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EXAMINING THE ROLE OF MEMORY IN SOCIAL COGNITION

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R. Nathan Spreng

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EXAMINING THE ROLE OF MEMORY IN SOCIAL COGNITION

Topic Editor:
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The function of memory is not only to recall the past, but also to form and update models of our experiences and use these models to navigate the world. Perhaps the most complex environment for humans to navigate is the social one. Social dynamics are extraordinarily complex, unstructured, labile and difficult to predict. However, successful navigation of the social world is essential to forming and maintaining interpersonal relationships. Little research has examined the role that memory plays in social behavior and interpersonal sensitivity. There is growing evidence that recalling personally experienced events (autobiographical memory) and inferring the mental states of others (mentalizing or theory-of-mind) share an extensive functional neuroanatomy. The functional overlap between autobiographical memory and mental inference has been hypothesized to facilitate the integration of personal and interpersonal information. This integration may provide a means for personal experiences to become social conceptual knowledge that, in turn, informs strategic social behavior. In this process, we project our memories onto others in order to better understand and empathize with them.

A number of fundamental questions remain about the relationship between memory and social cognition. Do we need a record of the past to navigate the social world adaptively? How is social conceptual knowledge represented, updated, and used to guide social behavior? What is the role of implicit memory on social judgments? How does social cognition interact with capacity limits in working memory? Is there something unique about the neural coding of social information in memory?

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Examining the role of memory in social cognition

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The function of memory is not only to recall the past, but also to form and update models of our experiences and use these models to navigate the world. Perhaps, the most complex environment for humans to navigate is the social one. Social dynamics are extraordinarily complex, unstructured, labile and difficult to predict. Successful navigation through our many social landscapes is essential to forming and maintaining the durable social bonds necessary for physical and mental health. Until recently, little research has examined the role that memory plays in social behavior and interpersonal sensitivity. There is growing evidence that recalling personally experienced events (autobiographical memory) and inferring the mental states of others (mentalizing or theory-of-mind) share an extensive functional neuroanatomy (Buckner and Carroll, 2007; Spreng et al., 2009; Spreng and Grady, 2010; Rabin et al., 2010) and may be critical for adaptive social cognition. The functional overlap between autobiographical memory and mental inference has been hypothesized to facilitate the integration of personal and interpersonal information (Spreng and Mar, 2012). This integration may provide a means for personal experiences to become social conceptual knowledge that, in turn, informs strategic social behavior. In this process, we project our memories onto others in order to better understand and empathize with their experiences (Perry et al., 2011).

The contributions to this Research Topic have examined this intersection between cognitive and social neuroscience, exploring the importance of memory to social cognition. What has become increasingly clear is that memory interacts with social cognitive processes in a diversity of meaningful and interesting ways. This interaction is reflected here through a range of individual differences, neuropsychological and developmental studies. The convergence of findings across the papers is very encouraging and provides good support for the central proposition that memory is a significant contributor to adaptive social cognition. The emergent themes are briefly reviewed here along with a few concluding remarks on future research directions.

The constructive nature of memory, whereby elements of a prior experience are woven back together during recollection, also supports imagination, whereby elements of disparate prior experiences are woven together in novel ways (Schacter et al., 2012). In this way, the network of brain regions supporting the recollection of prior experiences also allows one to imagine the experiences of other people (Hassabis et al., 2013). Gaesser (2012) proposes that this process may facilitate empathy and promote prosocial behavior. The constructive nature of memory also leaves recollection subject to distortions (Schacter, 2012). Brown et al. (2012) argue that this malleable nature of memory serves a socially adaptive function: The content of personal memories merge in the process of social interaction and this, in turn, fosters a sense of collective identity. The work of Lindner et al. (2012) suggests that there may be certain boundaries to this effect, however, that are driven by group membership.

In navigating the social world, we must often retrieve, maintain, manipulate, and update the information we have about other people. Meyer and Lieberman (2012) review the literature examining the unique neural dynamics underlying social working memory. In an empirical paper, Artuso et al. (2012) explore factors that impact working memory updating for faces. Cassidy and Gutchess (2012) provide preliminary evidence for a social memory system, potentially dissociable from the hippocampal declarative memory system. They found that amygdala and ventromedial prefrontal cortex integrity in older adults was associated with the successful retrieval of impressions for others (2012).

When one considers the broad range of interpersonal interactions encountered on a daily basis, it becomes clear that there are substantial differences in how people are able to navigate social situations. Some of these differences may relate to how we use memory in a social context. Ciaramelli et al. (2013) found that memory for previous episodes modulates the empathic response to others in a similar situation. Yang et al. (2012) found that the propensity for one to spontaneously relate one's personal memories to that of another individual predicted medial temporal lobe connectivity measured during resting-state fMRI.

It is becoming increasingly clear that the loss of a record of the personal past in neurological populations impairs the ability to adaptively navigate the social world. Four research articles converged around this central point with potentially intriguing implications for clinical practice. Davidson et al. (2012) reported that patients with amnesia are less likely to form and maintain social bonds, and have a smaller social network size. Adult onset hippocampal amnesia patients reported lower levels of trait empathy and demonstrated no increase in prosocial behavior with an empathic mood induction (Beadle et al., 2013). Consistent with recent neuroimaging findings demonstrating that the hippocampus is engaged during theory of mind of personally familiar individuals but not unfamiliar ones (Rabin and Rosenbaum, 2012), a patient with developmental amnesia was specifically impaired in providing a rich description of events related to oneself and close others, but not unfamiliar others (Rabin et al., 2012). Also examining developmental amnesia resulting from perinatal hypoxia, Staniloiu et al. (2013) found impairments on complex social judgment and perception tasks. Similar findings have been observed in neuropsychiatric disorders that are known to impair social cognition. In a longitudinal case study charting the development of a child with autism spectrum disorder, Bon et al. (2012)

present an evolving picture of atypical autobiographical memory functioning. In their review, Dimaggio et al. (2012) report that shared impairments in autobiographical memory and mentalizing are present in both psychiatric and personality disorders and these deficits need to be considered in treatment and intervention protocols.

Memory and social cognition are diverse concepts. This Research Topic reveals multiple points of convergence, from imaginative and empathic experience to the idea of a discrete social memory system. The importance of memory to social cognition also emerged in the context of memory disorders with important rehabilitation implications. As a collection, these works have begun to explore how our past experiences come to bear on our ability to navigate the social world, yet a number of fundamental questions remain. How are social experiences distilled into meaningful and flexible representations? By what mechanism is social conceptual knowledge represented, updated, and used to guide social behavior? What is unique about the neural coding of social information in memory? How do these sociomnemonic processes relate to the functions of the default network and other large-scale brain network interactions? Delineating these relationships will reveal how we use a record of the past to successfully navigate through our many and varied social landscapes.

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Constructing memory, imagination, and empathy: a cognitive neuroscience perspective

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Studies on memory, imagination, and empathy have largely progressed in isolation. Consequently, humans' empathic tendencies to care about and help other people are considered independent of our ability to remember and imagine events. Despite this theoretical autonomy, work from across psychology, and neuroscience suggests that these cognitive abilities may be linked. In the present paper, I tentatively propose that humans' ability to vividly imagine specific events (as supported by constructive memory) may facilitate prosocial intentions and behavior. Evidence of a relationship between memory, imagination, and empathy comes from research that shows imagination influences the perceived and actual likelihood an event occurs, improves intergroup relations, and shares a neural basis with memory and empathy. Although many questions remain, this paper outlines a new direction for research that investigates the role of imagination in promoting empathy and prosocial behavior.

Keywords: episodic memory, episodic simulation, mental simulation, imagination, functional magnetic resonance imaging, empathy, prosocial behavior

INTRODUCTION

Every day there are families with an inept cat marooned in a tree, friends with a couch to be moved, neighbors' homes damaged by a storm, pedestrians hit by a car: people in need of help. To the sufferers' benefit, other people tend to provide assistance, sometimes at a great cost to personal welfare (Hein et al., 2010). Partly accounting for why such selfless behaviors exist, some researchers have proposed humans' rampant evolutionary success is due to our species' ability to understand, collaborate with, and help others (Tomasello, 2000; Nowak and Highfield, 2011). Contributing to these abilities is our capacity for empathy. A term used to describe various concepts in the social psychology literature, empathy is a multifaceted construct that has included vicariously experiencing another person's emotions (affect-sharing), deliberately considering another person's perspective in order to understand their thoughts and feelings (mentalizing), and a desire to improve another person's welfare (prosocial concern; Zaki and Ochsner, 2012). For the purposes of this paper, I use empathy to imply the latter construct, viewing the former two as means of – but not always – eliciting empathy and prosocial behavior (Batson, 1991).

There are several factors known to modulate willingness to help (e.g., closeness of a relationship, social norms), but predominate among them is mentalizing the perspective of the person in need. Adopting the other person's perspective focuses our attention on how he or she is affected by an adverse situation, eliciting an empathic feeling that then increases the perspective-taker's willingness to help (Batson, 1991; see, Epley et al., 2006; Barber et al., 2010; for mentalizing conditions that elicit egotism). But that might not always be the case. In contrast to mentalizing, a path to facilitate helping that is less reliant on emotional concern may come from episodic simulation, the ability to vividly imagine specific personal events. While mentalizing and episodic simulation are related in that both processes consist of a mental shift away from the immediate environment and into hypothetical experiences (Buckner and Carroll, 2007), the content of those hypothetical experiences differs across these processes. Whereas mentalizing involves inferring mental states from another person's perspective, episodic simulation involves imagining scenarios specific in time and place from a first-person perspective.

In recent years, the functional role of memory has extended beyond remembering the past to include imagining the future (Addis et al., 2007; Schacter et al., 2008; Szpunar, 2010). One prominent theory, the *constructive episodic simulation hypothesis*, posits that the cognitive raw materials of imagined future experiences are bits and bobs of episodic memories (Schacter and Addis, 2007, 2009). The flexibility of constructive memory promotes the recombination of details gleaned across past episodic experiences into novel representations of future events that allow individuals to readily confront previously un-encountered situations (Schacter et al., 2008; Buckner, 2010). The adaptive function of imagining events is thought to mainly derive from the opportunity to "test out" one or more versions of what might happen by simulating the outcome of anticipated future events. Simulation reduces the cost of engaging in behavior while supporting planning and prediction, which enables humans to learn from simulated missteps without actually lifting a foot (Buckner and Carroll, 2007; Gilbert and Wilson, 2007; Schacter and Addis, 2007; see, Schacter, 2012 for a comprehensive review). Here, I offer an additional function for episodic simulation that has not previously been considered: facilitating socially desirable actions.

In what follows, I selectively piece together work from across the cognitive and social domains of psychology and neuroscience, marshaling support for the role of episodic simulation in understanding and helping others. First, I will review studies that demonstrate imagination's effect on the perceived likelihood that an event will happen, an effect that is likely to extend to imagined helping. Second, I will then look at recent promising work that demonstrates imagination's positive impact on empathy biases against dissimilar others. Third, I will briefly examine the neural basis of episodic simulation and empathy by highlighting overlapping brain regions and contemplate the shared cognitive processes these regions may support. Finally, I highlight what I think will be productive avenues for future research exploring episodic simulation's contribution to empathy.

IMAGINING MAKES IT SO

Relief that people in need will receive is partially dependent on the extent that others are willing to offer assistance; the more willing someone is to help, the more likely the person in need will gain relief. This point seems obvious, but it is easy to mistake self-evidence for inconsequence. While prosocial behavior is pervasive it is by no means assured (Batson et al., 1997). Evaluating one's willingness to help in any meaningful way requires a person to reflect on the perceived probability that he or she will help someone. Although there is currently no direct evidence that imagining helping increases willingness to help, there is relevant, though mostly disconnected, work from the memory and social judgment literatures.

Memory researchers have long been interested in the fallible nature of memory, attempting to understand why memories are imperfect re-constructions, rather than literal reproductions, of past experiences (Bartlett, 1932; Schacter, 2001). In the mid-1990s, studies on imagination inflation showed that imagining a novel event increased the perceived likelihood that it occurred in one's past, and in some cases led to rich false memories of experiences that never occurred (Hyman and Pentland, 1996; Garry and Polaschek, 2000). Less interested in past events, social psychologists have found that imagining hypothetical events increases the perceived probability that the event will occur in the future (Carroll, 1978; Anderson, 1983; Greenwald et al., 1987). Examining decision-making heuristics, Carroll (1978) initially demonstrated imagination's influence on predictions. Prior to the 1976 presidential election, subjects imagined events related to either a Ford or Carter victory and later were instructed to predict the likelihood that either candidate would win. The candidate that subjects imagined winning was rated more likely to win.

More recent work has shown this effect for simulating specific future social experiences (e.g., a family gathering, job interview, or first date). Simulating the same experience multiple times increased estimates of perceived plausibility for future experiences. Further, ratings of simulated detail, ease, and emotional intensity tracked with plausibility (Szpunar and Schacter, 2012). Although relatively little is known about the neural basis of these imagination inflation effects, tentative evidence from related work on imagination suggests that activity in the precuneus may drive increased plausibility ratings (Weiler et al., 2010). Thus, imagining (possibly mediated by the precuneus) makes it so, or at least makes it *seem* so.

Critical to assessing the potential contribution of imagination to helping others is to determine imagination's influence on actual behavior. A recent study on voting intentions found that imagination influenced self-perceptions (including perceived probability of voting), which subsequently influenced the likelihood that the subject would vote a day later (Libby et al., 2007). Consistent with the facilitating effect of imagined behavior on actual behavior, other researchers found that imagination increased estimated willingness to subscribe to a local cable company immediately following imagining the benefits and services the company offered. Strikingly, 2–3 months later, imagination-inflated estimates predicted actual subscriptions (Gregory et al., 1982, experiment 4).

Currently, it remains unknown whether imagining helping others will increase our willingness to help and subsequent helping behavior. However, based on research from cognitive and social psychology showing imagination's facilitating effect on perceived probability across a variety of situations, the effect will likely extend to prosocial behavior. Despite an absence of research on imagination inflation and empathy, a good deal is known about the positive effect of imagination on intergroup relations, a topic I turn to next.

IMAGINATION FOSTERS POSITIVE INTERGROUP RELATIONS

Human helping behavior is pervasive, but this empathic response to alleviate another person's suffering is diminished or absent when the sufferer is a member of a different social, racial, or cultural group (Cuddy et al., 2007; Cikara et al., 2011). To the betterment of intergroup relations, however, several techniques have been shown to reduce prejudice and empathy directed at outgroup members (Batson and Ahmad, 2009). One particular effective technique for improving intergroup attitudes and reducing prejudice involves simply imagining a positive interaction with an outgroup member (Crisp and Turner, 2009).

Imagined social contact offers a flexible and relatively minimal manipulation that can elicit robust prosocial change. For example, young subjects who spent 1 min imagining a positive interaction with an elderly person showed reduced ingroup bias compared to participants who imagined an outdoor scene or merely thought about an outgroup member. Imagined contact reduced anxiety about interacting with an outgroup member and increased willingness to work with outgroup members (Turner et al., 2007). Imagined contact may even promote intentions to engage in future contact (Husnu and Crisp, 2010), and reduce implicit prejudice (Turner and Crisp, 2010).

While imagined contact is a useful technique for improving intergroup relations, it is unlikely to be as effective as face-to-face contact (Turner et al., 2007). Part of the reason for this difference may be that direct perception leads to relevant knowledge being more cognitively available than imagined events (Tversky and Kahneman, 1973). Perhaps the closer an imagined event approximates a genuine percept (i.e., the more coherent, vivid, and detailed an event in the mind's eye) the greater its cognitive and behavioral sway would be (Anderson, 1983; Crisp et al., 2010). Therefore, if one could boost the vividness and detail of an imagined intergroup interaction, then perhaps the prosocial effectiveness of imagined contact would be enhanced.

Husnu and Crisp (2010) hypothesized that more elaborate imagined contact would enhance intentions of future contact with outgroup members and that subjective ratings of vividness would mediate this enhancement. Elaboration was manipulated by instructing subjects to specifically envision when and where they would come into contact with an imagined outgroup member (i.e., high elaboration condition) in contrast with the previously used imagined contact condition that did not require subjects to specify when and where (i.e., low elaboration condition). The researchers found that high elaboration increased vividness and intentions to interact with outgroup members in the future. Furthermore, vividness predicted willingness to interact while controlling for changes in attitude and anxiety. The more vivid an imagined event was, the greater the willingness to interact.

Interestingly, the qualities of the event that were manipulated for the purposes of elaboration closely resemble defining features of episodic experiences: contextual and temporal specificity (Tulving, 2002). Based on studies of episodic memory and imagination that have found greater hippocampal activity when more vivid and detailed events are subjectively experienced (Addis et al., 2004; Addis and Schacter, 2008), an intriguing possibility is that the hippocampus may instantiate the effect of vividness on intergroup cognition.

In regards to memory and intergroup relations, Husnu and Crisp (2010) found that – irrespective of the elaboration condition – remembered past experiences positively predicted vividness of imagined events and willingness to interact with outgroup members in the future. This makes theoretical sense if, when constructing imagined events, bits and bobs of episodic details are gleaned across memories. Broadly consistent with the theories on imagination and memory (Ingvar, 1979; Tulving, 1985; Schacter and Addis, 2007), memory appears to support – or at least to enrich – imagination. And, it would seem, in the service of prosocial behavior. It is worth noting, however, that the imagined contact literature has relied heavily on self-reported measures of prosocial behavior, causing some to question the practical significance of these measures (Bigler and Hughes, 2010). This emerging literature awaits further experiments using objective behavioral measures. Yet, evidence from Turner and Crisp (2010) finding positive changes in implicit prejudice reduces some of these concerns (Crisp and Turner, 2010). Thus far, I have largely focused on psychological evidence that indicates a cognitive relationship between memory, imagination, and empathy. Further support comes from emerging evidence of a shared neural architecture.

A SHARED NEURAL BASIS

The neuroscience on memory and imagination has developed largely independently from the neuroscience on social cognition (broadly) and empathy (specifically). Although initial findings from brain-damaged amnesic patients suggest that brain regions supporting memory and imagination may not be *necessary* to complete some mentalizing tasks (Rosenbaum et al., 2007), work from various clinical populations (e.g., Lombardo et al., 2007) and neuroimaging studies demonstrate that brain systems supporting memory and imagination may *shape* empathy. Demonstrating a link between memory for personal experiences and empathy, Lombardo et al. (2007) found that differences in self-referential memory between autistic patients and healthy controls disappeared when measures of empathy were included as a covariate (see also Corcoran and Frith, 2003; Lee et al., 2004 for co-morbid deficits in schizophrenia). Conversely, independence across these mental processes also exists. For example, older adults show diminished abilities to remember the past and imagine the future (Addis et al., 2008; Gaesser et al., 2011), yet they exhibit preserved levels of trait empathy across the lifespan (Gruhn et al., 2008). These behavioral findings underscore a complex relationship between processes, suggesting that memory and imagination may contribute to, but are distinct from, a capacity for empathy.

Here, I will briefly examine preliminary neuroimaging findings that are beginning to subvert theoretical autonomy across these processes, shedding light on a shared constellation of brain regions within the default network, recruited for remembering and imagining specific personal experiences as well as understanding and empathizing with others. To the extent that the brain is functionally localized, this anatomical overlap represents a cognitive interaction across faculties, signifying contributions of one faculty to another or component mental processes recruited by all faculties (Henson, 2005; Bressler and McIntosh, 2007; Hein and Knight, 2008). These findings raise more questions than they answer and pave the way for a promising new line of research.

While functional neuroimaging studies have provided initial evidence of the neural overlap between memory, imagination, and social cognition in the default network (Spreng et al., 2009; Spreng and Grady, 2010; Spreng and Mar, 2012), unexamined in these studies is the neural relationship of memory and imagination with empathic concern and action. However, recent neuroimaging studies are beginning to uncover commonalities.

Investigating the neural conditions that facilitate prosocial thoughts and behavior, Masten et al. (2011) found that regions of the default network were more strongly activated when subjects viewed social exclusion (i.e., a person in need) during a ball-tossing game compared to when they viewed social inclusion. Greater activity was observed for the mPFC and precuneus when subjects viewed social exclusion compared to inclusion. Further, after controlling for trait empathy levels in an exploratory mediation analysis, only activity in the mPFC positively predicted prosocial behavior (e.g., consoling the excluded player outside of the scanner; see also Rameson et al., 2012; Waytz et al., 2012).

Investigating the neural substrates of an enhanced empathy bias toward ingroup members relative to outgroup members, Mathur et al. (2010) showed that, across individuals, the difference in mPFC activity when observing someone in need (e.g., in a natural disaster) for ingroup versus outgroup members predicts state empathy and willingness to donate money and time to help ingroup members. Future work may want to investigate whether instructions similar to those used in the aforementioned imagined contact literature would boost mPFC activity and subsequent helping behavior.

One possible explanation for the involvement of the mPFC across these studies on empathy comes from its role in self-referential processing (Amodio and Frith, 2006). Psychological research has previously demonstrated that subjects who view a person in need as more similar to themselves show heightened empathetic concern for the similar-to-self person in need (Cialdini et al., 1997). Neuroimaging studies show the mPFC is preferentially activated when mentalizing about similar and psychologically close others (Krienen et al., 2010; Tamir and Mitchell, 2011; Denny et al., 2012). Therefore, mPFC activity may support empathy to the extent that it reflects a perceived self-other overlap, as greater mPFC activity may indicate an increase in perceived self-other similarity (Masten et al., 2011; Rabin and Rosenbaum, 2012).

The preceding studies typically interpret activity within the default network as a proxy of mentalizing processing. However, because similar regions are activated under conditions of episodic simulation (Schacter et al., 2008), it could be the case that this activity represents constructing vivid scenarios rather than simulating thoughts and feelings in some cases or perhaps shared component processes, such as self-referential processing. Further investigation is needed to adequately tease apart the entangled relationship across these cognitive processes in order to characterize the independent or interactive contributions of episodic simulation and mentalizing to prosocial cognition and behavior.

CONCLUSION AND FUTURE DIRECTIONS

Humans are a preeminent evolutionary success story because we work as a horde, a cognitively sophisticated and helpful horde. Multiple cognitive tools are thought to support our prosocial tendencies (Tomasello, 2000; de Waal, 2008). Prominent among these tools are the capacity to infer others' mental states and an empathic emotional response to others' plights (Batson, 1991). Here I have outlined the speculative possibility that episodic simulation of specific vivid and coherent scenarios may also foster helping behavior. Suggestive evidence from imagination inflation, imagined contact, and the neuroscience of memory, imagination, and empathy hints at a socially enhancing function for constructive memory and imagination.

To be clear, I am not proposing the adaptive function of promoting prosocial behavior to be mutually exclusive with other proposed functions of episodic simulation (e.g., "trying out" alternative scenarios in order to plan and predict the future). Nor am I advocating that episodic simulation will always be associated with prosocial behavior, but rather make the more modest claim that it may support prosocial behavior in healthy individuals and that promoting prosocial behavior may constitute the primary advantage (Nowak and Highfield, 2011). It is likely that imagination will only be beneficial to the extent that these simulations accurately reflect reality. And, while simulations of events can often be error prone (Dunning, 2007; Gilbert and Wilson, 2007), I am encouraged by a recent meta-analysis highlighting the relative accuracy of simulations (Mathieu and Gosling, 2012). There may also be particular circumstances in which episodic simulation could in fact reduce prosocial behavior. If the content of the simulation is focused on negative consequences associated with helping, such as damage to the self, then simulation may reduce the likelihood of intervening. Whether episodic simulation *can* be used to promote prosocial behavior, and whether episodic simulation *normally* promotes prosocial behavior are open questions of applied and theoretical relevance.

Future research is needed to establish the parameters under which episodic simulation may influence empathy and prosocial behavior. Of theoretical importance will be delineating the contributions of episodic simulation from known mental processes that influence prosocial behavior (e.g., mentalizing and affect-sharing). It may be the case that episodic simulation facilitates helping as a result of interacting with perspective taking or affect-sharing. For example, adopting a person in need's perspective may very well guide imagining how to appropriately help someone, or perhaps the facilitating effect of episodic simulation will be partially attributed to making more cognitively available the perspective of another person's thoughts and feelings. However, these interactions are unlikely to fully account for an increase in willingness to help to the extent that the effect of imagination inflation, which holds for non-social events, and the effect of increased temporal and contextual specificity of an event (both of which are definitional qualities of episodic simulation but not of mentalizing or affect-sharing) improving intentions to interact with outgroup members extend to helping behavior.

Identifying the precise degree of independence and interaction between the scenario construction and self-referential aspects of episodic simulation from traditional accounts of fostering empathy is paramount to determining the contribution of episodic simulation to prosocial behavior. An interesting question is whether episodic simulation could boost prosocial behavior in the absence of the capacity for perspective taking. One possibility is that semantic knowledge or episodic memories of past related helping experiences could be used to guide or inform episodic simulations of helping events without relying on perspective taking. For instances, perhaps the semantic knowledge that slow elderly people typically benefit from help crossing roads triggers an episodic simulation of how best to accompany a specific person upon observing an elderly person, cane in hand, waiting on a street corner, thereby promoting prosocial behavior.

Mechanistically, it remains unknown whether the effects of imagination will be primarily mediated by vividness and detail of the scenario (possibly substantiated in the hippocampus and precuneus), or by a self-other identity merging (possibly substantiated in the mPFC), or by some combination of the two. Specifying the effect of emotion is also of interest. Although mentalizing is well known to promote prosocial behavior by increasing emotional concern for others, there is currently no empirical evidence that the facilitating influence of imagining would also operate through emotional concern, but this does not dismiss a role for emotion in some capacity mediating the influence of simulation on prosocial behavior. Indeed, the increase in perceived likelihood that an imagined event will occur was restricted to emotional events in Szpunar and Schacter (2012) and imagining a positive social tone has been integral to eliciting imagined contact effects (Crisp and Turner, 2009).

At this point we are left to speculate and await empirical investigation to substantiate and critically evaluate the ideas outlined in this article. To the extent that a goal of society is to maximally foster these social abilities, identifying and examining all the mental processes that influence empathy and prosocial behavior is critical. Psychology and neuroscience have already illuminated several cognitive strategies for fostering empathy and prosocial behavior. But I wonder if perhaps humans are equipped with at least one more empathic tool: episodic simulation.

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Memory's malleability: its role in shaping collective memory and social identity

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If anything has been learned about memory, it is that it is fragile and error prone (Schacter, 2001; Loftus, 2005). Far from being a verbatim record of the past, memory is well understood as a reconstructive process replete with distortions, and at times, gross inaccuracies. Although often associated with negative consequences (Wells and Olson, 2003; McNally and Geraerts, 2009) there is growing evidence to suggest that memory's imperfections may also be a virtue (Schacter, 2012; Schacter et al., 2011). The reconstructive nature of memory is believed to provide greater cognitive flexibility (Schacter and Addis, 2007), underlie mental time travel (Schacter et al., 2008; Szpunar, 2010), and support the construction and maintenance of self-identity and life-stories (Greenwald, 1980; Markus and Nurius, 1986; Bruner, 1991; Baerger and McAdams, 1999; Conway and Pleydell-Pearce, 2000; Wilson and Ross, 2001). We argue here that memory's malleability benefits more than just the self – the same attitudes, schemata, and social and physical environments that render an individual's memory unique can also transform initially disparate memories into shared recollections. It is our proposition that autobiographical memories are simultaneously reconstructed to be distinct from that of another person and converge with it as a result of social interactions. Through this convergence, emerges collective memory that will in turn establish a collective identity and promote sociality. Our aim here is to bridge the gap between individual and collective memory by discussing several lines of research elucidating the processes by which the malleability of memory promotes the formation of shared memories.

THE PSYCHOLOGICAL STUDY OF COLLECTIVE MEMORY

Collective memories are a community's shared renderings of the past that help shape its collective identity (Halbwachs, 1950). From this perspective, they are the collective variant of autobiographical memories, which are individually held memories that help shape personal identity. The identity-constructing function of collective memories implies that not all shared memories are collective memories. That is, a memory can only be considered collective if it is widely shared and if it helps to define and bind together a group (Assmann, 1995). For example, Americans are, to a degree, Americans because they possess shared renderings of the past, and Americans differ from Russians, in part, because the two hold different shared memories for similar historical events. For instance, these two nations remember War World II differently. Americans tend to remember D-Day as being the most important battle of the war; Russians remember the most important battle as the Battle of Leningrad (Wertsch, 2002). Their different memories help shape the way Russians and Americans see their place in the world and how they conceive of themselves as a nation.

Whereas psychologists have largely remained on the sidelines of collective memory research, the last few years has evidenced a growing body of literature relevant to the psychological study of collective memory (Cuc et al., 2006; Barnier and Sutton, 2008; Stone et al., 2010; Coman and Hirst, 2012). It seeks to examine the cognitive mechanisms underlying how individual memories emerge, spread, and become shared across a community. These cognitive mechanisms often involve memory distortions, but as we shall see, these distortions are often shared across community memories, and as a result lead to shared memories.

Probably the best understood mechanisms for creating shared memories has been discussed in a various ways since Bartlett (1932) first introduce the notion of schema. He suggested that shared memories may be formed through social interactions because community members, whom are raised together, attend the same school, read the same books, and generally share many of the same experiences, will possess similar schemata, and in turn will shape the way community members remember their past. Take, for example, Hastrof and Cantril's (1954) study of Dartmouth and Princeton students' memories of a critical football match between the two schools; within group memories were similar, whereas across the two populations, the memories were dissimilar.

Despite these results, it is not always the case that a shared culture and shared schemata will dominate the shaping of one's memory. Community members achieve their individuality, in part, because they possess unshared attitudes and schemata. The discrepancies, as such, can lead members of the same community to remember a shared event quite differently. Paradoxically, individually distinct memories can still become shared over time. What makes us claim that memory is well-designed for the formation of collective memory is that there are a variety of mechanisms and processes that will lead to mnemonic convergence, in spite of the dissonance that exists among rememberers.

These mechanisms can shape and reshape memory through a variety of means. We focus here on conversational interactions. Although memory may have a number of functions (Bluck, 2003), the communicative function of memory may be uniquely human (Pillemer, 1992), and talking about the past is a pervasive part of everyday life (Hirst and Echterhoff, 2012). Pasupathi et al. (2009) found that 62% of events recorded in diary entries had already been discussed the evening after they had occurred. Similarly, Harber and Cohen (2005) found that after 33 students visited a morgue on a field trip, 881 people knew of the visit after three conversational exchanges had taken place. Furthermore, eyewitnesses tend to talk to other co-witnesses after witnessing incidents (Skagerberg and Wright, 2008).

When investigating how conversations shape memory studies to date have focused primarily on the impact a speaker has on a listener's memory. Whereas Echterhoff, Higgins, and others have focused on the reflexive influence a speaker can have on reshaping his or her memory, leading to mnemonic convergence between speaker and listener, a so-called *shared reality* (Hirst and Echterhoff, 2008; Echterhoff et al., 2009), speakers can have a unilateral influence on a listener's memory, leading to a similar shared reality.

SOCIAL CONTAGION

Through acts of social remembering individuals become vulnerable to incorporating details about the past that they did not actually experience. That is, conversations can serve as a mechanism enabling the spread of a memory from one person to another. This process is often referred to as social contagion. Social contagion can be traced back to the classic work of Loftus and colleagues (Echterhoff et al., 2005; Loftus, 2005). Although Loftus did not frame her work in terms of social contagion research, these experiments and others (Loftus, 2005) have consistently demonstrated that social interactions (e.g., what an experimenter says to a participant) can be an effective means for implanting false memories. For example, in these studies participants were asked to view a series of slides depicting a traffic accident. After the initial viewing, an experimenter provided them with additional information describing the accident, information that at times contradicted the content in the original images. After the post-event information was given to the subject, participants were asked to recall what they had seen. Across numerous studies Loftus and colleagues have demonstrated the ability to implant false memories for a wide range of events including getting lost in a grocery store, knocking over a wedding cake, and seeing Hanna–Barbara cartoon figures at Disneyland (Loftus, 2005).

Although the implantation of false memories often occurred from exposure to a social stimuli, studies directly examining how the effects of social interactions on memory have shown that social interactions are particularly effective methods for shaping memories. For example, Meade and Roediger (2002) asked participants to view a complex image. Afterward, a confederate discussed the image with the participant, providing false information relating to the original image. Post-discussion, participants were asked to individually recollect what they had originally seen. Although subjects were more likely to incorporate related, novel information into their recollections, even unrelated/unexpected implanted content was included and accepted as a valid memory. Wright et al. (2000) found that two people unknowingly integrated their individual memories of slightly different pictures with that of his or her peer. Cuc et al. (2006) went even further – groups of four were asked to first individually recollect the story they had just read, and then to discuss it with each other, and found across several studies that conversations are an effective means for transforming how different version of the past can converge into a more uniform memory.

The relationship the listener has with the speaker impacts what is transmitted within the conversation. Individuals are prone to conformity; they are not bent on providing novel information to a group recollection. The rememberers are following the conversational maxim – *say no more than is necessary* (Grice, 1975). What goes unsaid during the initial stages of conversation will be less likely to be included in the final shared memory. In essence, conversation and by extension memory transmission is sometimes a democratic process – frequency of participation determines how much influence one has over the group recollection. Put simply, the more one dominates a conversation the greater impact they will have on shaping the group's collective memory (Cuc et al., 2006), a conversational role referred to as the "dominant narrator." In fact, dominant narrators appear to be more effective in shaping collective memory than perceived experts (Brown et al., 2009).

SOCIALLY SHARED RETRIEVAL-INDUCED FORGETTING

Collective memory is inherently selective (Rajaram and Pereira-Pasarin, 2010; Hirst and Echterhoff, 2012). When people recall the past some details are retrieved while other fail to enter into conversation. The consequence of those items not retrieved has become of increasing interest in understanding how distinct memories become increasingly similar across individuals. Hirst and colleagues (Stone et al., 2012) have conducted studies applying the retrieval-induced forgetting (RIF) paradigm (Anderson et al., 1994) to social interactions. RIF in individuals consistently show that recalling an item inhibits the accessibility of categorically related information. In other words, retrieving a piece of information, a part of memory, makes it harder to remember unrecalled related information than if the individual had not retrieved any aspect of that memory at all. Modifying this paradigm to social interactions, similar patterns were found. That is, when people converse about the past evidence of RIF patterns emerge not only for the person doing the recalling but for the person listening to the speaker as well (socially shared RIF, SS-RIF; for a review see Stone et al., 2012). Hirst and colleagues posit that this occurs when the listeners concurrently retrieves with the speaker. SS-RIF has been found in free flowing conversations (Cuc et al., 2007), flashbulb memories (Coman et al., 2009), and in clinical populations (Brown et al., 2012). Interestingly, this effect was found even when speakers and listeners possessed similar, but not identical memories. Coman et al. (2009) asked individuals, unknown to each other, who had been living in New York City on 9/11 to recall their memories of that day. The results showed unmentioned details related to what was recalled became not only harder for the speaker to later remember but also in the listener as well, even though the speaker did not share these exact memories. These findings suggest that when people collectively recall the past, the act of retrieval has the potential to induce forgetting across individuals in similar ways, and like social contagion can also be an effective means for creating collective memories.

Are there certain conditions that increase the probability that a speaker can induce forgetting in a listener? A recent study by Barber and Mather (2012) found that RIF in speakers and listeners was greater when both participants were of the same gender, whereas neither the valence of the memory exchange (i.e., neutral versus negative) nor the age cohort of the participants had significant influence on the rate of forgetting. Barber and Mather's (2012) findings suggest that affiliation between speaker and listener may enhance forgetting. Emotion may also play a role. Brown et al. (2012) asked combat veterans with and without PTSD to study and selectively recall either trauma or neutral stimuli. Although equal levels of forgetting were found for neutral information, individuals with PTSD exhibited greater levels of induced forgetting, individually and socially, for trauma-related stimuli. Future studies will benefit from elucidating more clearly the conditions when social forgetting will and will not occur.

CONCLUSION

This paper has illustrated the capacity for memory's malleability to facilitate sociality and transform individual memories into shared, and subsequently collective memories. The transformation of individual memory into collective memory can be seen as an emergent and recursive system(s). We argue that the mechanisms that guide mnemonic convergence are in it of themselves social mediators. The porous nature of memory helps an individual maneuver through a social world that consists of an aggregate of autobiographical memories, and in so doing the individual as such engenders collective remembrance. Coman and Hirst (2012) found that mnemonic influences, such as social contagion and SS-RIF, are transitive and strengthen as they propagate. The plurality of the process is inevitable given the multiple environments individuals exist within. What begins as a dyadic exchange, results in a cohesive network, that is sustained by a multiplicity of convergences within and between groups.

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When do we confuse self and other in action memory? Reduced false memories of self-performance after observing actions by an out-group vs. in-group actor

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Observing another person performing an action can lead to a false memory of having performed the action oneself – the observation-inflation effect. In the experimental paradigm, participants first perform or do not perform simple actions, and then observe another person perform some of these actions. The observation-inflation effect is found when participants later remember performing actions that they have merely observed. In this case, self and other are confused in action memory. We examined social conditions of this self-other confusion when remembering actions, specifically whether the effect depends on the observed actor's group membership. In our experiment, we manipulated group membership based on physical appearance, specifically complexion of the hands. Fair-skinned participants observed either an in-group (i.e., fair-skinned) or an out-group (i.e., dark-skinned) actor. Our results revealed that the observed actor's group membership moderated the observation-inflation effect: False memories were significantly reduced when the actor was from the out-group (vs. in-group). We found no difference to a control condition in which the actor wore black gloves, suggesting that distinctiveness of perceptual or sensory features alone (due to the out-group member's dark skin) is not critical. We discuss these findings in light of social-neuroscience studies demonstrating the impact of an observed person's group membership on motor simulation. Overall, our findings suggest that action memory can be affected by a ubiquitous feature of people's social perception, that is, group-based social categorization of others.

Keywords: self-other confusion, group membership, action memory, false memory, motor simulation, perceptual distinctiveness

INTRODUCTION

Imagine that you watch a cooking-show on television while you are preparing dinner yourself. Sometime later, after you have left the house, you find yourself wondering whether you actually switched off the stove. Clearly, correctly remembering whether one has performed an action is crucial for successfully managing everyday life. Did you just observe the TV-cook switching off his or her stove, or did you do it yourself? Recent research shows that observing another person's action can lead people to mistakenly remember that they have performed the action themselves (Lindner et al., 2010; Schain et al., 2012). The present research was conducted to investigate conditions under which such false self-attributions of actions are more or less likely to occur. We focused on social conditions, specifically the observed actor's membership in the observer's in-group (vs. out-group).

In the initial experimental demonstration of the effect, Lindner et al. (2010) asked participants to perform or to read simple action statements, like "*Unlock the lock*" or "*Shake the bottle.*" Afterwards, participants were asked to observe another person perform some of the actions they had and some of the actions they had not previously performed themselves. Two weeks later, a surprise source-memory test revealed that observation of other-performed actions had inflated false memories of self-performance. Thus, this effect has been referred to as *observation inflation* (see also *imagination inflation*, i.e., false memories of self-performance from imagination; Garry et al., 1996; Goff and Roediger, 1998).

The observation-inflation effect reveals the profoundly social nature of memory inasmuch as it entails a confusion of self and other in recollecting actions. Thus, this phenomenon is a prime example of how our contact with the social world affects our memory (see Echterhoff and Hirst, 2009; Hirst and Echterhoff, 2012). Because we constantly observe others performing actions, there are countless occasions that potentially could trigger subsequent false self-attributions of actions. But do we indiscriminately incorporate others' actions into our own action memories? Or do such self-other confusions depend on social characteristics of the observed actor?

Research on social perception and interpersonal processes suggests that we are more likely to adopt, or to be affected by, the experiences of others who are more (vs. less) close and similar to ourselves (Aron et al., 2004). A key component involved in feelings of closeness and similarity is another person's group membership. One of the first things we do when we are observing another person – often automatically and spontaneously – is to categorize her or him (Macrae and Bodenhausen, 2000). Using cues like a person's age, gender, and race we sort people into different social groups that are either like us (i.e., the in-group) or not like us (i.e., the out-group).

Regarding the present phenomenon, there is ample evidence that people more readily adopt and incorporate the inner states of in-group (vs. out-group) members (Echterhoff et al., 2009; Cikara et al., 2011). This bias has been found for affects and emotions (Xu et al., 2009; Avenanti et al., 2010; Azevedo et al., in press), but also for memory (Echterhoff et al., 2008, in press).

So far, only few studies have examined whether and how memory for another person's features and actions is influenced by the person's group membership. For example, people are better in remembering in-group than out-group faces (see Meissner and Brigham, 2001; Young et al., 2012), and memory for negative out-group behavior is better than for positive out-group behavior (Howard and Rothbart, 1980). Furthermore, people are more likely to confuse the sources of recalled statements when the sources belong to the same (vs. a different) ethnic or racial group (Taylor et al., 1978; Stangor et al., 1992). With the present research we specifically examined whether false action memories from observation also depend on the observed others' group membership.

While the impact of group membership on action memory in general and false action memory in particular has not been investigated, there are potentially relevant findings outside the memory literature. Studies on action perception hint at a consistent pattern between observation of others' actions and their group membership. In one study, Müller et al. (2011) employed the social Simon task (Sebanz et al., 2003) to measure coordinated action between interaction partners. It was found that participants' reaction times were decelerated when interacting with an out-group (vs. in-group) member, indicating that co-representations of actions are only formed when coordinating with in-group members. Similarly, people exhibit increased cortical sensitivity when observing errors in action execution of someone who is similar (vs. dissimilar; Carp et al., 2009; Newman-Norlund et al., 2009; Kang et al., 2010). Furthermore, Gutsell and Inzlicht (2010) found that motor simulation during action observation was substantially decreased when observing out-group (vs. in-group) members. Taken together, actions of out-group members tend to be processed less preferentially and represented less readily in the observer than actions of in-group members. Accordingly, the potential of observed actions to induce false action memories in the observer should be less pronounced after observation of an out-group (vs. in-group) member.

The present study was designed to test this prediction. We manipulated a person's group membership by presenting either a fair-skinned (in-group) or a dark-skinned (out-group) actor to fair-skinned observers and predicted that a self-other confusion in action memory should be accentuated after observation of an in-group member, but reduced after observation of an out-group member.

A reduced observation-inflation effect after observation of an out-group member could be due to mere perceptual distinctiveness of the dark-skinned hands. To control for this possibility, participants in a control group observed an actor wearing black gloves (see Avenanti et al., 2010; Azevedo et al., in press). Whereas an approach drawing on perceptual distinctiveness predicts the least false memories after observation of a person wearing black gloves, an intergroup-bias approach suggests a reduced observation-inflation effect exclusively after observing an out-group member, but not after observing a person wearing black gloves.

MATERIALS AND METHODS

PARTICIPANTS

Fifty-eight students at the University of Münster (mean age = 21.9, $SD = 4.7$, 11 men) participated in this study for partial course credit. All participants were fair-skinned. The study was approved by the local ethics committee. The guidelines of the Declaration of Helsinki and standards of the American Psychological Association were followed. Informed consent was obtained from all participants.

DESIGN

A 2 (observation, Phase 2: observed vs. not observed) × 3 (group membership of observed actor, Phase 2: in-group vs. out-group vs. control) design was used, with the first variable manipulated within participants. The main dependent measure was the relative frequency of false *performed*-responses for actions that were only read but not performed in Phase 1.

MATERIALS AND PROCEDURE

We adapted the procedure introduced by Lindner et al. (2010). The experiment was computer-based and consisted of two sessions, separated by a 2-week interval. Participants were tested individually in both sessions.

In Phase 1, for each participant 40 action statements were randomly chosen from a pool of 60 action statements and presented at the center of a 22-inch TFT-LCD display in a random order. Half of the action statements had to be performed, the other half were only read. Assignment of items to these two types of encoding was also randomized. At the beginning of each trial, the name of a specific object (e.g., *Lock*) appeared on the screen. Objects were hidden behind a visual cover, thus participants waited until the experimenter had placed the required object in front of them. Next, a perform instruction (*Please perform*) or a read instruction (*Please read*) appeared on the screen and was followed by the specific action statement (e.g., *Unlock the lock!*). Participants now performed or read out the action statement once before moving on to the next trial.

In Phase 2, half of the action statements performed in Phase 1 and half of the action statements read in Phase 1 were randomly chosen and presented. Each presentation of an action statement was followed by a corresponding video showing the specific action repeatedly over the course of 15 s. To maintain participants' attention, an observation task was introduced: Participants were asked to count the number of action repetitions after each video and enter their final count. Overall, each action statement and the corresponding video were presented five times in a random order, resulting in a total of 100 trials for Phase 2.

In the *in-group* condition, videos of the torso, forearms, and hands of a German, fair-skinned female actress (24 years) were presented from a second-person perspective (352 kb/s, 960 × 530 pixels, see **Figure 1**). In the *out-group* condition, actions were performed by a Sri Lankan, dark-skinned female actor (21 years, see **Figure 2**). A pretest ($N = 17$ women; mean age $= 22.18$; $SD = 2.19$) confirmed that the different ethnicities could be easily derived from the videos. Participants rated sample videos with regard to the estimated likability for several countries and regions on a seven-point Likert scale (one being *very unlikely*, seven being *very likely*). Compared to the in-group actress, the out-group actress was perceived as significantly less likely to be from Germany [out-group: $M = 3.1$, $SD = 1.8$; in-group: $M = 6.2$, $SD = 1.1$; $t(16) = 5.83$, $p < 0.001$, $d = 1.41$], and more likely to be from South Asia [out-group: $M = 5.1$, $SD = 1.8$; in-group: $M = 2.5$, $SD = 1.2$; $t(16) = 6.75$, $p < 0.001$, $d = 1.64$]. For the *control* condition, the actor (22 years) wore black gloves during action performance. The actor's actual skin color (fair) was not visible at any time (see **Figure 3**).

Two weeks later, the 40 old action statements were randomly presented in a surprise source-memory test along with 20 new action statements. Participants indicated for each action statement whether it was performed, read, or not presented during Phase 1.

FIGURE 1 | Screenshot of action video *Unlock the lock!* presented in the *in-group* condition.

Our hypotheses refer to false *performed*-responses, that is, *performed*-responses to actions only read in Phase 1. An observation-inflation effect was defined as a significant increase in false *performed*-responses for items observed compared to items not observed in Phase 2. Accordingly, the magnitude of the effect was defined as the difference in false *performed*-responses between items observed and not observed in Phase 2.

RESULTS

To test our hypotheses, we ran planned pairwise comparisons (Type I error threshold $= 0.05$). Accordingly, p-values are one-tailed.

Table 1 contains the means and standard deviations of false *performed*-responses for the three experimental conditions (in-group actor vs. out-group actor vs. control). We found significant observation-inflation effects in all three conditions, the in-group condition, $t(19) = 6.40$, $p < 0.001$, $d = 1.43$, the out-group condition, $t(18) = 6.32$, $p < 0.001$, $d = 1.44$, and the control condition, $t(18) = 4.17$, $p < 0.001$, $d = 0.96$, respectively. Thus, all participants were prone to falsely claiming that they had performed actions themselves when in fact they had only observed another person performing these actions.

Importantly, the magnitude of the effect, that is, the difference in false *performed*-responses between observed and not observed items, was a function of the actor's group membership (see **Figure 4**). As predicted, planned comparisons indicated that the effect was significantly lower in the out-group than in the in-group condition, $t(37) = 2.06$, $p = 0.02$, $d = 0.65$. No significant difference was found between the control condition and the in-group condition, $t(37) = 0.83$, $p = 0.21$, $d = 0.27$, or between the control condition and the out-group condition, $t(36) = 0.84$, $p = 0.20$, $d = 0.27$.

We also conducted additional analyses to examine the role of other alternative processes (differences in task motivation, attention, or a general response bias) that could account for the present findings. First, we analyzed performance on the counting task that was administered in Phase 2 (that is, the counting of observed action repetitions). Mean accuracy rates varied between 0.79 and 0.85, and did not differ between the three experimental conditions,

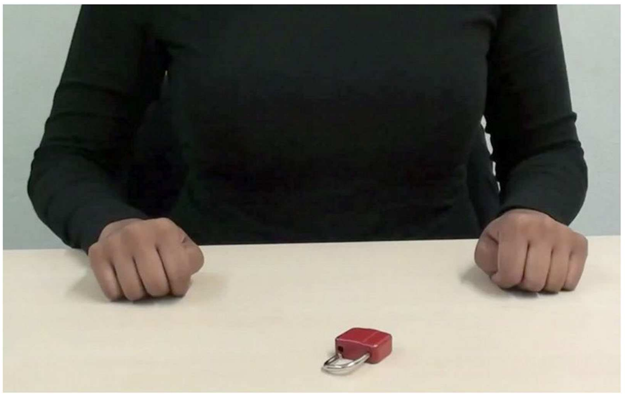

FIGURE 2 | Screenshot of action video *Unlock the lock!* presented in the *out-group* condition.

FIGURE 3 | Screenshot of action video *Unlock the lock!* presented in the *control* condition.

Table 1 | Mean proportion of performed-responses as a function of encoding in Phase 1, observation in Phase 2, and observation group.

Encoding, Phase 1	Observation, Phase 2					
	In-group		Out-group		Control: black gloves	
	Observed	Not observed	Observed	Not observed	Observed	Not observed
Performed	0.79 (0.17)	0.46 (0.15)	0.80 (0.14)	0.56 (0.23)	0.72 (0.16)	0.58 (0.21)
Read	0.27 (0.18)	0.06 (0.08)	0.18 (0.15)	0.05 (0.10)	0.24 (0.17)	0.08 (0.10)
Not presented	–	0.02 (0.04)	–	0.01 (0.02)	–	0.01 (0.03)

Standard deviations are given in parentheses. Proportions represent the frequency of performed-responses divided by the number of all responses for a corresponding item type.

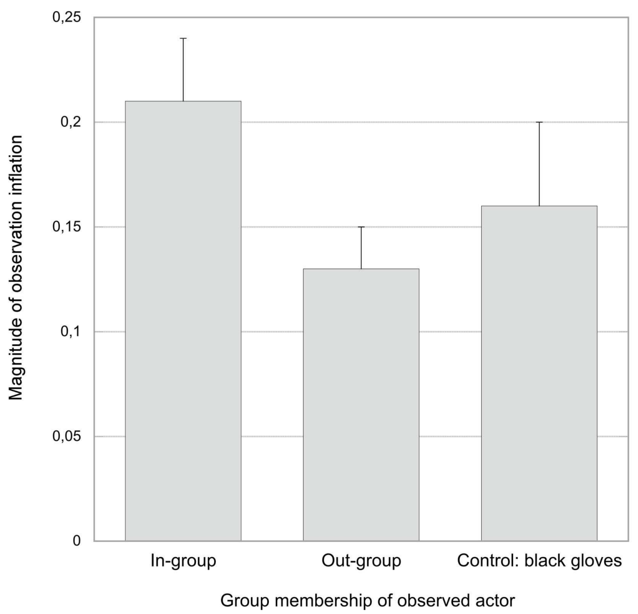

FIGURE 4 | Magnitude of the observation-inflation effect as a function of group membership of the observed actor. Error bars represent the standard error of mean.

$F(2, 51) = 1.34$, $p = 0.27$, $\eta_p{}^2 = 0.05$. This finding is inconsistent with the notion that the reduced observation-inflation effect in the out-group condition is due to decreased task motivation or visual attention, which could impair source memory in general.

Furthermore, the rate of false *performed*-responses to completely new items (not presented in Phase 1 and not observed in Phase 2) was close to zero, ranging from 0.01 to 0.02 in all the three experimental groups. Thus, differences in a general response bias toward claiming actions as self-performed cannot account for the difference in observation inflation found in the earlier main analysis.

DISCUSSION

Observation of another person performing a simple action can lead to a false memory of having performed this action oneself, that is, the observation-inflation effect (Lindner et al., 2010). The present study extends this initial finding inasmuch as it shows that the ethnic group membership of the observed person – conveyed by mere skin color – has an impact on the magnitude of the observation-inflation effect. Compared to an in-group (i.e., a fair-skinned) actor, the observation of an out-group (i.e., a dark-skinned) actor led to a significant reduction in false self-attributions of action performance after two weeks. As predicted from a social-psychological account of intergroup bias, such a reduction was not found for the observation of an actor wearing black gloves.

Our findings resonate well with research on reduced motor simulation of actions of out-group (vs. in-group) members. Building on research on mirror-neuron activity and shared motor representations, Lindner et al. (2010) hypothesized that motor simulation during action observation might be the core mechanism behind the observation-inflation effect. Apparently, people do not co-represent or share out-group members' actions to the same extent than in-group members' actions. Indeed, an EEG-study by Gutsell and Inzlicht (2010) suggests that covert vicarious action performance depends on an observed actor's group membership. These authors asked fair-skinned Canadians to either perform a target action themselves or to observe an in-group member (Caucasian) vs. an out-group member (African-Canadian, East-, or South-Asian) performing this same action. In these different conditions, they measured suppression of EEG activity in the mu frequency bandwidth over the primary motor cortex, which is thought to index the degree of motor simulation. Gutsell and Inzlicht found that both, performing an action oneself and observing an in-group member performing an action, elicited mu suppression. However, there was no significant mu suppression, that is, engagement in motor simulation, when observing an out-group member.

Furthermore, our results for the black-glove control condition are consistent with findings by Avenanti et al. (2010). These authors asked fair- and dark-skinned participants to observe the hands of either a fair-skinned, a dark-skinned, or an (artificially) violet-skinned actor experiencing pain (vs. no pain). The findings revealed sensorimotor resonance, indicating neuronal simulation of the observed pain, for observation of the in-group member, but not of the out-group member. They also found that observers simulated the pain of the violet-skinned actor, but to a smaller extent than for the in-group member. Analogous to this finding, in our study, the observers might have felt uncertain about the group membership of the person wearing black gloves. Hence, the observation of the glove-wearing actor would elicit only an intermediate level of motor simulation.

How can biased motor simulation account for the present memory effects? The bulk of the motor simulation literature, including studies on intergroup differences (Xu et al., 2009; Avenanti et al., 2010; Gutsell and Inzlicht, 2010; Azevedo et al., in press), has focused on the processes ongoing *during* observation. However, a few studies have shown that motor representations from observation are reactivated during retrieval (Senkfor et al., 2002; Wutte et al., 2012). Consistent with a motor-simulation account of the present false memory effect, Wutte et al. (2012) found overlapping neural activation in motor areas when participants remembered self-performed and observed movements.

Our findings extend the common understanding of the emergence of false memories of self-performance. Explanations of related false action memories, specifically the imagination-inflation effect (Goff and Roediger, 1998), have invoked the misattribution due to similarity of sensory features. According to this account, which draws on the source-monitoring framework (Johnson et al., 1993), non-self-performed actions (e.g., merely imagined actions) are attributed to self-performance to the extent that the sensory features of action memories from the competing sources are similar (vs. dissimilar). For instance, after vividly imagining the action of shaking a bottle, people may later remember perceptual details and features, such as shape and color of the bottle, or fingers grasping the bottle; because these features are similar to the features contained in memories of self-performed actions, an originally imagined action may be misattributed to previous self-performance. Conversely, by this view, the availability of distinctive perceptual features at retrieval prevents such misattributions.

Our findings are not easily reconciled with this account. Because hands wearing black gloves are more salient and perceptually more distinct from fair-skinned hands than dark-skinned hands, the sensory-feature account of misattribution would predict that this condition results in the lowest rate of false action memories. However, observation inflation was lowest in the out-group condition, indicating that group membership rather than perceptual distinctiveness was critical in forming false memories of self-performance. This result is in line with earlier findings (Lindner et al., 2010, Exp. 3).

Still, whereas similarity of perceptual features is not sufficient to account for the pattern of results that we found in the current study, the distinctiveness of such features may still moderate the effect under certain circumstances. Schain et al. (2012) manipulated perceptual distinctiveness by using the actor's face as a visual identity cue. They found that observation inflation is diminished when a central identity cue, that is, the actor's face, was available and attended to by observers. In light of these previous findings, one might wonder why the non-self cues employed here, dark skin or black gloves, did not eliminate false self-attributions to a greater extent. It could allow observers to apply a rule such as "*I did not wear black gloves/my skin is not that dark, so it was not me who performed this action*" to avoid false self-attributions.

This issue can be resolved by arguing that the face is probably a more effective and distinctive identity cue than are skin color or a piece of clothing. The face offers various features (e.g., color of the eyes, size of the nose, shape of the forehead, etc.), which collectively signal a *Not-me*-response. Also, the detection and identification of others' faces are exceptionally important in social development and social cognition (Zebrowitz, 1997), and humans, including newborns, have a pronounced tendency to direct their visual attention to others' faces (Johnson and Morton, 1991). However, for engagement and modulation of motor simulation to occur, skin color has not to be highly salient – the observers' categorization into an in-group vs. an out-group member is sufficient to alter shared motor representations in the observer.

To conclude, in the present study, we focused on physical similarity in terms of skin color to manipulate group membership. Future studies should examine whether our results generalize to other cues of group membership that are not conveyed by physical appearance and to other types of group membership than ethnicity. For instance, would we find the same bias when ethnicity is conveyed solely by verbal labels, such as first names that are typical for specific groups? And will observation inflation be higher if the actor shares, for example, the same values, the same profession, or the same interest as the observer?

With this study we have shown that people are less prone to confuse self and other in action memory when they have observed an out-group (vs. in-group) member. As we have argued, our findings are not easily explained by the similarity or distinctiveness of perceptual features, but are consistent with an account of intergroup biases in motor simulation. Future studies should seek further evidence for the underlying mechanisms in this fascinating new domain of memory research.

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Social working memory: neurocognitive networks and directions for future research

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Navigating the social world requires the ability to maintain and manipulate information about people's beliefs, traits, and mental states. We characterize this capacity as *social working memory* (SWM). To date, very little research has explored this phenomenon, in part because of the assumption that general working memory systems would support working memory for social information. Various lines of research, however, suggest that social cognitive processing relies on a neurocognitive network (i.e., the "mentalizing network") that is functionally distinct from, and considered antagonistic with, the canonical working memory network. Here, we review evidence suggesting that demanding social cognition requires SWM and that both the mentalizing and canonical working memory neurocognitive networks support SWM. The neural data run counter to the common finding of parametric decreases in mentalizing regions as a function of working memory demand and suggest that the mentalizing network can support demanding cognition, when it is demanding social cognition. Implications for individual differences in social cognition and pathologies of social cognition are discussed.

Keywords: mentalizing, working memory, default mode network, social neuroscience, social cognitive affective neuroscience

Whether keeping track of friends' perspectives during conversation, a roomful of colleagues' beliefs during a conference, or the political ideology of someone we just met, we constantly juggle social cognitive information. Smooth social interaction requires keeping track of various amounts of social information, such as the particular characteristics and relationships among people. Indeed, the "social brain hypothesis" suggests that the fundamental evolutionary constraint leading to increased human brain size, relative to body size, was the need to manage social cognitive demands (Dunbar, 1998).

In cognitive psychology, the process commonly associated with holding multiple pieces of information in mind simultaneously is known as working memory. While there is a great deal of research on the brain mechanisms guiding working memory, tests of working memory have almost exclusively focused on cognitive or perceptual information and have not examined *social working memory (SWM)* for the kinds of social cognitive information that is important for successful social interaction. There are at least two critical barriers that likely prevented research on SWM in the past. First, past research finds similar patterns of behavioral performance across social and non-social cognitive processing demands (Kinderman et al., 1998; German and Hehman, 2006; Apperly et al., 2007). It has therefore been taken for granted that both forms of information processing rely on one working memory system. However, brain imaging research suggests that social cognitive and non-social cognitive information processing rely on distinct brain systems (Kampe et al., 2003; Fox et al., 2005; Mitchell et al., 2005; Ciaramidaro et al., 2007), suggesting that SWM and cognitive working memory (CWM) may rely on distinct, though perhaps correlated, neural mechanisms. Second, the dominant paradigms in social neuroscience show little-to-no variability in the amount of information they require, or working memory demand (Fletcher et al., 1995; Brunet et al., 2000; Walter et al., 2004). The past decade of research has focused on which brain regions engage in a binary fashion to social relative to non-social cognitive tasks. While this has been useful in delineating brain networks engaged in social cognition, it has overshadowed the possibility that these systems are sensitive to SWM demands and show variability in activation across individuals.

We recently reported findings suggesting that SWM may rely on both social cognition and canonical working memory brain networks (Meyer et al., 2012). Here, we review evidence in support of the idea that demanding social cognition may require SWM, that individual differences in neural responses to SWM may explain variance in individual differences in social cognitive ability, and suggest that research on SWM may help address remaining gaps or untested assumptions in social cognition research, as well create novel ways to improve social cognitive function.

WHAT IS SOCIAL WORKING MEMORY?

Social working memory is working memory for social cognitive information, and will tend to engage during a process referred to as "mentalizing." Mentalizing is an umbrella term used to describe the ability to think about mental states, traits, beliefs, and intentions (Frith and Frith, 2003). Arguably, complex mentalizing depends on some form of working memory: when considering and attributing mental states to the self and others, people must access, maintain, and manipulate information about the person (self or other) and draw some sort of conclusion about their related mental state. This is similar to the idea that when solving a math problem, people must access and hold representations of the numbers to be manipulated in order to derive an answer (Siegler, 1987, 1988; Geary and Burlingham-Dubree, 1989; Geary and Wiley, 1991; Geary et al., 1993; Ackerman, 1996; Timmermans and Van Lieshshout, 2003; Bjorklund et al., 2004) – and indeed, arithmetic computation is inextricably linked to working memory (e.g., Geary et al., 2004; Wu et al., 2008; Meyer et al., 2010).

Behavioral evidence for SWM comes from studies showing that as social cognitive load increases, mentalizing performance decreases (Kinderman et al., 1998; Rutherford, 2004; Apperly et al., 2007), a behavioral profile consistent with working memory research which suggests that working memory is a limited capacity system (see; Miyake and Shah, 1999 for a review). For example, adults show increased errors on mentalizing tasks as a function of the number of embedded beliefs maintained (i.e., "Bob thinks that John knew that Mary wanted to go to the shop"; Kinderman et al., 1998). Although previously not specified as working memory tasks, such multiple embedding tasks could be conceived of in terms of working memory processes. That is, a correct answer to questions about what Bob thinks requires not only difficult grammatical constructs, but also the active maintenance of belief and desire representations for John and Mary. Likewise, dual-task methodology has shown that performing mentalizing tasks while simultaneously engaging in auditory (McKinnon and Mascovitch, 2007) and verbal working memory (Gilbert et al., 1988) decreases accuracy on various kinds of mentalizing tasks (e.g., theory of mind ToM, trait inference).

The guiding assumption of these approaches is that there is a limited pool of working memory resources and depleting the pool, either concurrently or prior to mentalizing, reduces the resources available for performing the mentalizing task. In fact, the "cognitive load" method in social cognition (i.e., manipulating CWM demand concurrently or prior to performing a social cognition task and measuring how load effects performance; Gilbert et al., 1988) and the "strength models" of cognitive resources (i.e., that there is one pool of limited resources supporting effortful cognition; Baumeister et al., 1998) seem to depend on this assumption. An alternative hypothesis, however, is that these tasks reflect different patterns of working memory system exhaustion, although both forms correspond with deteriorating mentalizing performance (i.e., different means to the same end). In this scenario, studies that ramp up social cognitive load may exhaust both a specialized SWM system and general CWM system, whereas those enhancing CWM demands may direct attention away from social information processing mechanisms toward CWM mechanisms (see **Figure 1B**). As will be shown in the subsequent section, brain imaging evidence suggests that this alternative hypothesis may better explain otherwise undetectable mechanistic differences guiding similar behavioral performance in mentalizing across social and non-social load manipulations.

MENTALIZING AND COGNITIVE WORKING MEMORY RECRUIT DISTINCT NEUROCOGNITIVE NETWORKS

SOCIAL COGNITION AND THE MENTALIZING SYSTEM

Mentalizing, or thinking about the psychological characteristics of others, whether it is thinking about their current mental state (beliefs, desires, intentions) or psychological aspects of their personality (traits), reliably recruits functional activation in the so-called "mentalizing network" consisting of medial frontoparietal regions [medial prefrontal cortex (MPFC); precuneus/posterior cingulate cortex (PC/PCC) along with temporoparietal junction (TPJ), temporal poles (TP), and posterior superior temporal sulcus (pSTS; Van Overwalle, 2009; Lieberman, 2010)]. This network is recruited when people draw inferences about the mental states of others either by assessing a person's state of mind, the emotional reactions they are likely to feel in response to particular events, or the likely behaviors they will engage in based on their intentions and current events (Kampe et al., 2003; German et al., 2004; Walter et al., 2004; Ciaramidaro et al., 2007). This network is also reliably recruited when people think about the psychological traits of other people, such as when they are learning about and judging someone's personality (Mitchell et al., 2004, 2005; Harris et al., 2005; Heberlein and Saxe, 2005). Consistent with these functional findings, recent findings using structural brain imaging suggest that individual differences in the gray matter structures of the mentalizing system correlates with social cognitive competence and even social network size (Powell et al., 2010; Lewis et al., 2011).

Importantly, the functional MRI studies investigating mentalizing compare brain activation in response to easy social cognitive tasks (e.g., deciding whether adjectives like "charming" could be used to describe people) relative to easy non-social tasks (e.g., deciding whether adjectives like "orange" could describe objects). Prior to our study (Meyer et al., 2012), no research had examined whether and how these regions respond to increases in the amount of social information to be maintained or manipulated during mentalizing. As will be revealed in the subsequent sections, hypothesizing how the mentalizing system may respond to increasing demands in social cognition is not straightforward, and examining this question may reveal interesting insights into the functional dynamics of the mentalizing and CWM networks.

THE NEUROCOGNITIVE NETWORK SUPPORTING CWM AND ITS ANTI-CORRELATION WITH THE MENTALIZING NETWORK

Despite the lack of research on SWM, there is a longstanding line of research on CWM, which offers a backdrop for examining whether the mentalizing system may respond similarly to regions supporting CWM. In general, CWM is the ability to maintain and manipulate increasing amounts of information at once. In typical studies of CWM, participants are instructed to maintain or manipulate spatial information (the location of shapes) or verbal information (the order of letters in a string; Smith et al., 1996; D'Esposito et al., 1999) and brain imaging studies using these paradigms consistently report activation in a lateral frontoparietal network consisting primarily of dorsolateral prefrontal cortex (DLPFC), lateral parietal cortex, as well as supplementary motor area (SMA; Goldman-Rakic, 1994; D'Esposito et al., 1999; Rypma et al., 1999; Wager and Smith, 2003). Specifically, activity in these regions increases as the amount of information in CWM increases (Braver et al., 1997; Rypma et al., 1999).

Importantly though, the neural regions previously implicated in CWM are often thought to be functionally distinct from the brain regions associated with mentalizing (medial frontoparietal

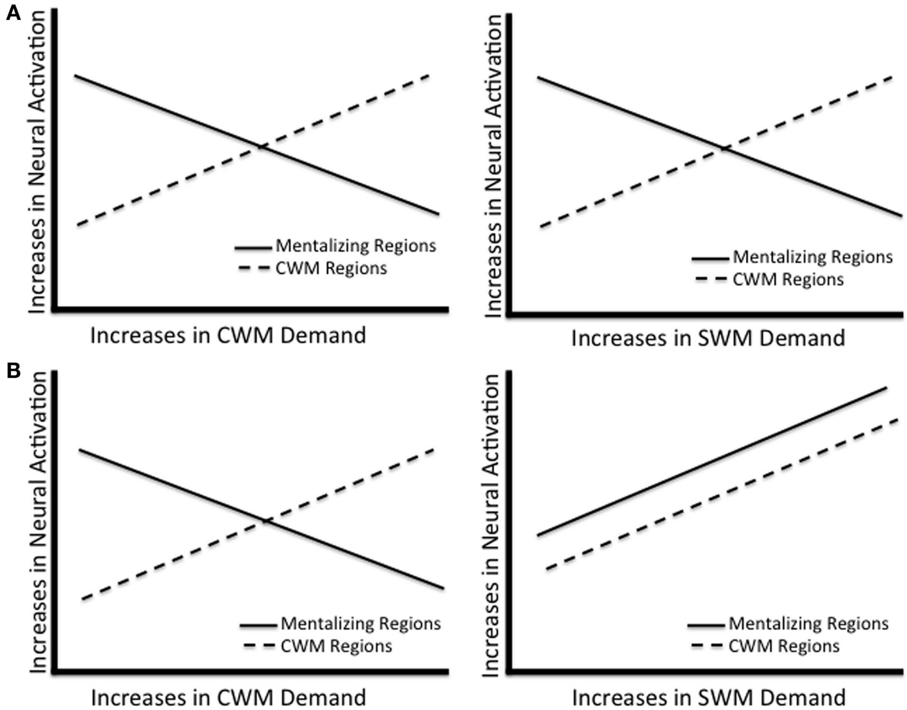

FIGURE 1 | Models of how the CWM and mentalizing regions respond to working memory demand. (A) Reflects the possibility that mentalizing regions do not support any working memory. **(B)** Reflects the possibility that mentalizing regions do not support non-social working memory, but do support social working memory.

cortex, TPJ, TP, and pSTS; e.g., Fox et al., 2005). In fact, brain regions associated with mentalizing seem to interfere with cognitive demands, including working memory (McKiernan et al., 2003; Greicius and Menon, 2004; Li et al., 2007; Anticevic et al., 2010; Metzak et al., 2011). That is, while increased activation in the lateral/SMA network supports cognitive processing, regions in the mentalizing network decrease in activation during cognitive processing. These regions have become known (outside of social neuroscience) as the "default network" (Raichle et al., 2001), so named because they are highly active when participants are passively resting in the scanner (i.e., by default), but show reduced activation, or deactivation, during task performance. **Figure 2** shows the anatomical regions associated with the mentalizing network, the default network, and their overlap based on the results from a term-based meta-analysis software, *Neurosynth* (Yarkoni et al., 2011).

A reliable finding is that the default network and lateral frontoparietal network show an inverse pattern of activation both at rest (Shulman et al., 1997; Greicius and Menon, 2004; Fox et al., 2005) and during CWM (Greicius et al., 2003; McKiernan et al., 2003; Metzak et al., 2011). For example, one study manipulated CWM demand with easy, medium, and difficult auditory detection CWM trials. Not only did the CWM network show parametric *increases* in activation, but also regions in the default network showed parametric *decreases* in activation, as a function of CWM trial difficulty (McKiernan et al., 2003). There is also evidence that failure to deactivate regions in the default network during CWM tasks interferes with activating the canonical working memory regions (Greicius and Menon, 2004) and may contribute to poorer cognitive performance (Weissman et al., 2006; Kelly et al., 2008). While these and related findings could suggest that the default network does not support working memory and instead its activation interferes with working memory processes, another possibility is that this network can support working memory when the content is social, and hence anti-correlations with canonical working memory systems is limited to non-social forms of working memory.

Taken together, findings from three literatures offer different pieces of information relevant to understanding SWM. First, social cognitive neuroscience research finds that a specific set of brain regions activate in response to mentalizing (i.e., medial frontoparietal cortex, TPJ, TP, and pSTS; the "mentalizing network"). Second, the CWM literature shows that a different set of brain regions (lateral frontoparietal network and SMA, the "canonical working memory network") support CWM. Specifically, these regions show a parametric response to CWM demands, which provides a possible pattern to look for when examining which brain regions support SWM. Third, extensive research on the default network shows that there is a network of regions whose functional activation is tightly coupled, most robust at rest, and deactivates during demanding cognition, including CWM. What is fascinating about this literature in the context of SWM is that this default network is anatomically similar to the mentalizing network. Whether and how the mentalizing and CWM networks could support SWM is

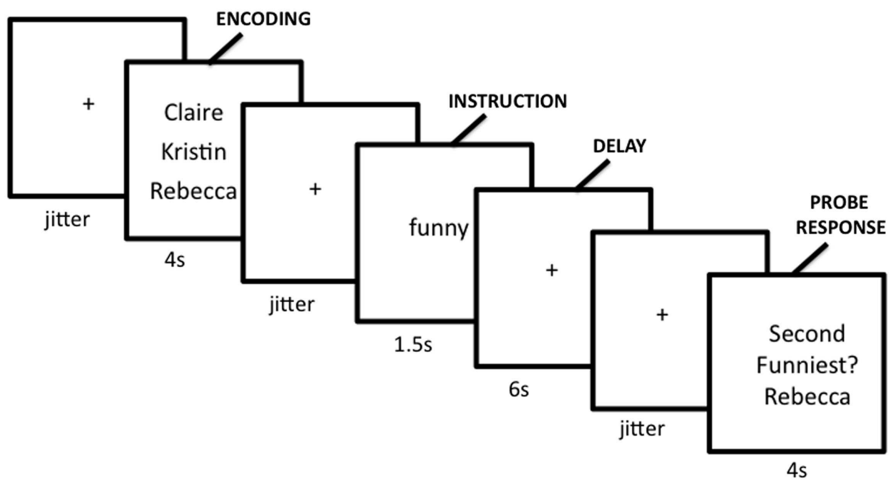

FIGURE 2 | Social working memory task.

an intriguing theoretical question, which will be addressed in the subsequent section.

MENTALIZING UNDER CWM AND SWM LOAD

Most social neuroscience research on mentalizing has used relatively simple mentalizing tasks. When performance measures are reported in fMRI studies of social cognition, they are often near ceiling (Fletcher et al., 1995; Brunet et al., 2000; Walter et al., 2004), implying relative ease. In fact, even 4 year olds achieve high levels of performance on many of the fMRI-based social cognition tasks given to adults (Wimmer and Perner, 1983; Sommer et al., 2007). Therefore, whether the mentalizing network supports complex social cognition, like SWM, remained untested. However, four studies have explored how juggling increased non-social information, or CWM, affects mentalizing system activation during social cognition (den Ouden et al., 2005; Kellermann et al., 2011; Rameson et al., 2012; Spunt and Lieberman, 2012a). For example, requiring participants to maintain a string of numbers while empathizing with others' emotional states relative to empathizing without maintaining numbers showed reduced activation in several regions of the mentalizing system [e.g., dorsomedial prefrontal cortex (DMPFC), MPFC, VMPFC, PC, pSTS, TP; Rameson et al., 2012]. A similar pattern of results extends to mental state inferences: requiring participants to maintain a complex sequence of digits (e.g., 937–6542) relative to a simple sequence of digits (e.g., 888–8888) while determining characters' intentions showed reduced activation in mentalizing regions (DMPFC, TP; Spunt and Lieberman, 2012a).

While these studies show that mentalizing regions reduce activation in response to CWM, they cannot speak to how the mentalizing network responds to working memory demands with social cognitive content. Given the fact that this system supports mentalizing, but also deactivates in response to canonical working memory demand (McKiernan et al., 2003; Metzak et al., 2011), it is not entirely clear how the mentalizing network would respond to working memory load in the social domain (i.e., social load). For example, one possibility is that mentalizing regions do not support effortful processing at all. If this were the case, then mentalizing regions may be insensitive, or even reduce activation, in response to demanding social cognition like SWM. This would be consistent with default network characterizations of brain regions associated with mentalizing, whose activation to date has been portrayed as reflecting non-effortful cognitive processing, and even postulated to interfere with effortful cognition (Sonuga-Barke and Castellanos, 2007; **Figure 1A**). An alternative possibility, however, is that mentalizing regions are specialized to respond to demands in social cognition. Thus, while they *reduce* activation in response to CWM and other non-social forms of effortful cognition, they also *increase* activation in response to SWM and other forms of effortful social cognition (**Figure 1B**). If this were the case, then mentalizing regions do not support non-effortful cognition *per se* as suggested by the default network literature, but instead support effortful social cognition.

To test these competing hypotheses, we recently examined how the mentalizing regions respond to SWM (Meyer et al., 2012). We developed a delayed-response working memory task that varied working memory load in the social domain on a trial-by-trial basis (**Figure 3**). During scanning, participants completed trials in which they encoded names of two, three, or four of their friends, mentally ranked their friends along a trait dimension during a delay period, and answered a true/false question about the rankings. Parametric analyses showed increases in the mentalizing system (DMPFC, PC/PCC, TPJ) and canonical working memory system [DLPFC, superior parietal lobule (SPL), SMA] as a function of the number of friends considered along a trait dimension during delay and probe-response periods (**Figures 4A,B**). Our data are therefore consistent with the hypothesis that the mentalizing regions can support effortful social cognition. Additionally, the CWM network also showed parametric increases in activation suggesting that although these two networks often operate inversely, in the context of SWM they may operate in conjunction. Thus, there may be two separable networks supporting SWM:

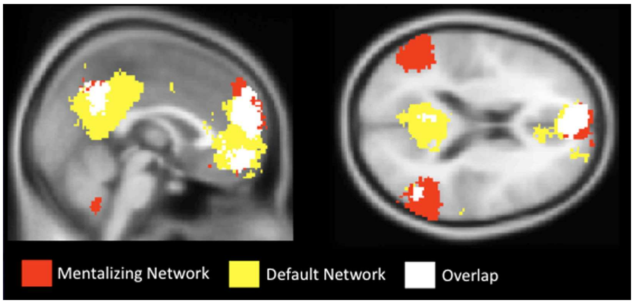

FIGURE 3 | Results from a term-based search on Neurosynth, which synthesizes fMRI data extracted from published articles. The mentalizing network, shown in red, was created with the search term "mentalizing." The default network, shown in yellow, was created with the search term "default." White areas indicate overlapping areas of activation.

the mentalizing network, which may be specifically involved in SWM and the canonical working memory network, which may be involved in all known forms of working memory.

These results suggest there might be multiple routes by which secondary tasks inducing CWM or SWM load might impair primary task performance in cognitive or social domains. Given that mentalizing regions commonly involved in social cognition are typically deactivated during effortful cognitive tasks, social load might impair cognitive task performance to the extent that there is negative connectivity between mentalizing and canonical working memory regions. In this hypothesized case, SWM load would not deplete canonical working memory resources, but instead suppress them to the extent to which the two systems are wired to compete. In contrast, non-social cognitive load might deplete canonical working memory controlled processing resources directly. Under many conditions, these two mechanisms might produce similar behavioral outcomes as a function of working memory load, but under others they may not. Connectivity-based suppression versus within system overloading might, for instance, lead to different performance outcomes immediately after the competing demand is eliminated. Future research should examine how the social or cognitive content of secondary tasks differentially lead to resource depletion and whether different neural markers of depletion lead to distinct behavioral responses.

These results are also consistent with a handful of recent studies, which have found that in certain contexts the default network and lateral frontoparietal regions can increase activation in conjunction (see; Spreng, 2012 for review). For example, these networks show positive functional connectivity when participants plan future, personal goals such as "how to find a good job" (Spreng et al., 2010), and co-activation during personal simulations that are goal oriented (Gerlach et al., 2011), creative idea generation (Ellamil et al., 2012), and mind-wandering (Christoff et al., 2009; Christoff, 2012). These studies may link to SWM in a variety of ways. On the one hand, each of these studies involve generating internal, subjective content, and it makes sense to think that SWM does as well: thinking about mental states requires the internal generation of mental state content. On the other hand, each of these past studies may involve social cognition. Even during mind-wandering, we may spontaneously think about our own and others intentions. Another interesting future question to explore is whether one function of the default network is to process social information, and its more natural, externally valid relationship with the lateral frontoparietal network is co-activation to better allow humans to navigate their social world. If this were the case, then past studies showing anti-correlations with the lateral frontoparietal system may be incidental to paradigms that engage demanding cognition for externally invalid stimuli.

While both the mentalizing and CWM networks showed parametric increases in response to SWM load, we found that only parametric increases in the mentalizing network correlated with a standardized measure of perspective-taking ability (**Figures 4C,D**). Specifically, individuals higher in trait perspective-taking were more likely to show load-dependent parametric increases in MPFC (Brodmann area 10), perhaps suggesting that individuals with greater perspective-taking ability are more able to exert intentional effort in MPFC. Interestingly, this is the only region of the frontal cortex known to be disproportionately larger in humans than other primates after scaling for body size (Semendeferi et al., 2001). In humans, individual differences in MPFC size correlate with social cognitive competence and social network size (Powell et al., 2010; Lewis et al., 2011). To tease apart the causal nature of these kinds of findings, a recent study measured macaque cortex size prior to and after living in groups of 1–7 macaques (Sallet et al., 2011). Rostral prefrontal cortex, a region suggested to be homologous to human BA 10, showed significant increases in gray matter structure as a function of larger group size. Thus, to the extent that the macaque findings parallel human findings, increasing social cognitive demands may cause growth in brain structures like BA 10. Our functional finding and the previous structural findings in humans and macaques dovetail nicely with the social brain hypothesis, which emphasizes that demanding social information processing may have been critical in the expansion of prefrontal cortex size in humans (Dunbar, 1998).

FUTURE DIRECTIONS IN SWM RESEARCH

PROBING THE MENTALIZING SYSTEM WITH SWM PARADIGMS

Together, functional and structural findings implicate the mentalizing network in social cognition. Yet the component process each region plays in mentalizing is still an open question, although some speculations have been suggested. In a recent review of mentalizing brain imaging studies, Lieberman (2010) found that across 45 different studies/tasks, DMPFC (BA 8/9) was reported in 91% of studies, whereas TPJ was reported in 59%, TP was reported in 52%, pSTS, and PC/PCC each 39%, and MPFC (BA 10) in 33%, suggesting that DMPFC may play a broad role across different kinds of mentalizing. Interestingly, the second most reported region from the meta-analysis was the TPJ, whose role in mentalizing is still heavily debated. For example, some researchers argue that TPJ activation during mentalizing, over and above attentional demands, reflects social cognitive processing (Young et al., 2010), while others argue that TPJ activation during mentalizing may entirely reflect attention orientation, rather than mentalizing-content-specific computations (Mitchell, 2008). The TPs are highly active when viewing faces and names of familiar people (Sugiura et al., 2006) yet are also associated with semantic knowledge (Schmolck

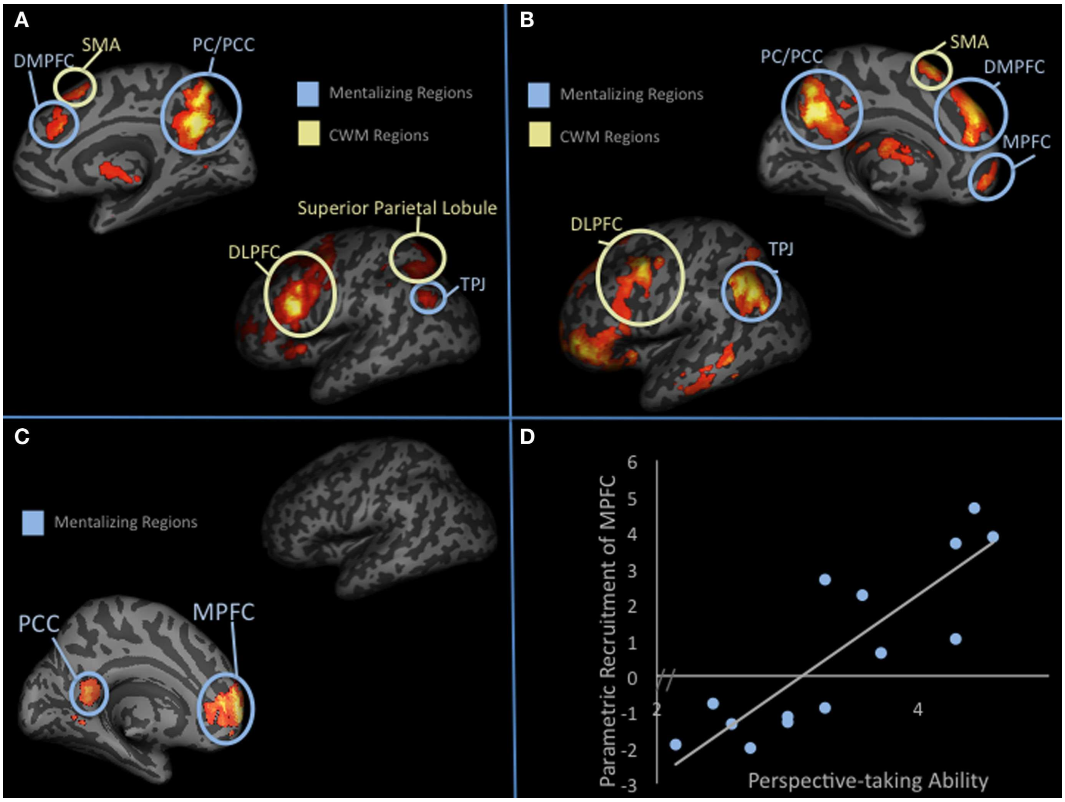

FIGURE 4 | Parametric increases in response to SWM. (A) shows parametric results (i.e., increases in activation as a function of thinking about 2, 3, or 4 friends) from whole-brain analysis during the delay period. **(B)** Shows parametric results (i.e., increases in activation as a function of thinking about 2, 3, or 4 friends) from whole-brain analysis during the probe-response period. **(C)** Parametric increases in activation as a function of social load during the delay period that correlates with trait perspective-taking scores. **(D)** Graphical display of the correlation shown in **(C)**.

et al., 2002; Bayley and Squire, 2005) and have been proposed to underlie social norm, rule-based or script knowledge guiding mentalizing (e.g., Lambon Ralph et al., 2009; Van Overwalle, 2009). The pSTS, on the other hand, appears to be sensitive to biological motion (e.g., Noguchi et al., 2005), which may help guide inferences about people's mental states (Baumeister et al., 1998).

Importantly, not only are all of these interpretations relatively speculative, none of them attempt to make sense of these regions' *interactive roles* in mentalizing. A SWM framework may help unravel the specific component processes these regions may play in mentalizing. For example, one working memory model suggests that a general, or "central executive" system orchestrates the holding of mental representations in mind, while content-specific sub-systems grounded in subdivisions of the parietal cortex code for visuo-spatial and lexical content that is fed forward to the central executive system (Baddeley, 2002). Likewise, demanding social cognitive processing in general, and SWM in particular, may rely on the DMPFC to function as a social-central executive system, whereas TPJ, TP, pSTS, and MPFC may function as SWM sub-systems that feed forward task-specific content. Alternatively, other working memory models suggest that rather than specialized systems dedicated to holding content-specific information in mind, working memory is supported by reactivation of previously stored long-term memories (Anderson, 1983; Cowan, 1995; Ruchkin et al., 2003; Lewis-Peacock and Postle, 2008). It seems possible that mentalizing region activation during SWM may reflect reactivation of previously stored episodic memories, a possibility which could be explored in the future with techniques such multivariate pattern analysis.

In addition to open questions surrounding functional roles of regions within the mentalizing system, the general operating characteristics of this network (i.e., not just *that* regions respond to certain stimuli, but *how* they respond, for example as a linear, quadratic, or cubic function) remains almost entirely unexplored in social neuroscience. Nonetheless, it has become increasingly clear that complex cognitive processes likely emerge from the interactions between and within brain regions that compose networks showing specific functional profiles (Bressler and Menon, 2010). As described previously, there is an overlap between regions of the mentalizing network and one of the core large-scale brain networks typically referred to as the default network (Gusnard et al., 2001; Spreng et al., 2009). Thus, an intriguing future direction for mentalizing research is to move beyond the region-by-region approach and explore how these regions' functional properties interact as a dynamic network to support mentalizing. SWM paradigms may be particularly useful in this endeavor, as network analyses on subtle manipulations in the mentalizing-content managed in SWM (traits versus beliefs, familiar versus unfamiliar others) may show unique functional relationships across regions within the mentalizing system.

Finally, in everyday life, SWM will often require not only juggling internal mental states, but also external characteristics, such as emotional expression, identity, and action understanding. Studies on working memory for facial identity tend to find increased activation in the fusiform face area (FFA) in addition to activation increases in canonical working memory regions (Druzgal and D'Esposito, 2001, 2003). However, in many of these studies, only facial identity is maintained during a delay. In one study that required the maintenance of facial identity and emotion, the FFA did not show a delay period response. Instead, the amygdala, hippocampus, and lateral orbitofrontal cortex showed sustained increases during the working memory delay period for both identity and emotion trial types (LoPresti et al., 2008). LoPresti et al. (2008) suggested that the FFA may facilitate simple forms of facial working memory, but that it may not be sufficient for maintaining more complex facial information in working memory. An interesting future direction will be to expand on the LoPresti et al. (2008) findings by combining the maintenance of mental states along with emotions and identities to examine how brain regions previously implicated in facial processing interact with the mentalizing system during SWM.

In the context of action identification, a large literature implicates the mirror neuron system, which is neuroanatomically distinct from the mentalizing system, in simulating others' minds by decoding their behavioral intentions (Aron et al., 1992; Di Pellegriono et al., 1992; Keysers and Gazzola, 2010; Spunt and Lieberman, 2012b). To date, no study has examined the potential working memory properties of the mirror neuron system, although one study has demonstrated that the mirror neuron system may engage more automatically than the mentalizing system (Spunt and Lieberman, 2012a). One interesting possibility is that the mirror neuron and mentalizing system may differ in their working memory properties and future research will be needed to disentangle how we maintain, manipulate, and bind representations of actions and mental states during SWM.

INFORMING THE DEBATE BETWEEN MENTALIZING AND EXECUTIVE FUNCTIONS

Mentalizing research has its roots in developmental and comparative psychology that, for several decades, has examined "ToM," or the *ability* to represent internal mental states (Premack and Woodruff, 1978). A fundamental question in this line of research surrounds how humans are able to understand that people have internal mental states that often times are distinct from our own subjective experience. A longstanding debate in the ToM literature surrounds whether a ToM requires executive functions, or the suite of cognitive abilities including working memory, planning, attention, problem solving, inhibition, and mental flexibility. As it stands, researchers asking this question tend to adhere to one of two sides of a debate. Many suggest that ToM requires executive function ability, including working memory (Hala et al., 2003). Evidence in support of this position comes from (1) developmental findings showing that children on average do not pass the false belief task (a measure of ToM; see; Wimmer and Perner, 1983) until 4 years of age (Gopnik and Astington, 1988), which coincides with the development of working memory (Carlson and Moses, 2001; Tamm et al., 2002); (2) performance on working memory tasks correlates with ToM ability in children (Gordon and Olson, 1998); and (3) adult performance on ToM tasks decreases as a function of task demand (McKiernan et al., 2003; German and Hehman, 2006; Apperly et al., 2007).

Evidence in support of the other side of the debate – that ToM is a specific conceptual knowledge that does not necessitate executive function – (for a discussion, see; Bloom and German, 2000) garners support from brain imaging studies showing that ToM relies on mentalizing regions, rather than brain regions associated with executive function (Baumeister et al., 1998; Lieberman, 2010). In addition, neuropsychological evidence, particularly from research on individuals with Autism Spectrum Disorder (ASD), is consistent with the idea that ToM is distinct from executive functions. Individuals with ASD show deficits in mentalizing, including ToM. However, some evidence suggests that these deficits can persist while executive functions including working memory remain intact (Ozonoff and Strayer, 2001). In addition, children under the age of 4 show improved performance on ToM tasks when cognitive demands are reduced (Lewis and Osborne, 1990; Wellman and Bartsch, 1998; Yazdi et al., 2006), suggesting that the role of executive functions including working memory in ToM may be an artifact of the arbitrary cognitive demands required in false-belief reasoning *per se*, not ToM in particular.

In both sides of the debate, it is assumed that ToM and executive functions are mutually exclusive. An alternative possibility, however, is that mentalizing requires a specific social executive function system, which is distinct from the domain-general executive function system, and is designed to handle increasing amounts of beliefs, traits, and mental states. Consistent with this suggestion, the mentalizing network, which supports ToM, was found to increase linearly as a function of SWM load, as did the CWM system (Meyer et al., 2012). It is possible that parametric increases in the CWM system reflect domain-general working memory demands in the SWM task (i.e., the temporal and spatial ordering of names and/or verbal rehearsal). However, the mentalizing-specific demands (i.e., thinking about the traits of an increasing amount of people) are likely supported by the functionally distinct mentalizing system. In the case of ASD, the domain-general executive functions may be intact, while the domain-specific social executive system may be compromised. Likewise, extant ToM tasks may vary in manipulating social versus cognitive demands and may in turn differentially exhaust one or both executive systems.

SOCIAL COGNITIVE PATHOLOGIES, SOCIAL COGNITIVE ABILITY, AND INTERVENTIONS

Many psychiatric conditions including schizophrenia, social anxiety, and ASD show dual or differential deficits in social cognition and working memory. Understanding how the mentalizing and CWM networks contribute to SWM may offer important insight into how these systems contribute to various psychological disorders and the kinds of interventions that might benefit them. For example, working memory and ToM are impaired in patients with schizophrenia (Goldman-Rakic, 1994; Pickup and Frith, 2001; Couture et al., 2006). Individuals with social anxiety show working memory deficits, but enhanced working memory for socially salient words (Amir and Bomyea, 2011). Similarly, a hallmark of autism is the impaired ability to relate to and take the perspective of others (Baron-Cohen et al., 1985; Dawson and Fernald, 1987). Interestingly, research on working memory capacity in individuals with ASD is mixed (Bennetto et al., 1996; Russell et al., 1996; Ozonoff and Strayer, 2001; Williams et al., 2006), with some research finding that working memory capacity is relatively intact in high-functioning individuals (Bennetto et al., 1996; Ozonoff and Strayer, 2001). It is possible that social cognitive deficits in these and other disorders may be better characterized with the inclusion of a social cognition task like SWM that varies in difficulty level.

Outside of psychopathology, SWM capacity may also explain variance in healthy individual's social cognitive abilities and broader "social intelligence." If, as suggested by Bower (1975), the purpose of working memory "is to build up and maintain an internal model of the immediate environment and what has been happening in our world," then SWM should be similarly significant. In daily life, much of what one would qualify as "happening" that should require working memory comprises information about people's psychological characteristics, their mental states, and the relation of these across individuals. On the cognitive side, working memory capacity and lateral frontoparietal activity has been linked to cognitive abilities ranging from math and reading to IQ (Daneman and Carpenter, 1980; Conway et al., 2003; Geary et al., 2004). Similarly, with our SWM paradigm, we identified regions that increased with social load and showed a positive association with self-reported perspective-taking ability (Davis, 1983). Although both lateral and medial frontoparietal networks increased with load in this task, only medial frontoparietal regions showed significant correlations with self-reported perspective-taking ability (see **Figures 4B,C**). Additionally, medial frontoparietal regions only showed this effect when load-level was taken into account. General responses, collapsing across load-level, showed no correlation with trait perspective-taking ability. Perspective-taking is considered an effortful social cognitive process (Davis et al., 1996; Epley et al., 2004) and greater self-reported perspective-taking is associated with better social functioning (Davis, 1983). This finding is therefore consistent with the suggestion that individual differences in medial frontoparietal activation during SWM may explain variance in real-world social cognitive ability.

Paralleling recent findings with working memory (Klingberg et al., 2005; Jaeggi et al., 2008, 2011), it is also plausible that SWM training could benefit the everyday social cognitive success of individuals with social cognitive deficits and even individuals with normal social cognitive performance. A handful of recent studies, while controversial (for critical reviews of WM training transfer effects see: Melby-Lervåg and Hulme, 2012; Redick et al., 2012; Shipstead et al., 2012), suggest that working memory training not only improves working memory, but these improvements generalize to improved cognitive reasoning and fluid intelligence (Klingberg et al., 2005; Jaeggi et al., 2008, 2011). For example, after completing a working memory intervention, children with attention-deficit hyperactivity disorder (ADHD) showed improvements in working memory capacity, response inhibition, and complex reasoning. In addition, the participants' parents reported that their children's ADHD symptoms improved both post-training and after a 3 month follow-up assessment (Klingberg et al., 2005). Similarly, Jaeggi et al. (2008) found that in psychologically healthy adults with normal IQ, working memory training corresponded with improvements in fluid intelligence, or the ability to reason and solve new problems independent of previously acquired knowledge. While preliminary, these findings suggest that working memory ability may be plastic, and that training working memory may help to improve other forms of general cognitive reasoning. By extension, SWM training may be a way to improve both SWM (i.e., how many people can someone think about at once) and other forms of social cognitive reasoning (i.e., perspective-taking) in both atypical and typical populations.

Another interesting hypothesis related to enhancing cognitive ability is the potentially greater efficiency of SWM, relative to non-SWM. Other cognitive operations are facilitated when put in a social context. For example, performance on the Wason card selection task, a measure of conditional reasoning, improves when conditional rules are based on social contracts relative to non-social contingencies (see Cosmides and Tooby, 1992). Similarly, because social cognition may come more readily to individuals, engaging SWM may facilitate recruitment of the lateral frontoparietal working memory network via the mentalizing system, and improve working memory performance.

CONCLUSION

Working memory research has focused on the basic building blocks that allow us to handle representations of our immediate environment, but has neglected to incorporate relevant social information that makes up much of our mental processing. Research reviewed here suggests that demanding mentalizing can be conceived as requiring SWM. Interestingly, the picture that is beginning to emerge is that SWM may rely on two functionally distinct neurocognitive networks: The mentalizing network and the canonical working memory network. While the mentalizing network reduces activation under CWM load, it appears to increase activation, alongside the canonical working memory system, while under SWM load. These findings have theoretical implications for the functional properties of the default network and the neural systems that support social cognition, as well as practical implications for future research in social cognitive training.

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How do we update faces? Effects of gaze direction and facial expressions on working memory updating

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The aim of the study was to investigate how the biological binding between different facial dimensions, and their social and communicative relevance, may impact updating processes in working memory (WM). We focused on WM updating because it plays a key role in ongoing processing. Gaze direction and facial expression are crucial and changeable components of face processing. Direct gaze enhances the processing of approach-oriented facial emotional expressions (e.g., joy), while averted gaze enhances the processing of avoidance-oriented facial emotional expressions (e.g., fear). Thus, the way in which these two facial dimensions are combined communicates to the observer important behavioral and social information. Updating of these two facial dimensions and their bindings has not been investigated before, despite the fact that they provide a piece of social information essential for building and maintaining an internal ongoing representation of our social environment. In Experiment 1 we created a task in which the binding between gaze direction and facial expression was manipulated: high binding conditions (e.g., joy-direct gaze) were compared to low binding conditions (e.g., joy-averted gaze). Participants had to study and update continuously a number of faces, displaying different bindings between the two dimensions. In Experiment 2 we tested whether updating was affected by the social and communicative value of the facial dimension binding; to this end, we manipulated bindings between eye and hair color, two less communicative facial dimensions. Two new results emerged. First, faster response times were found in updating combinations of facial dimensions highly bound together. Second, our data showed that the ease of the ongoing updating processing varied depending on the communicative meaning of the binding that had to be updated. The results are discussed with reference to the role of WM updating in social cognition and appraisal processes.

Keywords: biological binding, social cognition, appraisal, gaze direction, facial expression, facial dimensions, working memory

INTRODUCTION

Gaze direction and facial expression are crucial components of face processing, particularly because they communicate the intentions of others, and, in general, being able to read the mind from the face is important not only for social interaction but is also advantageous for navigating in a social environment. Previous studies demonstrated that the influence of gaze direction on the perception of human faces varies depending on the behavioral intention associated with the facial emotion that is expressed (e.g., Adams and Kleck, 2003; Conty et al., 2012). Direct gaze enhances the perception of approach-oriented facial emotional expressions, such as anger or joy, while averted gaze enhances the perception of avoidance-oriented facial emotional expressions, such as fear or sadness. Indeed, facial expression and gaze direction are associated to signal these basic behavioral tendencies and their processing appears to be combined.

Appraisal theories of emotion (e.g., N'Diyae et al., 2009; Mumenthaler and Sander, 2012) emphasize the fact that the combination of gaze direction and facial expression indicates to the perceiver the degree of self-relevance of the seen face. For instance, for survival, the self-relevance of a threat signaled by a fearful face should increase when the face is looking at something away from the observer. This is because the averted gaze signals where in the environment a threat may come from. Whereas the opposite should be true for an angry face looking straight at the observer since the direct gaze indicates impending aggression toward the observer him-herself. Therefore, the appraisal of the face also provides important social information to be processed and then to be taken into account.

Not only are facial emotional expressions and gaze direction included in the evaluation process to determine the behavioral intention of the other person and the relevance to oneself, but their bound processing appears to occur rapidly and automatically, as Milders et al. (2011) demonstrated through an attentional blink task. In fact, they found that specific emotions were detected more frequently when associated with specific gaze directions. Namely, fearful faces were detected more frequently with averted than with direct gaze, whereas angry and happy faces were detected more frequently with direct than with averted gaze. Similarly, Ricciardelli et al. (2012) found that angry faces displaying direct gaze produced no attentional blink, indicating that such a threatening combination of facial expression and gaze direction was processed fast and automatically, probably by virtue of its high social and adaptive value.

Therefore, there is evidence, from the domain research of perception, emotion and attention, of an enhanced processing of specific and highly communicative combinations of gaze direction and facial expression. Moreover, there is also some evidence of the influence of gaze and facial expression on face memory. In particular, poorer memory for angry faces that were initially presented with averted gaze as opposed to direct gaze has been reported (Nakashima et al., 2012). The appraisal of a face (i.e., deceptive faces) influences its encoding in the memory (e.g., Yamagishi et al., 2003; Bayliss and Tipper, 2006). Surprisingly however, it is unknown whether and how the highly communicative combinations of gaze direction and facial expression affect working memory (WM), a function of primary importance for ongoing processing and for dealing with either environmental stability or flexibility (e.g., Kessler and Meiran, 2008).

Working memory is a dynamic cognitive system and it is likely to work largely through the mechanism of updating which is responsible for the fast processing and appraisal of information useful to our current goals. Updating can be conceptualized in terms of the maintenance and inhibition of information, since its function is to maintain goal relevant information and to inhibit information that is irrelevant (see Morris and Jones, 1990; Palladino et al., 2001; Oberauer, 2005). Indeed, this function of updating should be especially observed and important when we are engaged in processing social salient stimuli such as faces. In fact, in order to read the social meaning of a face, we have to quickly select relevant information from it and, when needed, to update it. Particularly, this is true for the information coming both from facial expression and gaze direction which represent highly communicative and changeable aspects of faces (see Haxby et al., 2000). Thus, when living in a social world, being able to quickly detect changes in faces and to update them is undoubtedly beneficial in terms of the ability to evaluate the face and understanding its meaning. The WM updating mechanism should be certainly involved in all these social cognitive abilities but it has not been studied using face as stimulus.

Recently, basic research in WM has addressed the role of binding (or association/combination) as an important factor in explaining performance. Moreover, the ability to build-up, maintain, dismantle, and recreate a binding has been considered a primary source of individual and age-related differences (see Oberauer, 2005; Schmiedek et al., 2009). Bindings may also represent different types of relational memories: for example, between stimuli and their features (e.g., item-color) or between unrelated stimuli that have highly similar characteristics (e.g., item–item, see Piekema et al., 2010).

A recent study by Artuso and Palladino (2011) investigated how bindings may affect the updating process in WM. Specifically, they manipulated the arbitrary association between two consecutive items, i.e., letters; for example, if *BFC* is a set of items, a binding could be the combination between *B* and *FC*, or *BF* and *C*. They created a computerized task where they manipulated the strength of the binding through the perceptual similarity with which the stimuli were bound together. They found that stronger bound perceptual configurations (i.e., stimuli depicted using identical colors), needed longer latencies to be updated, compared to weaker bound configurations (i.e., stimuli depicted in different colors; for details see Artuso and Palladino, 2011, see Results *On-line: Perceptual binding*). The finding was similar to that found with stimuli characterized by phonological similarity (Guérard et al., 2009). Altogether, these results show that WM performance is affected by the strength with which stimuli are bound together by some kind of similarity (e.g., perceptual or phonological), at least for stimuli with no, or very little, biological relevance.

A relevant methodological aspect of the Artuso and Palladino's (2011) study was that in the task they measured on-line response time (RT), an alternative way to assess WM thought to represent a more sensitive index of the process occurring during the task, thus enabling a more direct and clear-cut measurement of the updating process (e.g., Kessler and Meiran, 2008; see the Method and the Results for further details). In the study by Artuso and Palladino (2011) trials were composed of steps requiring the performance of different cognitive operations, i.e., studying, maintenance, or updating of information. Interestingly, the authors showed that on-line RT was useful to track the updating process: participants' RTs were longer in updating steps, when compared to either maintenance or studying steps. This supported the view that updating is much more effortful, relative to simple memory maintenance of information (see Results *On-line*: *Updating effects*; see also Palladino and Jarrold, 2008).

It's worth noting that all of the aforementioned studies used high bound stimuli, but with no biological and communicative value; in other words, arbitrarily created stimuli. Further, such stimuli combinations do not have a role of primary importance either in terms of ongoing behavior or in terms of appraisal processes of the stimulus. We believe that the two dimensions of gaze direction and facial expression can be reasonably considered and treated as a special kind of binding, i.e., a biological binding. This is because of their biological, social, and communicative value, and due to the fact that they are preferentially processed in combination (e.g., Adams and Kleck, 2003; Conty et al., 2012). Therefore, the updating of these bindings should be particularly meaningful in a social environment. Thus, respect to stimuli with no explicit biological value (such as letters or digits), they might have a different impact on WM updating. We believe, in fact, that faces represent one of the main stimuli whose processing undoubtedly contribute to building-up and maintaining an internal model of what has been, and is happening in our social world. This is analogous to what has been reported for the on-line maintenance and manipulation of other pieces of social information (e.g., thinking about the psychological characteristics of people, see Meyer et al., 2012). Consequently, the updating of crucial and communicative components of the face (such as gaze direction and facial expression) is necessary to handle representations of the immediate social environment.

In the present study, we tested the impact that biological bindings may have on WM updating. By biological binding we mean different combinations between facial dimensions.

Our aim was twofold. First, to investigate whether when stimuli have a biological value, the strength of their bindings was detrimental or beneficial on updating performance. In particular, in Experiment 1 we regarded as high biological bindings the combinations between approach-oriented facial expressions (i.e., joy) and direct gaze and those between avoidance-oriented facial expressions (i.e., fear) and averted gaze. The reason was because they were previously found to be perceived and processed strongly bound together and to have a role in appraisal processes (e.g., N'Diyae et al., 2009). Whereas, we regarded as low biological bindings those combinations in which approach-oriented facial expressions were combined with averted gaze, and avoidance-oriented facial expressions were combined with direct gaze. We hypothesized that, by virtue of their biological, social, and communicative value, the strong combinations of gaze direction-facial expression, i.e., high bindings, should be updated faster than the weak gaze direction-facial expression combination, i.e., low bindings. Therefore, we assumed that this biological binding might be beneficial to WM updating given its relevance and its function of maintaining an internal model of social environment (see also Meyer et al., 2012), and also because they are processed fast and automatically (Milders et al., 2011; Ricciardelli et al., 2012).

Second, we aimed to study whether (as we expected) the impact of biological bindings on WM updating is affected, thus varies, as a function of the social and communicative value of the facial dimensions considered. In fact, given that the combination of gaze direction and facial expression also conveys the relevance of the face for the observer (i.e., face appraisal, see e.g., N'Diyae et al., 2009), it would be possible that this piece of information also has to be dealt with by WM memory updating. To this end, we compared the biological binding between the two highly social/communicative dimensions of gaze direction and facial expression (see Experiment 1), with the biological binding between two less social/communicative dimensions such as eye color and hair color (Experiment 2). According to human genetic studies (e.g., Sulem et al., 2007; Sturm, 2009), high binding conditions were represented by combinations which have been reported to occur more frequently bound together, such as blue eyes-blonde hair, whereas low binding conditions were represented by combinations which have been reported to occur less frequently bound together, such as, e.g., blue eyes-brown hair.

MATERIALS AND METHODS

PARTICIPANTS

Participants were undergraduates from the University of Pavia. Twenty took part in Experiment 1 (mean age = 23 years, SD = 2.54; 14 females) and 20 took part in Experiment 2 (mean age = 24.6 years, SD = 3.06; 16 females). None of them participated in both experiments. All volunteered in exchange for partial course credit, gave informed consent and were naïve as to the purpose of the experiment.

APPARATUS AND MATERIALS

For both Experiment 1 and 2 a novel computerized updating task was devised starting from a previous one (see Artuso and Palladino, 2011). Stimuli were presented on a 17″ monitor driven by an Asus computer, located 60 cm from the observer. Stimulus presentation and response registration were controlled by the SuperLab software.

The stimuli were color photographs of faces selected from the Radboud Faces Database by Langner et al. (2010) and measured $5.6 \times 6.8°$. For Experiment 1 10 faces were selected (five female and five male) showing joyful, fearful, or neutral facial emotional expressions. A face with the neutral facial expression was always presented at the start of the trial to allow participants some time to adapt to the processing of a complex visual stimulus such as a human face (stimulus adaptation; see also below). Each facial expression was taken with gaze either direct or averted. Gaze direction and facial expression combinations were counterbalanced within faces. For Experiment 2 10 different faces were selected from the same database, displaying direct gaze, and neutral facial expression. Five were female and five male, and showed blue or dark eyes and blonde or brown hair. Each blonde/brown hair face was taken with eyes either blue or dark. As in Experiment 1, at the start of the trial there was an adaptation phase in which a face with the neutral facial expression displaying direct gaze and with a combination of eye-hair color in accordance with the binding trial (i.e., high or low, see below) was always presented. Eye and hair color combinations were counterbalanced within faces.

PROCEDURE AND DESIGN FOR EXPERIMENT 1

Participants were told that the experiment was composed of trials varying in length, randomized in the experiment. They were presented with a number of faces, displayed in the center of the screen one at a time. The number of the faces displayed varied from two to four faces. As suggested by updating literature which emphasizes the use of an unknown list length to have the participant process each incoming item (see Morris and Jones, 1990), we presented lists of different length, so as to increase task variability and to make the end of the list unpredictable to participants.

Their task was to memorize the displayed faces and, in case, to compare and substitute the information of two consecutive faces, in terms of a specific facial dimension. At the end of the trial they were asked to recall the information of the last or next-to-last face. Therefore, in order to correctly perform the task they had to keep in mind two consecutive faces. Furthermore, during the task participants were instructed to respond as accurately and quick as possible, so that they were not encouraged to process the stimuli strategically. For half of the trials, participants received the specific instruction to focus on and memorize gaze direction disregarding facial expression; for the other half, to focus on and memorize the emotional expression, disregarding gaze direction. See **Figure 1** for an example.

All the trials had the same procedure: an initial stimulus adaptation phase, two memory phases, one or two updating phases followed immediately by a recall test phase.

In the stimulus adaptation phase, a neutral face gazing straight ahead was presented. Then, the instruction on which facial dimensions the participant had to focus (gaze direction vs. facial expression) was presented. The participants had to press the spacebar to start the experimental part of the trial.

In the memory phases, participants had to study, memorize, and maintain the information about each face. Thus, after two

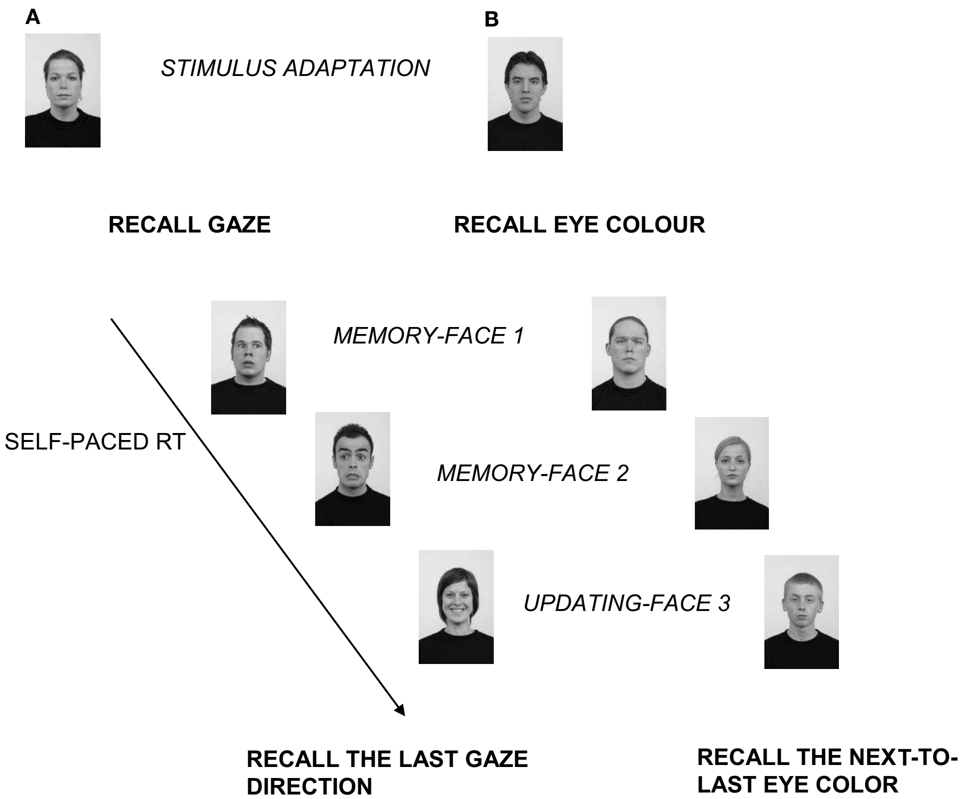

FIGURE 1 | An example of the sequence of events present in a trial requesting one update from Experiment 1 (A) and Experiment 2 (B). **(A)** After the initial stimulus adaptation phase, the participants were instructed to focus on and memorize the direction of the gaze of the face, disregarding the facial expression. After reading the instruction, they had to press the spacebar to see each face of the trial sequence. The self-paced experimental part of the trial started when the first face (Face 1, displaying here an averted gaze) appeared. Since the participants' task was to recall at the end of the trial either the direction of the gaze or the facial expression of the last/next-to-last of the seen faces, they had to memorize the direction of the gaze of Face 1 and to keep it in mind. Then, when the participants pressed the spacebar, the second face (Face 2) was presented. Here again, the face showed an averted gaze. At that point, participants had in mind the gaze direction of the first two faces (averted–averted). Next, when the third face appeared displaying direct gaze, an updating phase took place. In it the participants had to substitute the direction of the gaze of the first memorized face with the most recent memorized one. Namely, they had to substitute the direction of gaze of Face 1 with the direction of gaze of Face 3, thus updating their representation. They now had in mind the new association of gaze direction: averted-direct. Finally, at the end of the trial, at the recall test phase, in this case they had to recall the most recent memorized gaze by pressing the key corresponding to direct gaze on the keyboard. **(B)** In Experiment 2 the sequence of events was the same as in Experiment 1 but the instruction request here was to focus on and memorize either eye color (shown here) or hair color. The stimuli here are reproduced in grayscale and are not drawn to scale.

memory phases, they had to maintain the information about two consecutive faces.

In the updating phase, after the first two studied faces, when a third face was displayed (and sometimes a fourth), the participant had to compare it (or them) with the previously studied faces and to substitute it when necessary, as exemplified by **Figure 1A**. This comparison/substitution process represented the updating function in terms of maintenance of information and inhibition of irrelevant information, through its replacement (see also Introduction).

At the end of each trial, according with the initial instruction, participants were asked to recall either gaze direction or facial expression of the last studied face or the next-to-last studied face. The recall request (which face had to be recalled) was displayed in the center of the screen. Participants responded by pressing on the computer keyboard one of two keys for gaze direction ("M" for direct gaze, "Z" for averted gaze), and another two for facial expression ("A" for a joyful face, "L" for a fearful face).

The task was self-paced, that is, participants pressed the spacebar to start each trial and after each phase of the trial (i.e., adaptation, instruction, memory, updating), in order to carry on with the task. This allowed the participants to study the stimuli at their own pace enabling a less biased performance. Classically, in updating literature the pace of the task is established by the experimenter. However, it has been observed that fixing stimulus presentation pace might create both recency and anxiety effects (e.g., Bunting et al., 2006; Palladino and Jarrold, 2008). To avoid this risk, we used a self-paced stimuli presentation. The RT for each of the memory and updating phases was collected as dependent variables. In addition, accuracy at the final recall test was measured.

After 16 practice trials, a total of 144 trials, divided in four experimental blocks, were presented individually to participants. The order of presentation of the blocks was counterbalanced across participants.

The variables of interest were Binding, Facial Dimension, and Phase. Binding was randomized between trials, whereas Facial Dimension was blocked, as participants received half of the blocks with the instruction to focus on gaze direction and the other half with the instruction to focus on emotional expression.

Binding represented the strength of the specific biological combinations of gaze direction and facial expression. High bindings were the combinations of gaze direction-facial expression (i.e., joy-direct gaze; fear-averted gaze) previously found to be perceived and processed strongly bound together. Low bindings were the combinations of gaze direction-facial expression (i.e., joy-averted gaze; fear-direct gaze) found to be perceived and processed weakly bound together. Facial Dimension represented the stimulus dimension (gaze direction or facial expression) which participants were instructed to memorize/update and to recall at the end of the sequence. The Phase variable corresponded to the different process involved in each specific phase of the task: memory or updating.

PROCEDURE AND DESIGN FOR EXPERIMENT 2

The procedure in Experiment 2 was exactly the same as in Experiment 1, except that the Facial Dimension of interest was represented by eye color or hair color, and thus the Bindings were different combinations of eye color-hair color. Specifically, high bindings were combinations which have been reported to occur strongly bound together (i.e., dark eyes-brown hair; blue eyes-blonde hair); whereas low bindings were combinations which have been reported to occur bound together more weakly (i.e., blue eyes-brown hair; dark eyes-blonde hair; see e.g., Sulem et al., 2007). At the recall test phase, participants had to press the same keys used in Experiment 1 except that now they indicated the two dimensions of eye color and hair color. Namely, participants responded by pressing keys on the computer keyboard ("M" for blonde hair, and "Z" for brown hair, and "A" for blue eyes, and "L" for dark eyes).

RESULTS

Only trials in which the recall was correct were analyzed in both Experiment 1 (97.78%) and Experiment 2 (93.36%). As we obtained high accuracy at recall, in line with previous findings (e.g., Artuso and Palladino, 2011), we focused our analysis only on task self-paced RTs, which have been shown to be much more sensitive to the updating process (see Kessler and Meiran, 2008; Artuso and Palladino, 2011). It is worth mentioning that the traditional updating measure is accuracy, which is used in the running memory span task (Morris and Jones, 1990) and similar tasks. However, it has been shown that accuracy (i.e., the number of correctly remembered items) tends to combine all the processes active during the task, collapsing them into a global index of memory efficiency, and to mask their separate contributions. Thus, in order to avoid this problem, and following some recent contributions to the update literature (e.g., Kessler and Meiran, 2008; Artuso and Palladino, 2011) we adopted the self-paced RT as a more direct measurement of the updating process.

Table 1 | Mean reaction times in ms and standard deviation (in brackets) from Experiment 1 subdivided for each condition.

		High binding	Low binding
Memory	Gaze direction	576.58 (12.30)	669.52 (20.39)
	Facial expression	649.27 (3.71)	697.11 (11.89)
Updating	Gaze direction	778.88 (29.25)	837.38 (17.53)
	Facial expression	653.09 (22.18)	667.17 (9.40)

DATA TREATMENT

Response times exceeding individual participant means for each condition by more than three intra-individual standard deviations were considered outliers in both Experiment 1 (4.43%) and Experiment 2 (7.28%) and therefore excluded from the analyses. The RTs for each memory and updating phase were calculated as follows. At the memory phases, as well as the updating phase, the RT was computed starting from the onset of the first face until the participants (having memorized/updated the face) pressed the spacebar to continue the task and see the next face. Then, the mean RTs were computed for each specific phase. The mean RTs of the memory phases were computed averaging the RTs of all the memory phases of each trial. An analogous procedure was used to calculate the mean RTs of the updating phases.

EXPERIMENT 1

Experiment 1 RTs were entered in an ANOVA with Binding (high, low) × Facial Dimension (gaze direction, facial expression) × Phase (memory, updating) as within-subjects factors. The inter-participant means of RTs are shown in **Table 1**.

The main effects were all significant. The main effect of Binding, $F(1, 19) = 206.01$, partial $\eta^2 = 0.98$, $p < 0.001$, showed quicker RTs for high bindings ($M = 664$ ms; SD = 5.89 ms) than for low bindings ($M = 717$ ms; SD = 8.72 ms). The main effect of Facial Dimension, $F(1, 19) = 176.21$, partial $\eta^2 = 0.90$, $p < 0.001$, showed longer RTs for processing gaze direction ($M = 715$ ms, SD = 12.37 ms) than for facial expression ($M = 666$ ms, SD = 8.37 ms).

In addition, the main effect of Phase, $F(1, 19) = 446.02$, partial $\eta^2 = 0.99$, $p < 0.001$, showed that updating phases required longer RTs ($M = 734$ ms, SD = 8.60 ms) than memory phases ($M = 648$ ms, SD = 5.90 ms).

The two-way interaction between Binding and Facial Dimension was also significant, $F(1, 19) = 80.97$, partial $\eta^2 = 0.81$, $p < 0.001$. *Post hoc* planned comparisons, $t(19) = 25.90$, $p < 0.001$, showed a greater advantage for facial expression processing (vs. gaze direction) in low binding conditions, relative to high binding conditions, $t(19) = 5.31$, $p < 0.001$. A possible explanation for this result is that facial expressions may be treated as global configurations, whereas gaze direction is likely to be considered as a single component of a face, thus requiring a more analytical approach to be processed (see also Discussion).

The two-way interaction between Binding and Phase was significant as well, $F(1, 19) = 36.28$, partial $\eta^2 = 0.66$, $p < 0.001$. *Post hoc* planned comparisons showed that updating phases always required longer RTs than memory phases, both in high binding conditions, $t(19) = 26.15$, $p < 0.001$, and in low binding ones,

Table 2 | Mean reaction times in ms and standard deviation (in brackets) from Experiment 2 subdivided for each condition.

		High binding	Low binding
Memory	Hair color	625.26 (49.24)	659.66 (66.28)
	Eye color	628.26 (42.84)	629.32 (64.40)
Updating	Hair color	654.24 (34.21)	745.26 (89.00)
	Eye color	642.45 (42.35)	674.68 (83.13)

$t(19) = 24.16$, $p < 0.001$. Moreover, although RTs in high binding conditions were faster compared to low binding conditions in the memory phase, $t(19) = 19.12$, $p < 0.001$, in the updating phase the advantage for high binding conditions was smaller, but still significant, $t(19) = 13.52$, $p < 0.05$. See **Figure 2A**.

The three-way interaction was not significant, $F < 1$.

EXPERIMENT 2

Experiment 2 RTs were entered in an ANOVA with Binding (high, low) × Facial Dimension (eye color, hair color) × Phase (memory, updating) as within-subjects factors. The inter-participant means of RTs are shown in **Table 2**.

The main effects were all significant. The main effect of Binding, $F(1, 19) = 14.61$, partial $\eta^2 = 0.44$, $p < 0.001$, showed quicker RTs for high bindings ($M = 637$ ms; SD = 28.70 ms) than for low bindings ($M = 677$ ms; SD = 67.08 ms). The main effect of Facial Dimension, $F(1, 19) = 35.58$, partial $\eta^2 = 0.65$, $p < 0.001$, showed longer RTs for processing hair color ($M = 671$ ms, SD = 44.72 ms) than for eye color ($M = 643$ ms, SD = 49.19 ms).

In addition, the main effect of Phase, $F(1, 19) = 21.75$, partial $\eta^2 = 0.53$, $p < 0.001$, showed that updating phases required longer RTs ($M = 679$ ms, SD = 53.67 ms) than memory phases ($M = 635$ ms, SD = 48.57 ms).

The two-way interaction between Binding and Facial Dimension was also significant, $F(1, 19) = 101.11$, partial $\eta^2 = 0.84$, $p < 0.001$. *Post hoc* planned comparisons, $t(19) = 23.70$, $p < 0.001$, showed a greater advantage for eye color processing (vs. hair color) in low binding conditions, relative to high binding conditions. The results can be accounted for by the fact that eyes are components of face which receive high priority in processing (see e.g., Henderson et al., 2005); consequently, they are processed faster and more efficiently than other face components.

The two-way interaction between Binding and Phase was significant as well, $F(1, 19) = 21.68$, partial $\eta^2 = 0.53$, $p < 0.001$. *Post hoc* planned comparisons showed that RTs in high binding conditions were faster than low binding conditions at the memory phase, $t(19) = 18.22$, $p < 0.05$, and this difference increased at the updating phase, $t(19) = 21.43$, $p < 0.001$. Moreover, updating phases always required longer RTs than memory phases, but less so in high binding conditions, $t(19) = 11.23$, $p < 0.05$ than in low binding conditions, $t(19) = 22.35$, $p < 0.001$. See **Figure 2B**.

Again, the three-way interaction did not reach significance, $F < 1$.

GENERAL DISCUSSION

The present study is original in terms of bringing together two distinct areas of research: WM updating and the perception of faces, in particular the processing of biological binding between facial dimensions. It provides an initial answer as to how the bindings between facial dimensions that have an important social and communicative value are updated; a function of WM that is important for guiding our social behavior.

The aim of the study was to investigate how the biological binding between different facial dimensions may impact updating processes in WM. Two new results emerged. First, in contrast to previous findings for non-biological bindings, faster processing times were found for the updating of combinations of facial dimensions highly bound together; second, our data showed that the ease of updating highly bound facial dimensions varied depending on the communicative and social meaning of the binding to be updated.

In terms of the first result, our data indicate an advantage in the updating of high biological binding. Thus, WM updating seemed to benefit when different facial dimensions were highly bound together. This is a new and original result, not evident in the existing updating literature, which has focused on other kinds of bindings, i.e., non-biological bindings, arbitrarily created, such as between letters or digits. In fact, previous findings showed that when stimuli with no social/biological value were highly bound, their binding had a negative impact on WM performance (e.g., Guérard et al., 2009; Artuso and Palladino, 2011). Indeed, when the binding was based on phonological or perceptual similarity, high bindings required longer RTs to be dismantled, updated and re-created. Conversely, in the present study, where biological bindings were considered, the stronger they were combined the faster they were updated. This advantage is likely to be due to the fact that faces are important stimuli for social and interpersonal behavior. Therefore, when living in a social world these stimuli need to be updated quickly in order to be beneficial for our social behavior. These results are important because they suggest that updating processes support face processing in a way that is consistent with keeping track of the communicative value of facial dimension bindings. In this respect, the inclusion in our study of non-biological bindings would not have been informative of the effect of social and communicative salience of the binding on WM updating.

An alternative explanation is also possible. High biological bindings are not updated faster to allow the tuning of WM to an ongoing social environment, rather, their faster updating is a consequence of being well-learned, due to their enhanced perceptual processing (e.g., Adams and Kleck, 2003). In other words, it is thanks to a learning process that they have a more rapid access to WM. Therefore, these highly bound combinations could just work more effortlessly, more fluently, than the processing of weakly bound combinations. If this is the case, then WM updating would benefit indirectly by a faster analysis of the relevant stimulus dimension. However, although plausible and worthy of further research, this explanation is unlikely and should be regarded with some caution. In fact, the results on the updating of well-learned bindings with stimuli having no biological value (e.g., 12 taken as a well-learned memory binding) indicate that the strength of this binding was not enough to produce an advantage in updating (Artuso and Palladino, 2012).

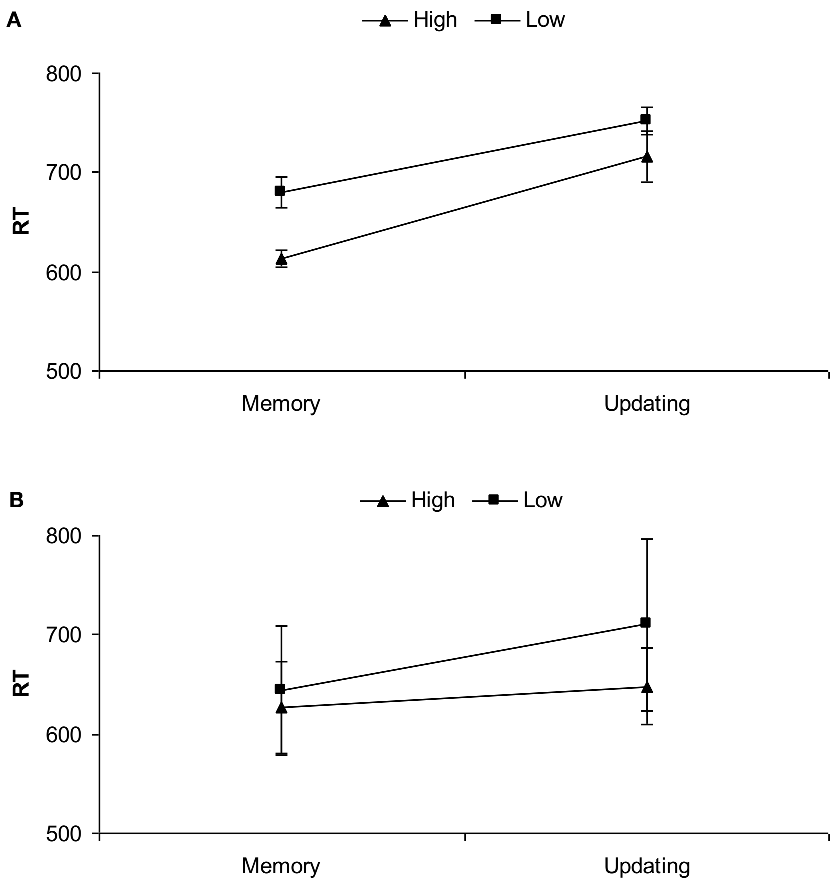

FIGURE 2 | Mean RTs (ms) and updating phases as a function of high and low biological bindings for Experiment 1 (A) and Experiment 2 (B). Bars show standard deviations.

A related issue is also worth mentioning. Different kinds of bindings do exist (e.g., Piekema et al., 2010; see also Ecker et al., 2012). In the present study, we focused our investigation on the updating of the binding between two dimensions of the same kind of stimulus, that is the face. However, in the traditional updating literature, usually the bindings between different stimuli (e.g., letter–letter) are investigated. Thus, the advantage we found in the updating of high binding conditions might also be ascribed to the different type of binding, i.e., of different dimensions of the same stimulus. To clarify this point, further studies will be needed to separate these different bindings and their biological value.

The present results show that the processing of facial expression was faster than that of gaze direction, particularly in low binding conditions (see Experiment 1, Results). A possible explanation, as mentioned earlier, is that facial expressions may be treated as global configurations, whereas gaze direction is likely to be treated as a single component of a face. This is in accordance with neurophysiological results which show that the processing of the internal parts of a face, such as gaze direction, is slower than the processing of the same overall face (see e.g., De Souza et al., 2005). Conversely, in high binding conditions gaze direction and facial expression seem to have been processed in a more global or holistic way given that the difference between gaze direction and facial expression was significantly reduced.

Closely related to the updating processing, we found that the updating phases showed longer latencies than the memory phases. Thus, the updating phase was clearly different from the memory phase (i.e., longer latencies; see both Experiments but especially Experiment 1), as it required more effort to complete. This is in accordance with the traditional conceptualization of updating and is also consistent with previous findings which characterize memory and updating as distinct cognitive processes (e.g., Morris and Jones, 1990; Palladino and Jarrold, 2008; Artuso and Palladino, 2011). Indeed, when the memorized information became no-longer relevant and had to be substituted with new relevant information, this was more difficult than just the memorization of information. Thus, the results suggest that the task we devised was suitable and effective in distinguishing the memorization process from the updating process. In turn, it contributes to memory updating literature, by showing that similar processing effects can be found across different stimuli manipulations. Moreover, consistent with previous findings (e.g., Morris and Jones, 1990; Palladino et al., 2001), we found an effect of the number of updates, consisting of an increase in response latencies with the number of requested updates[1]

In addition, the fact that highly bound combinations had shorter latencies in memory phases, as well as in updating phases confirms that participants based their response on perceptual processing, combining the facial dimensions of the faces (i.e., gaze direction-facial expression and hair color-eye color), rather than verbalizing it. In other words, the fact that we found an advantage for high binding conditions at the memory phase as well as at the updating phase indicates that these conditions required less effort to encode and memorize. Moreover, the advantage found at the updating phase could not be based on a verbalization of facial dimensions, which would otherwise have produced the same effect on both low and high binding conditions.

In terms of our second result, although we found an overall advantage for the updating of high binding conditions, compared to memory, our data also suggests that the two bindings affected updating differently. Interestingly, for the highly bound combinations of gaze direction and facial expression, we found a large difference in response latencies between the memory and updating phases. On the contrary, for the binding between eye color and hair color, memory and updating phases were still different across high binding conditions, but their difference was reduced. In other words, our data shows that the binding between the dimensions which are genetically determined and having less communicative value (i.e., eye color-hair color) required less effort to update, since the difference between the study and updating phases was very small. In contrast, the updating of the binding between the two changeable and more communicative dimensions of gaze direction and facial expression was clearly more difficult, relative to the memory phase. This was a new and unexpected result, as one might have expected gaze direction and facial expression to be rapidly and efficiently updated given that they are facial aspects which can change quickly, and that their different combination have different communicative meanings (see Adams and Kleck, 2003; N'Diyae et al., 2009). Therefore, to respond promptly and adapt our behavior to their change, one would expect our cognitive system to be able to update them very quickly.

[1]Because it was beyond the scope of the present study, analyses involving the Number of Updates (or Load) as a factor were not reported in the main text. However, to relate our results to the existing literature we ran two further analyses including Number of Updates as a factor. For both Experiment 1 and Experiment 2 we entered RTs in an ANOVA with Binding (high, low) × Facial Dimension × (gaze direction, facial expression) × Phase (memory, updating) × Number of Updates (0, 1, 2) as within-subjects factors. For Experiment 1, as well as finding the same results as those reported in the main text (in which the Number of Updates factor was collapsed), we also found a significant main effect of Number of Updates, $F(2, 38) = 15.03$, partial $\eta^2 = 0.44$, $p < 0.001$. Means comparison, $t(19) = 22.31$, $p < 0.001$, showed longer RTs for processing trials requesting two updates, compared to trials with one update, and trials with no update (respectively, 664 vs. 643 vs. 636 ms). Similar results were found for Experiment 2. In particular, the main effect of Number of Updates was also significant, $F(2, 38) = 4.41$, partial $\eta^2 = 0.18$, $p < 0.01$. Means comparison, $t(19) = 15.22$, $p < 0.01$, showed longer RTs for processing trials requesting two updates, compared to trials with one update, and trials with no update (respectively, 632 vs. 618 vs. 604 ms). Overall, the results show that RTs increased with the number of requested updates. This effect is consistent with the updating literature (see e.g., Morris and Jones, 1990; Palladino et al., 2001) and offers further support to the reliability of our findings and the validity of our task.

We believe this result is interesting and we think this difference can be a consequence of the fact that the two high bindings require different updating processes. In particular, we might hypothesize that different cognitive processes come into play. For the binding between gaze direction and facial expression it is plausible that beyond studying the faces, memorizing and maintaining the relevant information, and updating their binding, participants also have to update the meaning of that binding. The meaning of the binding being its appraisal, i.e., the relevance of the stimulus to the observer (e.g., Mumenthaler and Sander, 2012). For example, if while the observer is looking at a happy face gazing straight ahead, the face suddenly becomes scared and moves the eyes toward a specific portion of space, the observer has to detect this change in gaze direction together with the emotion expressed, thus creating a new representation of the seen face, that is to update it. However, a second operation is also necessary: an updating of the appraisal of the seen face. In fact, the observer has to modify not only the combination between the two facial dimensions, but also the value and the meaning of that combination. This is particularly so, if the face which changes gaze direction and facial expression is also a new face as in the present study. So, if for instance the observer moves from a potentially pleasant stimulus to one which indicates a potential danger, she/he has to change the meaning of that face as well, in other words to update its ongoing cognitive appraisal.

In contrast, updating the color of the eye and the hair when highly bound together would require less or different cognitive processes. In fact, they appear easier and require less effort to update, as the updating phase latencies were not much longer than those of the memory phase. This might be because participants just have to study the faces, memorize, and update the relevant information, and update their binding, but no update of their meaning is probably necessary. In fact, these facial dimensions are less communicative and consequently they are not very relevant for the ongoing social and appraisal processes. Therefore, the observer is probably not continuously engaged in updating their meaning and their value for him/herself. This would explain why these combinations can be updated quickly.

Thus, the greater cost observed in the updating of highly bound combinations of gaze direction and facial expression, relative to their memorization (see Experiment 1), might reasonably be interpreted in terms of the amount and type of processes requested: the updating of the binding as well as the updating of the appraisal of that binding. Whereas, for the updating of highly bound combinations of eye and hair color, the updating of their meaning would not be needed, thus explaining the smaller cost of their updating compared to their memorization (see Experiment 2).

In low bound combinations, the differences were the same across the two kind of bindings (i.e., gaze direction-facial emotion and eye color-hair color) indicating that similar cognitive processes were taking place.

Therefore, it seems plausible that a cost in terms of cognitive processing which would be due to processing more social information, such as that found for the updating of highly bound gaze direction and facial expression, may translate eventually into an advantage for social cognition, because through the updating of the appraisal of a biological and highly communicative binding a more adaptive response to the environment can be given. Further investigations will be needed to corroborate our new results and to test this explanation.

Our results refer not only to the role of social stimuli in WM processes but are also informative about social cognition processes. Social cognition "refers to the processes that subserve behavior in response to conspecifics and in particular to those higher cognitive processes subserving the extremely diverse and flexible social behaviors seen in primates" (Adolphs, 1999, p. 469). Thus, to successfully live in a social environment, people must possess invariant representations of the immediate world but also be responsive to the unexpected changes, in particular changes in the behavior of others and in person perception: all aspects relevant for social cognition (see Macrae and Bodenhausen, 2000). This simultaneous stability and flexibility are likely to characterize social functioning as well as WM functioning. However to date, and to the best of our knowledge, only the study by Meyer et al. (2012) has specifically investigated the relationship between social cognition and WM. In a fMRI study, the authors, investigated which areas are recruited in a social WM task, i.e., mentalizing. Their results brought evidence for a specific social WM system which is recruited when we deal with social information. Therefore, they conclude by claiming that the purpose of social WM is to build-up and maintain an internal model of the immediate social environment and social world.

Our study resembles that of Meyer and co-workers in the sense that we also investigate how WM deals with pieces of social information, and in particular how WM is engaged in updating the faces of other people. As with mentalizing (see Meyer et al., 2012), face perception is thought to represent a building block of human social cognition.

Moreover, in line with the idea that the purpose of social WM is to keep track of the various social information which are crucial to navigating our social world and understand social interaction, our study is important because offers some first evidence of how the bindings between facial dimensions are updated. In particular, it suggests that the increase in social information conveyed by the binding with higher social and communicative value demands more WM resources to be updated. A possible reason for this is the necessity to also include in our internal model of the changeable social environment the immediate social or survival relevance of the stimulus to the observer. When perceiving faces this also results in being able to understand other people's intentions and mental states. Moreover, this is in line with the proposal that memory for another individual's face partly depends on an evaluation of the behavioral intention of that individual (Nakashima et al., 2012).

In conclusion, the present study indicates for the first time that updating of biological bindings benefits from the strength of their bindings. In addition, our study suggests that the ease of the ongoing updating processing in WM varies depending on the meaning of the facial dimension bindings that have to be updated, thus revealing a crucial role of WM updating in social cognition and appraisal processes.

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Structural variation within the amygdala and ventromedial prefrontal cortex predicts memory for impressions in older adults

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Research has shown that lesions to regions involved in social and emotional cognition disrupt socioemotional processing and memory. We investigated how structural variation of regions involved in socioemotional memory [ventromedial prefrontal cortex (vmPFC), amygdala], as opposed to a region implicated in explicit memory (hippocampus), affected memory for impressions in young and older adults. Anatomical MRI scans for 15 young and 15 older adults were obtained and reconstructed to gather information about cortical thickness and subcortical volume. Young adults had greater amygdala and hippocampus volumes than old, and thicker left vmPFC than old, although right vmPFC thickness did not differ across the age groups. Participants formed behavior-based impressions and responded to interpersonally meaningful, social but interpersonally irrelevant, or non-social prompts, and completed a memory test. Results showed that greater left amygdala volume predicted enhanced overall memory for impressions in older but not younger adults. Increased right vmPFC thickness in older, but not younger, adults correlated with enhanced memory for impressions formed in the interpersonally meaningful context. Hippocampal volume was not predictive of social memory in young or older adults. These findings demonstrate the importance of structural variation in regions linked to socioemotional processing in the retention of impressions with age, and suggest that the amygdala and vmPFC play integral roles when encoding and retrieving social information.

Keywords: impression formation, aging, memory, amygdala, ventromedial prefrontal cortex

INTRODUCTION

Structural changes to the brain accompany healthy aging (Hedden and Gabrieli, 2004), including cortical thinning, decreased intracranial volume (Salat et al., 2004), and more specific volumetric reductions in subcortical structures (Walhovd et al., 2005). These structural changes manifest in behavioral differences when compared to healthy younger adults. For instance, reductions in hippocampal volumes correspond with age-associated visual and verbal memory impairments (Soininen et al., 1994), age-related decrements in explicit memory performance (Raz et al., 1998), and longitudinal changes on aging-sensitive memory tests (Golomb et al., 1996).

Although aging also affects functional engagement of the hippocampus, including working (Mitchell et al., 2000), and episodic (Daselaar et al., 2003) memory processes, recent research suggests the existence of a functional neural mechanism underlying memory for social information, and that involves the recruitment of medial prefrontal cortex in contrast to the hippocampus (Mitchell et al., 2004; Gilron and Gutchess, 2012). Regions within this "social" memory system (e.g., dorsal and ventral medial prefrontal cortex) are recruited when learning and remembering social material, such as autobiographical memories (Gilboa, 2004), self- versus other-related items (Kelley et al., 2002), and impressions (Mitchell et al., 2004; Gilron and Gutchess, 2012). Like the relationship between hippocampal atrophy and memory for non-social material in healthy aging, social memory may be sensitive to age-related structural changes to more "social" brain regions. Thus, the relative integrity of these regions may be associated with the level of remembered social information in older, but not necessarily younger, adults.

Recent neuroimaging studies have begun to investigate how aging affects the neural underpinnings of social processing. These studies have found age-invariant neural recruitment in several social tasks, including self-referencing (Gutchess et al., 2007), theory of mind (Castelli et al., 2010), reaction to social affiliation and isolation (Beadle et al., 2012), and social evaluation (Cassidy et al., in press). Some age differences in neural recruitment in response to social stimuli have been identified, such as in the elaborative encoding of self-related information (Gutchess et al., 2010), and in mentalizing tasks (Moran et al., 2012). Thus, functional engagement of "social" brain regions may be intact in healthy aging to an extent. For instance, in easy tasks (Castelli et al., 2010) or tasks requiring a consideration of the self (Gutchess et al., 2007; Cassidy et al., in press), function within neural regions underlying social processing may be relatively spared. However, more difficult tasks or tasks that do not garner self-involvement may not similarly engage these regions in older adults (Moran et al., 2012).

Behavioral work evidences relative age-related sparing of social memory processes. In contrast to studies reporting age-related decline on hippocampally dependent memory tasks (Squire, 1992;

Grady et al., 2003; Dennis et al., 2008), other work evidences that older and younger adults similarly remember socioemotional information (Rahhal et al., 2002; May et al., 2005; Cassidy and Gutchess, 2012). In the present study, we focused on impression formation, an interpersonally relevant domain where older adults may be motivated to utilize and remember information. For example, older adults may be more sensitive than young adults to cues that can modify an initial first impression, as well as the diagnosticity of traits (Hess and Auman, 2001; Hess et al., 2005). Younger and older adults may similarly remember impressions (Todorov and Olson, 2008), predominantly when impressions are formed in a context emphasizing interpersonal relationships (Cassidy and Gutchess, 2012). Choosing a domain where older adults may not exhibit poorer memory than younger adults allows us to better examine if structural variation differentially affects memory in older over younger adults.

Considering the impact of structural variation within the neural regions underlying social processing offers a complementary approach to neuroimaging and behavioral studies to examine the preservation of memory for impressions with age. Such an approach could examine if older adults with more structural atrophy and thinning exhibit *poorer* social memory performance relative to older adults with less structural change. Previous research using healthy young adults and lesioned individuals has linked structural integrity of two regions implicated in impression formation and social evaluation, the amygdala (Todorov and Olson, 2008), and ventromedial prefrontal cortex (vmPFC; Milad et al., 2005), to socioemotional memory. Interestingly, vmPFC receives substantial input from the amygdala, and these regions are linked in several socioemotional processes, including emotional memory (Phelps et al., 2004) and reward expectancy and choice (Hampton et al., 2007). This relationship suggests that age-related structural variation within these regions may also extend to memory for impressions.

The amygdala is widely implicated in impression formation (Schiller et al., 2009; Baron et al., 2010) and its integrity is critical when remembering impressions (Todorov and Olson, 2008). Intact amygdala volume is also necessary for retrieving socially relevant information in response to visual stimuli (Adolphs et al., 1998), suggesting that among non-lesioned individuals, structural variation within the amygdala might correspond with the ability to remember impressions when viewing individuals previously paired with trait-inferring behaviors. Although results are mixed as to whether the amygdala undergoes significant age-related atrophy (Soininen et al., 1994; Jack et al., 1997; Good et al., 2001; Allen et al., 2005), potentially smaller amygdala volumes in older compared to younger adults might lead to differential behavioral performance. The relationship between amygdala volume and memory for impressions may be more apparent in older over younger adults, given that the sensitivity to detect behavioral changes may not manifest without substantial structural atrophy (Raz et al., 1998).

In younger adults, thicker vmPFC corresponds with enhanced extinction retention after a fear conditioning task (Milad et al., 2005). In addition, the relationship between vmPFC thickness and emotional learning correlates with extraversion, a personality characteristic that influences the social situations in which an individual will or will not participate (Rauch et al., 2005). vmPFC activity is implicated in numerous social processes, including the learning of social information (Behrens et al., 2008), empathy (Shamay-Tsoory, 2011), the analysis of social content (Schilbach et al., 2006), and social evaluation (Cassidy et al., in press). Although research documents overall age-related cortical thinning (Fjell et al., 2009), vmPFC may not undergo such stark structural changes (Salat et al., 2001). Even though older adults may experience relatively less vmPFC thinning compared to other regions, structural variation within this region might differentially affect performance on tasks engaging that area regardless of age, based on evidence that thickness in young adults relates to emotional memory performance (Milad et al., 2005), and this finding could extend to social memory tasks. More specifically, the integrity of this region may be critical in remembering valuable social information (e.g., aversive stimuli within a fear extinction paradigm) regardless of age. However, although memory for valuable social information may relate to vmPFC thickness in both younger and older adults, this relationship may be particularly prominent in an older population, who place more emphasis on personally salient socioemotional material than young (Fredrickson and Carstensen, 1990; Carstensen and Turk-Charles, 1994; Carstensen et al., 1999).

The current study investigated how structural variation within regions important to socioemotional (amygdala, vmPFC) and explicit (hippocampus) memory affects the retrieval of impressions in healthy aging. We predicted that older adults would have smaller amygdala and hippocampal volumes relative to young, but that there would not be an overall age difference in vmPFC thickness. We expected amygdala volume to be predictive of memory for impressions regardless of the context in which the impressions were formed, given the amygdala's widespread role in impression formation. We anticipated older adults would drive this relationship, given the expectation of the association with memory would be more pronounced for smaller amygdala volumes. We did not expect hippocampal volume to be predictive of memory for impressions, given lesion work showing that the hippocampus is not necessary to learn and retain person information (Todorov and Olson, 2008). If hippocampal lesion patients can successfully encode and retrieve impressions, age-related atrophy should also be unrelated to this ability. Finding a relationship between amygdala, and not hippocampal, integrity, and social memory would provide evidence for the existence of a social memory system potentially separable from hippocampally dependent memory systems. Given that vmPFC is engaged when processing socially meaningful information (e.g., self-related material), we expected that vmPFC thickness would predict memory for impressions in younger and older adults, but primarily in a context having significant social value. Because older adults are particularly sensitive to emotionally meaningful information, we anticipated that structural variation among older adults would drive this relationship.

MATERIALS AND METHODS

PARTICIPANTS

Fifteen older (61–85 years old, six males; $M = 72.80$, $SD = 6.91$) and 15 younger (20–29 years old, eight males; $M = 21.13$, SD = 3.00) adults recruited from Brandeis University and the surrounding community participated. The Brandeis University and Partners Healthcare institutional review boards approved this study, and participants provided written informed consent. Older adults were screened for cognitive orientation with MMSE scores >26 (Folstein et al., 1975; $M = 29.07$, SD = 1.33) to ensure no significant cognitive impairment, and were characterized on cognitive measures to assess comparability to others in the literature. Age groups had similar years of education and vocabulary scores (Shipley, 1986). Young adults had faster processing speed ($M = 83.60$, SD = 14.07) than older adults ($M = 53.87$, SD = 9.06), $t(28) = 6.88$, $p < 0.001$, using a digit-comparison measure (Hedden et al., 2002), and had higher letter-number sequencing scores (Wechsler, 1997; $M = 12.60$, SD = 2.80) than older adults ($M = 10.40$, SD = 2.77), $t(28) = 2.16$, $p = 0.04$.

STIMULI

Ninety-six images of Caucasian faces (evenly distributed across young/old and male/female) with neutral expressions, and rated for attractiveness, distinctiveness, and trustworthiness (Gilron and Gutchess, 2012), were drawn from the PAL database (Minear and Park, 2004). Each face was paired with a unique trait-inferring behavioral sentence, drawn from a dataset (Uleman, unpublished data) previously rated for trait convergence, arousal, and valence extremity by young and older adults (Cassidy and Gutchess, 2012). Forty-eight sentences inferred positive traits and 48 inferred negative traits.

PROCEDURE

Participants were told they would be forming impressions and making judgments of others. Participants practiced the task, receiving feedback on their responses, before completing the full task in the scanner. Description of functional data obtained from this task are reported elsewhere (Cassidy et al., in press). Stimuli were presented via E-Prime software (Psychology Software Tools, Pittsburgh, PA, USA).

Participants encoded 96 trait-inferring face-behavior pairs one at a time for 6000 ms. Participants were instructed to form impressions based on the face-behavior pairs, and then to answer the prompt displayed on top of the display (**Figure 1A**). One-third of the trials directed participants to the social-meaningful evaluation ("Do I want this person to play a role in my life?"), one-third to the social-irrelevant evaluation ("Does this person have a pet?"), and one-third to the non-social evaluation ("Does the sentence contain any three syllable words?"). Participants responded "yes" or "no" to the prompts via button box. Sentences of positive and negative valence, along with the four age-gender groups, were evenly distributed among the three evaluations. Attractiveness, distinctiveness, and trustworthiness ratings of faces did not differ by evaluation condition. Trials were interspersed with periods of delay ranging from 2000 to 20,000 ms (indicated by a fixation point at the center of the screen). These intervals were obtained using the Optseq program[1].

There was an approximately 7 min retention interval where participants did not perform any task. Participants then completed a self-paced retrieval task outside of the scanner (**Figure 1B**). All previously viewed faces were presented in one block, one at a time in a random order. Two trait adjectives were listed below each face. One was the correct response, inferred from the encoding behavior, and the other was a non-inferred lure unrelated to the target trait. Target traits were the most commonly generated impressions from norms (Uleman, unpublished data), and lure traits were experimenter-generated. Participants indicated which trait they remembered as associated with the face. Half of the presented lure traits had matching valence of the inferred trait without being synonyms (e.g., friendly versus generous), and half had unmatched valence of the inferred trait, but were not antonyms (e.g., friendly versus dull). Participants then completed additional cognitive measures.

ANATOMICAL DATA ACQUISITION

Data was collected via a Siemens Trio 1.5 T whole-body scanner (Siemens Medical Systems, Iselin, NJ, USA). High-resolution T1-weighted anatomical images were acquired using a multiplanar rapidly acquired gradient echo (MP-RAGE) sequence. All anatomies were reconstructed using FreeSurfer 5.0[2] running on CentOS 5.

Measurement of subcortical volume in individual participants

To assess amygdala and hippocampal volumes, we performed a quantitative analysis of T1-weighted MRI data using an automated segmentation technique widely used in volumetric studies (McDonald et al., 2008; Bickart et al., 2010). This method uses a manually labeled atlas dataset from 40 individuals to automatically segment and assign anatomical region-of-interest (ROI) labels to 40 different brain structures, including our *a priori* ROIs of the amygdala and hippocampus (**Figure 2A**). Regions are labeled based on probabilistic estimations, and the method is comparable to manual labeling (Fischl et al., 2002). Because subcortical volumes vary with head size, we performed our statistical analyses using amygdala and hippocampal volumes corrected for individual intracranial volume, a technique used in previous volumetric studies (O'Brien et al., 2006; Wright et al., 2006), including research in aging individuals (Walhovd et al., 2010; Jackson et al., 2011).

Measurement of cortical thickness in individual participants

To assess cortical thickness, we used the FreeSurfer surface-based analysis software tools, a method previously described in detail (Dale and Sereno, 1993; Fischl et al., 1999; Fischl and Dale, 2000). To summarize the technique, the anatomical scan for each participant was first used to segment cerebral white matter and to estimate the gray-white interface. Topological defects in this estimate were inspected by an experimenter and manually corrected, as needed, and this estimate was used as a starting point for a surface algorithm designed to obtain precise measurement of the pial surface. The cortical surface in each participant was then visually inspected for inaccuracies in segmentation. Next, thickness measures across the cortex were computed by finding the point on

[1] http://surfer.nmr.mgh.harvard.edu/opt-seq

[2] http://surfer.nmr.mgh.harvard.edu

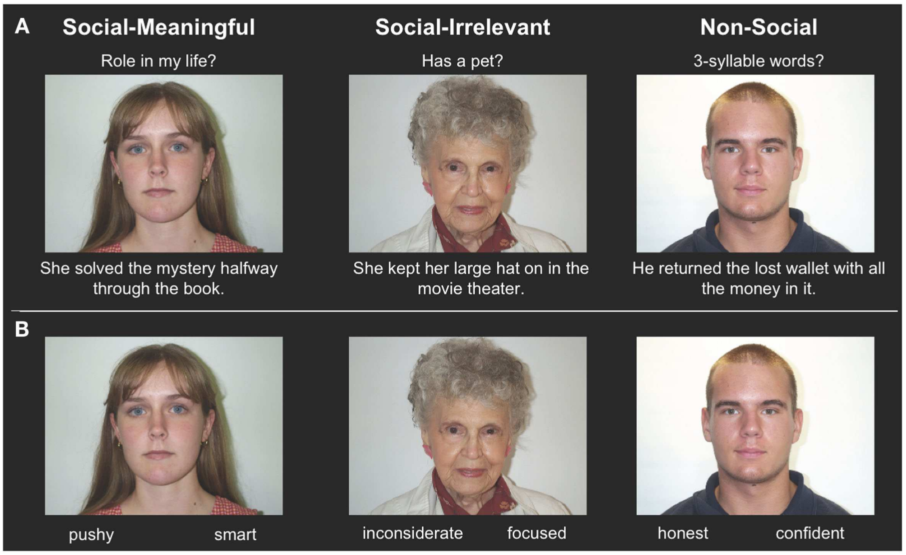

FIGURE 1 | (A) Example encoding stimuli, showing the three evaluation types (social-meaningful, social-irrelevant, and non-social) with example face-behavior pairs. The evaluation types were not explicitly labeled on the screen, and participants answered yes or no to the displayed prompt. **(B)** Example retrieval stimuli, showing examples of target and lure traits.

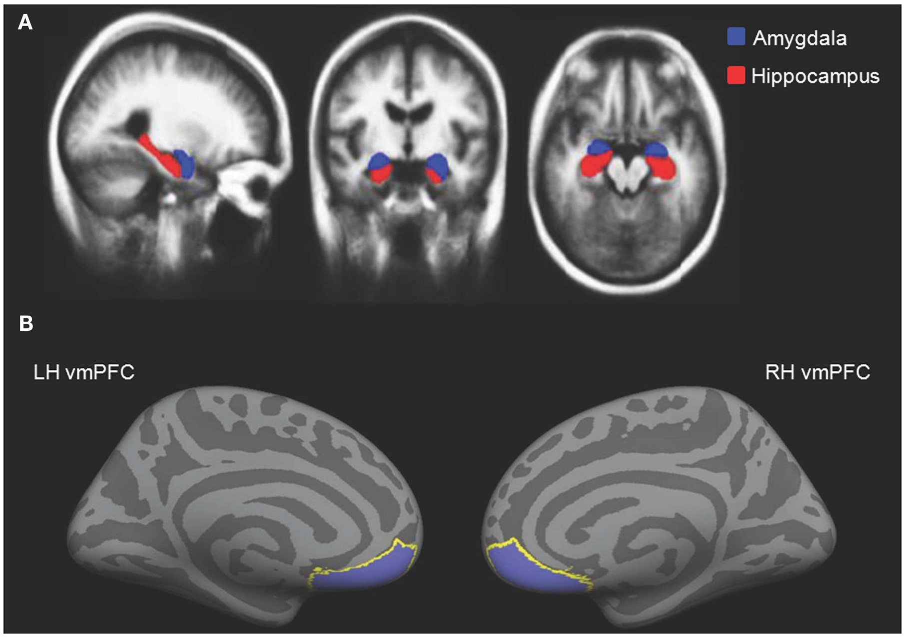

FIGURE 2 | (A) Independently defined anatomical volumetric ROIs of bilateral amygdala and hippocampus and **(B)** independently defined anatomical surface-based ROIs of bilateral vmPFC.

the gray-white interface that was closest to a given point on the estimated pial surface and averaging between these values in each participant (Fischl and Dale, 2000). The accuracy of this technique to obtain cortical thickness has been previously validated by comparisons with manual analysis on postmortem brains (Rosas et al., 2002), as well as direct comparisons with anatomical MRI data (Kuperberg et al., 2003), and has been used in research conducted in aging individuals (Desikan et al., 2009; Fjell et al., 2009). Our *a priori* ROIs for vmPFC were defined using the automatically delineated labels for left and right "medial orbitofrontal cortex" within FreeSurfer (**Figure 2B**; Fischl et al., 2004; Desikan et al., 2006).

Table 1 | Retrieval test accuracy (M, SD) for each age group split by evaluation type.

	Younger adults (*N* = 15)	Older adults (*N* = 15)	*t*-Statistic	*p*-Value
Social-meaningful	65.21% (10.62%)	63.33% (12.69%)	0.44	0.66
Social-irrelevant	66.67% (10.48%)	57.92% (13.15%)	2.02	0.05
Non-social	59.38% (9.30%)	50.42% (7.07%)	2.97	0.01

RESULTS

BEHAVIORAL DATA

We analyzed participants' accuracy (proportion of correct responses in remembering impressions) in the retrieval task using a 2×3 ANOVA with Age Group (young, old) as a between-groups factor and Evaluation (non-social, social-irrelevant, social-meaningful) as a within-group factor. See **Table 1** for a breakdown of performance by age group and evaluation type. There was a main effect of Age Group, $F(1, 28) = 5.58$, $p = 0.03$, $\eta_p^2 = 0.17$. Young adults had increased retrieval accuracy ($M = 63.82\%$, $SD = 7.23\%$) over older adults ($M = 57.22\%$, $SD = 7.90\%$). There was also a main effect of Evaluation, $F(2, 56) = 8.38$, $p = 0.001$, $\eta_p^2 = 0.23$. Contrasts showed that participants had better memory for impressions formed when making the social-meaningful evaluations ($M = 64.27\%$, $SD = 11.53\%$) than the non-social evaluations ($M = 54.90\%$, $SD = 9.40\%$), $F(1, 28) = 14.67$, $p = 0.001$, $\eta_p^2 = 0.34$. Participants also had better memory for impressions formed when making the social-irrelevant evaluations ($M = 62.30\%$, $SD = 12.50\%$) over the non-social evaluations, $F(1, 28) = 8.45$, $p = 0.01$, There was no difference in memory performance for impressions formed when making the social-meaningful versus social-irrelevant evaluations, $F(1, 28) < 1$, ns. There was no Age Group by Evaluation interaction, $F(2, 56) = 1.40$, ns.

BEHAVIORAL CORRELATIONS WITH AMYGDALA AND HIPPOCAMPAL VOLUME AND vmPFC THICKNESS

To assess overall positive relationships between structural variation and social memory, we examined the relationships between left and right hippocampal and amygdala volume (corrected for intracranial volume), as well as left and right vmPFC thickness, with overall retrieval accuracy in the memory test, while controlling for age. We also examined the relationship between structural variations in these regions with retrieval accuracy for impressions formed in each evaluation condition, while controlling for age. To assess whether young or older adults predominantly drove these relationships, we again calculated these relationships separately for each age group. We assessed the significance of the difference between Pearson correlation coefficients for young and older adults using the Fisher r-to-z transformation. Because we predicted positive correlations between volume and thickness with memory, one-tailed Fisher r-to-z transformations were used. All correlations reported for the amygdala and hippocampus were calculated after correcting for intracranial volume.

Amygdala

Older adults had smaller left amygdala volumes (range: 596–1526 mm^3, $M = 1107.67$ mm^3, $SE = 62.46$) than young (range: 1167–1904 mm^3, $M = 1481.67$ mm^3, $SE = 44.63$), $t(28) = 4.87$, $p < 0.001$. Older adults also had smaller right amygdala volumes (range: 826–1655 mm^3, $M = 1238.13$ mm^3, $SE = 60.17$) than young (range: 1227–1841 mm^3, $M = 1532.07$ mm^3, $SE = 55.63$), $t(28) = 3.59$, $p = 0.001$. These differences held when correcting for intracranial volume, $ps < 0.001$. When corrected for intracranial volume, there was a significant positive relationship between left amygdala volume and overall memory for impressions, controlling for age, $r(27) = 0.43$, $p = 0.02$, 95% CI [0.18, 0.64]. To assess whether structural variation within older adults primarily drove this relationship, we calculated this correlation split by age group. Left amygdala volume positively correlated with overall memory for impressions in older, $r(13) = 0.64$, $p = 0.01$, 95% CI [0.41, 0.85] but not younger adults, $r(13) = 0.09$, ns (**Figure 3A**). The difference between these two correlations was marginally significant, $z = 1.64$, $p = 0.05$. There was also a significant positive relationship between left amygdala volume and memory for impressions formed when making non-social evaluations, controlling for age, $r(27) = 0.43$, $p = 0.02$, 95% CI [0.07, 0.70]. However, when split by age group, this correlation was not significant among older or younger adults, $ps > 0.10$. Additionally, there was a positive relationship between left amygdala volume and memory for impressions formed when making the social-irrelevant evaluations in older adults, $r(13) = 0.51$, $p = 0.05$, 95% CI [−0.01, 0.85] whereas this relationship was not apparent among young adults, $r(13) = -0.23$, ns. The difference between these two correlations was significant, $z = 1.95$, $p = 0.03$. Controlling for age, there were no positive correlations found between right amygdala volume and memory for impressions, neither overall or in any of the three evaluation conditions. When split by age group, no positive relationships emerged.

Hippocampus

Older adults had smaller left hippocampus volumes (range: 2382–4072 mm^3, $M = 3109.40$ mm^3, $SE = 112.11$) relative to young (range: 3224–4656 mm^3, $M = 3921.73$ mm^3, $SE = 106.53$), $t(28) = 5.25$, $p < 0.001$. Older adults also had smaller right hippocampus volumes (range: 2532–4011 mm^3, $M = 3200.60$ mm^3, $SE = 111.22$) than young (range: 3250–4365 mm^3, $M = 3859.87$ mm^3, $SE = 94.93$), $t(28) = 4.51$, $p < 0.001$. These differences held when correcting for intracranial volume, $ps < 0.001$. When corrected for intracranial volume and controlling for age, there were no significant correlations between left or right hippocampal volume and overall memory for impressions or memory performance in any of the three evaluation conditions. When split by age group, there were also no significant correlations between increasing left or right hippocampal volume and overall memory or memory in any of the three evaluation conditions in young or older adults.

vmPFC

Older adults had thinner left vmPFC (range: 2.12–2.49 mm, $M = 2.27$ mm, $SE = 0.03$) relative to young (range: 2.16–2.79 mm, $M = 2.41$ mm, $SE = 0.05$), $t(28) = 52.38$, $p = 0.03$. However, older

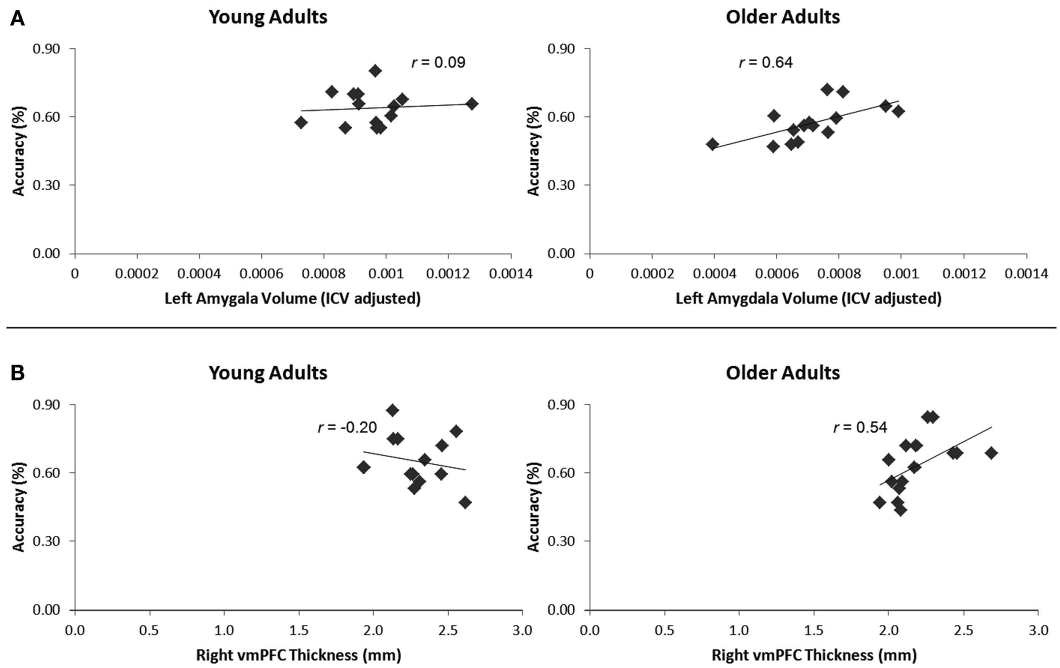

FIGURE 3 | (A) Increasing left amygdala volume, corrected for intracranial volume, corresponded with enhanced overall memory for impressions in older, but not younger adults. **(B)** Increasing right vmPFC thickness corresponded with enhanced memory for impressions formed when making the social-meaningful evaluations in older, but not younger adults.

adults did not have thinner right vmPFC (range: 1.94–2.69 mm, $M = 2.19$ mm, $SE = 0.05$) than young (range: 1.93–2.62 mm, $M = 2.29$ mm, $SE = 0.05$), $t(28) = 1.33$, $p = 0.19$.

When controlling for age, neither right nor left vmPFC thickness corresponded with memory for impressions formed in the interpersonally meaningful condition. However, given our *a priori* hypothesis that impressions formed in a socially meaningful context might be particularly salient for older over younger adults, we calculated correlations split by age group. In older adults, right vmPFC thickness positively correlated with memory for impressions formed when making social-meaningful evaluations, $r(13) = 0.54$, $p = 0.04$, 95% CI [0.30, 0.82], whereas this relationship was not evident among younger adults, $r(13) = -0.20$, ns (**Figure 3B**). The difference between these correlations was significant, $z = -1.96$, $p = 0.02$. When controlling for age, there were no positive correlations between left or right vmPFC thickness and overall memory for impressions or memory for impressions formed when making the social-irrelevant or non-social evaluations. When split by age group, there were also no positive correlations between increasing left or right vmPFC thickness and overall memory or memory for impressions formed when making the social-irrelevant or non-social evaluations.

DISCUSSION

This study investigated the possibility that older adults' ability to remember impressions might be associated with structural variation within brain regions previously implicated in socioemotional memory (vmPFC and amygdala) but not a region implicated in explicit memory (hippocampus), whereas young adults' memory performance might be less affected by structural variability. Although previous research has implicated hippocampal atrophy as being associated with behavioral performance on memory tasks (Golomb et al., 1993, 1996; Soininen et al., 1994; Raz et al., 1998), other work suggests the existence of a social memory system potentially separable from the hippocampally dependent explicit memory system (Mitchell et al., 2004). Although the neural underpinnings of impression formation may be relatively spared with age (Cassidy et al., in press), the structural integrity of regions implicated in these processes may affect the extent of successful retrieval of impressions. We show that variation in amygdala volume and vmPFC thickness corresponds with the extent of successfully retrieved impressions in older, but not younger adults, such that less structural atrophy in amygdala volume and thicker vmPFC are related to enhanced memory for impressions. In contrast, relative hippocampal volume did not correspond with memory for impressions, suggesting that social memory may be less affected by the structural integrity of the hippocampus, although additional research must replicate and expand upon this null finding. Prior research has demonstrated that lesions to the amygdala (Adolphs et al., 1998, 2005; Anderson and Phelps, 2001; Todorov and Olson, 2008) and vmPFC (Shamay-Tsoory et al., 2003, 2007; Koenigs and Tranel, 2007; Young et al., 2010) have many behavioral consequences for social cognition. Importantly, this study extends this literature to the structural changes accompanying healthy aging.

In older adults, left amygdala volume positively correlated with overall memory for impressions, whereas this relationship was not observed in the younger cohort. Previous research has shown that individuals with medial temporal lobe lesions extending into the amygdala and temporal pole have difficulty retrieving impressions of others (Todorov and Olson, 2008). Although the study also reported equivalent memory for impressions of others across younger and older adults, there was, however, a notably wide range in performance among the age groups, allowing for the possibility that structural variation in regions such as the amygdala could be associated with the level of memory performance. The current work suggests that variation in performance in older adults may depend in part on the extent of left amygdala atrophy. While some older adults may indeed remember impressions to the same extent as young in some circumstances (Cassidy and Gutchess, 2012), the integrity of the amygdala may correspond with the extent of age-related preservation. It is also noteworthy that, among all participants, left amygdala volume still positively correlated with retrieval of impressions when controlling for age. This suggests that regardless of age, left amygdala volume is critical in determining how well individuals remember impressions.

Moreover, it may be that amygdala volume may begin to affect memory for impressions once atrophy has passed a particular threshold, similar to the idea that the link between structural integrity and behavioral performance may not become apparent until brain regions lose a substantial portion of their volumes. For instance, Raz et al. (1998) found no relationship between limbic region structure and explicit memory until limiting their analysis to a subsample of individuals over 60 years old, where more age-related structural atrophy would be expected compared to a younger cohort. Differences in the extent of medial temporal lobe atrophy have also been shown to dissociate memory performance among individuals with probable Alzheimer's disease from age-matched controls (Scheltens et al., 1992). This may explain why in the current study, the relationship between amygdala volume and memory for impressions persisted among older, but not younger, adults.

Notably, this relationship was observed in the left, but not the right, amygdala. Left amygdala engagement has been implicated in the encoding of verbal affective information and detailed feature extraction, whereas right amygdala activity is involved in the retrieval of emotional visual information (Markowitsch, 1998). Because our retrieval task required participants to reflect on previously learned socioemotional verbal information, given the role of the left amygdala in encoding affective verbal information, it could indicate that left amygdala integrity would be particularly sensitive to the retrieval of impressions formed off the basis of verbal material. However, some work has evidenced that both left and right amygdala volumes are correlated with visual, but not verbal memory in aging (Soininen et al., 1994). The contribution of the amygdala bilaterally may be more pronounced for non-social tasks, whereas the present task, with its heavy emphasis on verbal information about behavior, may be more sensitive to the relative integrity of the left amygdala.

We also found that increasing right vmPFC thickness corresponded with enhanced memory for impressions formed in the socially meaningful context in older, but not younger adults. This was contrary to our hypothesis that both age groups' memory for impressions would be related to vmPFC thickness, given that previous fear extinction work in young adults showed that vmPFC thickness predicts emotional memory retention (Milad et al., 2005). Fear extinction work relies on a physiological reaction as evidence of prior learning, and not an explicit memory task as in the current study; thus the nature of retrieved information differs between the tasks. While some face stimuli had negative impressions associated with them, being asked to retrieve information about these individuals would not bring back memory of a painful experience, as in fear extinction work. Given that older adults have an increased focus on socioemotionally meaningful material relative to young adults, who have an overall information acquisition focus (Carstensen and Turk-Charles, 1994; Carstensen et al., 1999; Carstensen and Mikels, 2005), it might seem unsurprising that the relationship between vmPFC integrity and memory for impressions formed in a socially meaningful context was stronger for older compared to younger adults.

Interestingly, the relationship between right vmPFC integrity and impression memory occurred despite the fact that there was no age-related difference in right vmPFC thicknesses overall, and when combining the cohorts and controlling for age, the relationship between thickness and memory did not hold. While amygdala volume moderated overall memory for impressions in older adults, the extent of vmPFC thickness may play a more nuanced role in the ability to remember information older adults consider particularly valuable (e.g., impressions formed in a socially meaningful context). Lesion research has suggested that processes associated with vmPFC optimize decision-making processes by encoding a future goal's abstract value (Moretti et al., 2009). In the current work, older adults' right vmPFC thickness corresponded with memory for more impressions that had been formed when making a socially meaningful evaluation, consistent with the idea that older adults prioritize incoming socioemotional material (Carstensen et al., 1999). The vmPFC's role in memory was not evident among younger adults, perhaps because their overall focus on acquiring knowledge means that they value novel information regardless of the particular evaluation they make.

One limitation of the current work is the relatively small sample size for young and older adults (Ns = 15). Smaller sample sizes may not be substantial enough to reflect the large variations in brain structure seen in older adult cohorts (Raz and Rodrigue, 2006), particularly when capturing age differences in a cross-sectional, rather than longitudinal, design (Raz et al., 2005). Thus, while the present data may be considered preliminary evidence that structural variation within the amygdala and vmPFC, but not the hippocampus, leads to age differences in remembering impressions, null effects may be a result of small sample size, or a limitation of cross-sectional design. A more sensitive way for future research to estimate these differences would be to assess whether intraindividual structural change relates to age differences in memory, as previous research has shown that within-individual structural change is sensitive to cognition to a greater extent than cross-sectional estimates (Rodrigue and Raz, 2004).

Recently, cognitive neuroscience researchers have illustrated that low statistical power (Yarkoni, 2009) can lead to misleading correlations between brain activity and human behavior. It is important to note that the regions of interest in the current work were anatomically defined, and that anatomical information was correlated with human behavior using a similar methodology as prior work sensitive to these concerns (Bickart et al., 2010).

Correlating our behavioral data with anatomically defined regions of interest rather than functionally defined regions from previous analyses allows for the memory and neural measures to be considered independent. Further, despite our limited sample size, our hypotheses were *a priori* and derived from previous work demonstrating how amygdala and vmPFC integrity affect different aspects of social cognition. Nevertheless, it is important to consider the current study as preliminary evidence that amygdala and vmPFC integrity influence memory for impressions in older adults, and further work is needed.

Although this work may serve as a basis for future research, it is important for future studies to consider using samples with a full range of ages across the lifespan, instead of two distinct age groups. This may allow for greater variability in both volumetric and thickness measurements, as well as greater variation in memory performance. Future work might also consider different types of social memory. While the current work tested explicit memory for impressions, the integrity of social cognition regions may be particularly important in a more difficult memory task (e.g., free recall). It would also be of use for future studies to contrast social against non-social memory tasks, which would be expected to rely on the hippocampus. Showing dissociation between how the integrity of regions involved in social versus non-social cognition affect social and non-social memories, respectively, may further substantiate claims that social and non-social explicit memory rely on distinct neural substrates.

In summary, these findings are initial evidence that structural variation in amygdala volume and vmPFC thickness influence the extent to which older adults are able to successfully retrieve impressions. Moreover, the data provide preliminary support for the existence of a social memory system potentially separable from hippocampally dependent systems, as hippocampal integrity was not shown to predict memory for impressions in young or older adults despite significant structural atrophy in older adults compared to young. Although some research has shown that regions implicated in impression formation and social evaluation are functionally relatively spared with age (Cassidy et al., in press), the current study complements this work by showing that the integrity of regions involved in social processing and memory matter as well. Future work can clarify this relationship by testing how structural variation influences the accuracy of different types of social decisions (e.g., appropriate approach behavior in the face of a previously seen unsafe individual). Such work is critical, as our memories of others profoundly impact our social judgments and behaviors throughout the lifespan.

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Individualized theory of mind (iToM): when memory modulates empathy

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Functional neuroimaging studies have noted that brain regions supporting theory of mind (ToM) overlap remarkably with those underlying episodic memory, suggesting a link between the two processes. The present study shows that memory for others' past experiences modulates significantly our appraisal of, and reaction to, what is happening to them currently. Participants read the life story of two characters; one had experienced a long series of love-related failures, the other a long series of work-related failures. In a later faux pas recognition task, participants reported more empathy for the character unlucky in love in love-related faux pas scenarios, and for the character unlucky at work in work-related faux pas scenarios. The memory-based modulation of empathy correlated with the number of details remembered from the characters' life story. These results suggest that individuals use memory for other people's past experiences to simulate how they feel in similar situations they are currently facing. The integration of ToM and memory processes allows adjusting mental state inferences to fit unique social targets, constructing an individualized ToM.

Keywords: theory of mind, empathy, episodic memory, autobiographical memory, episodic simulation

INTRODUCTION

Humans have the ability and the need to interpret the mental states of other people, including their thoughts, feelings, and intentions. This ability, called "theory of mind" (ToM) is crucial for empathy, which includes representing other people's thoughts (referred to as "cognitive empathy") and experiencing affective states aligned to theirs (referred to as "affective empathy"; Amodio and Frith, 2006; de Vignemont and Singer, 2006; Zaki and Ochsner, 2012). Understanding the neural bases and the cognitive mechanisms of ToM is an important goal of research in cognitive neuroscience.

Recent reviews of functional neuroimaging (fMRI) studies have noted that brain regions supporting ToM and cognitive empathy overlap remarkably with those underlying autobiographical memory. The regions of overlap include the medial prefrontal and posterior cingulate cortex, frontal pole, inferior frontal gyrus, regions within the medial temporal lobe, superior temporal sulcus and middle temporal gyrus, and the angular gyrus (Buckner and Carroll, 2007; Rabin et al., 2010; Spreng and Grady, 2010; Zaki and Ochsner, 2012). These regions take part in the "default network," a set of interconnected brain regions whose activity typically is suppressed by stimulus-driven attention, and enhanced by internally focused activities (Buckner et al., 2008; Spreng and Grady, 2010).

What might be the functional meaning of this overlap? Some authors have suggested that, in order to infer others' mental states, individuals draw on past experience (Corcoran and Frith, 2003; Gallagher and Frith, 2003; Buckner and Carroll, 2007). Thus, individuals may understand how others feel because they recall having experienced similar episodes personally, and how they felt at that time. Batson et al. (1996), for example, found that participants who had experienced the same electrical shock as their confederates displayed a greater empathic response toward them relative to participants who never had experienced the shock. Likewise, participants who went through a similar experience as the protagonist in a story showed a greater empathic response toward the protagonist relative to participants who had never experienced such an event (Batson et al., 1996). Dimaggio et al. (2008) have shown that the more individuals are able to retrieve and reflect on episodes from their own life narratives, the more likely they are to decipher others' thoughts and emotions. According to the "episodic simulation hypothesis" (Buckner et al., 2008; Schacter et al., 2008), indeed, one fundamental function of episodic memory, beyond recalling the past, is enabling the formulation of flexible models of the future to inform choice. In the social domain, this may entail retrieving fragments of past events rich in experiential detail, recombining them to construct new scenarios suited to represent the situation currently faced, and pre-experiencing how we, or others, might feel in such situations. The hypothesis of a close relation between episodic memory and ToM processes is supported by evidence that episodic memory and ToM emerge close in time during development (Perner and Ruffman, 1995). Moreover, patient populations with ToM impairments, such as high-functioning autism (Adler et al., 2010) and schizophrenia (Corcoran and Frith, 2003), as well as patients with damage to the ventromedial prefrontal cortex (Stone et al., 1998; Stuss et al., 2001; Shamay-Tsoory et al., 2005, 2009; Ciaramelli et al., 2012) also show a (possibly parallel) impairment in autobiographical recollection (see Gilboa and Moscovitch, 2002; Dimaggio et al., 2012; for reviews), as well as functional abnormalities in the brain default network (e.g., Kennedy et al., 2006; Harrison et al., 2007).

On the other hand, a neuropsychological study of ToM in two amnesic individuals provided contradictory evidence. Rosenbaum et al. (2007) showed that, despite severely impaired autobiographical memory, amnesic patients were normally able to perform standard laboratory ToM tests that required them, for example, to identify whether a character unintentionally said something hurtful to another character, committing what is called a "faux pas" (Faux Pas Test; Stone et al., 1998). The finding that ToM may be intact in amnesic patients with impaired autobiographical memory poses constraints on the purported relation between episodic memory and ToM, indicating that, at least under some circumstances, ToM is independent of episodic memory. As Rosenbaum et al. (2007) speculate, indeed, detection of a faux pas may be achieved through the retrieval of semantic knowledge of how a person might stereotypically feel in a given situation, and of social etiquette (see also Spreng and Mar, 2012). For example, we know that people do not like being told that they look older than they are and we avoid making comments like that. To do so, we do not need to resort to episodic retrieval or simulation. The question remains, therefore, as to whether and why ToM would need the support of episodic simulation processes.

As much as semantic memory is about scripts and general knowledge about the world, it is not suited to capture the characteristics of unique individuals and unique situations. Exclusive use of semantic representations may be sufficient to infer what the average person is likely to experience in a given situation, which is what is required by most standardized ToM tests that employ strangers as the social targets (e.g., Stone et al., 1998; Baron-Cohen et al., 2001; Rabin et al., 2010; Spreng and Grady, 2010; St. Jacques et al., 2011). However, we typically do not reason about average strangers, but about distinct individuals, some of whom we know well, and with whom we interact. In this case, semantic representations, which only allow for stereotyped interpretations of others' behavior, are likely to be insufficient to make adaptive mental state inferences. In this case, episodic memory for shared experience may be necessary to tailor ToM processes on the social target we are interpreting, to construct what we call an "individualized" ToM (iToM). Suppose, for example, you have a friend that for all of his life has been said to look young for his age, and this was a problem in trying to get positions of responsibility. In this situation, one would abandon (semantic) social etiquette, and create instead a new, *ad hoc* rule of avoiding commenting on his youthful appearance.

THE PRESENT STUDY

Our hypothesis is that episodic memory is necessary to retrieve previously acquired information in order to derive tailored interpretations of others' behavior, allowing one to adjust ToM to fit unique social targets (iToM). To test this hypothesis, in the present study we had participants read about the lives of two individuals, one extremely unlucky in love, whose life was punctuated with episodes involving failures in intimate and romantic relationships, and the other extremely unlucky in professional life, whose life was punctuated with failures at school and at work. The two life narratives were rich in episodic and experiential detail. Participants' immediate free recall of the narratives provided us with a measure of recollection. Next, participants considered social scenarios that could or could not contain a faux pas, that is, a situation in which a character unintentionally hurt a second character (the victim), and participants had to detect the faux pas and report how much empathy they felt for the victim. We assessed both cognitive empathy and affective empathy. Critically, in some scenarios the faux pas concerned the victim's intimate/romantic relationships (Love scenarios), whereas in other scenarios it was about the victim's professional relationships (Work scenarios). For comparison purposes, generic violations of social norms not specifically involving intimate/romantic or professional relationships were also used. The type of social violation and the identity of the victim were experimentally crossed, such that the victim in the scenarios could be the characters participants had read about – one unlucky at work, one unlucky in love – as well as another character about whom participants knew nothing.

Our main prediction was that empathy toward the victim of a faux pas should be modulated by memory for the victim's life story. Thus, we expected more empathy for the victim unlucky in love in Love scenarios, and for the victim unlucky at work in Work scenarios. If this memory-driven modulation of empathy is based on the recollection of the victim's story, then a correlation should be expected between the entity of the modulation and the amount of detail recalled from victim's life story. We also investigated whether memory for the victim's life story would predict a better ability to detect social violations, i.e., ToM accuracy. To the extent that episodic memory and ToM recruit overlapping neural networks (Buckner and Carroll, 2007), one would expect a correlation between recall accuracy and faux pas recognition accuracy. On the other hand, it has been reported that trait empathy may be related to ToM and social cognitive functioning (Zaki and Ochsner, 2012). For example, individual differences in self-report measures of empathy track with activity in brain regions associated with mentalizing and ToM (Wagner et al., 2011). Moreover, patients with lesions in the ventromedial prefrontal cortex exhibit both low self-reported cognitive empathy (Shamay-Tsoory et al., 2009) and impaired understanding of other people's thoughts and intentions (Stone et al., 1998; Shamay-Tsoory et al., 2005; Ciaramelli et al., 2012). On this view, one may expect that participants with high levels of trait empathy, especially cognitive empathy, would be better able to adopt the perspective of the victims in the scenarios, and therefore adjust their empathic response depending on the identity of the victim.

MATERIALS AND METHODS

PARTICIPANTS

Thirty-one individuals were recruited for the study. Participants were tested at the Department of Psychology of the University of Toronto, Canada, and at the Department of Psychology of Northwestern University, USA. Two subjects were excluded from the study because part of the data was lost as a result of technical problems. The experimental group, therefore, was composed of 29 participants (11 males), with mean age of 22.38 years (range 18–37) and a mean education of 15.03 years (range 13–19). For four of the participants, cognitive empathy scores were not registered due to a malfunctioning of the computer program. Therefore, all the analyses involving cognitive empathy were run on 25 of the 29 participants. Participants were not taking psychoactive drugs, and were free from current or past psychiatric or neurological illness as determined by history. Participants gave written informed consent for the study, which was approved by the ethics committees of the University of Toronto and of Northwestern University. They received course credit or $10.

MATERIALS

The materials included two "life-stories" narrating excerpts from the lives of two fictitious characters, a faux pas recognition task, and the Interpersonal Reactivity Index Questionnaire (IRI; Davis, 1980).

Life-stories recall task

We created two stories narrating the lives of two fictitious characters, in the form of a series of episodes narrated in first person (see Life-stories in Appendix). The life story of one character concerned a series of events mainly involving failures in intimate and romantic relationships. For male participants in the experiment, this character, unlucky in love, was called Mike, whereas for female participants the character was called Susan. Life-stories were slightly adapted depending on the gender of the protagonist (see Life-stories in Appendix). The life story of the other character, on the other hand, concerned a series of events mainly involving failures in professional life. This character, unlucky at work, was called Adam and Jean for male and female participants, respectively. Thus, while Mike/Susan's life was punctuated by unsuccessful love-related events (e.g., *I just asked her for her name and she answered:* "*I am sorry, I am very busy and cannot waste my time!*"), Adam/Jean's life mainly involved work-related failures (e.g., *I have been hired recently, but I already had a hard time with my boss. He said that I had mistakenly filed some invoices, and that was a disaster*). Life-stories were rich in spatial, perceptual, and emotional details (e.g., [. . .] *the flat is on Queen West, on the second floor of a Victorian house painted in red with a blue ceiling It's just that sometimes I can feel like such a nothing*). Life-stories were subdivided *a priori* in conceptual units, each of which conveyed a bit of information, such as a unique occurrence, fact, statement, thought, etc. (see also Levine et al., 2002 for a similar segmentation procedure). In the first version of the life-stories, which was administered to participants tested at University of Toronto ($N = 14$), the love-related story contained 199 conceptual units, and the work-related story contained 233 conceptual units. Participants subsequently tested at Northwestern University ($N = 15$) received a slightly shortened version of the love-related story and the work-related story, which both contained 171 conceptual units.

Faux pas recognition task

Thirty-seven social scenarios were selected and adapted from the "Faux Pas Recognition Test" (Baron-Cohen et al., 1999) or the "Social Stories Questionnaire" (Lawson et al., 2004), or created *ad hoc* (see Faux Pas Scenarios in Appendix for the list of scenarios used). Twenty-seven scenarios contained a violation of accepted social norms (a faux pas): an individual said something awkward that may hurt someone (the victim). The remaining 10 scenarios involved neutral social interactions that did not contain any faux pas (Neutral scenarios). In eight scenarios, the faux pas hit the victim on his/her intimate/romantic relationships (Love scenarios; e.g., [. . .] *Susan wondered whether her boyfriend also remembered their anniversary. Then he came out of the shower. "What were you saying honey? I couldn't hear from the shower," asked the boy. Susan said: "I thought it would be nice to go out for dinner since today. . ." But he interrupted her: "Oh sorry honey, not today: I promised some colleagues I would join them for a drink! What about next Saturday?*"). In nine scenarios, the faux pas was about the victim's professional life (Work scenarios; e.g., *Susan went to say bye to the director of her office, because she was planning to leave for her holidays. [. . .].* "*Don't worry,*" *answered the director,* "*I don't think your absence will cause huge problems. Have fun!*"). Ten scenarios involved generic social violations that did not pertain specifically to the victim's intimate/romantic or professional life (Generic scenarios; e.g., *Susan had just met an Italian colleague, Paola. [. . .] Susan wanted to invite Paola for dinner to get to know her better.* "*Hey Paola, why don't you come over for dinner some time, we just bought a pasta machine and you could help us figure how to use it!*" *Paola answered:* "*Oh why not. . . but I guess you should be able to get it to work. Wasn't there an instruction manual?*").

All participants considered 20 scenarios: five Love scenarios, five Work scenarios, five Social scenarios, and five Neutral scenarios. Participants received slightly different sets of scenarios. This was done as part of a pilot research project testing the generalization of our effects to different types of materials, which was later discontinued. In all our analyses, we assessed (and controlled for) the effect of the different set of scenarios used. Twenty participants received Set A (Love scenarios #: 1, 2, 3, 4, 5; Work scenarios #: 1, 2, 3, 4, 5; Generic scenarios #: 1, 2, 3, 4, 5; Neutral scenarios #: 1, 2, 3, 4, 5; see Faux pas scenarios in Appendix), 4 participants received Set B (Love scenarios #: 1, 4, 6, 7, 8; Work scenarios #: 4, 6, 7, 8, 9; Generic scenarios #: 6, 7, 8, 9, 10; Neutral scenarios #: 3, 4, 6, 7, 8), and five participants received Set C (Love scenarios #: 1, 4, 6, 7, 8; Work scenarios #: 4, 6, 7, 8, 9; Generic scenarios #: 6, 7, 8, 9, 10; Neutral scenarios #: 4, 6, 8, 9, 10). Each scenario was presented three times. One time the victim of the faux pas was Mike/Susan (the character unlucky in love), one time it was Adam/Jean (the character unlucky at work), and one time it was Jason/Patricia, a character participants did not know anything about. The order of the scenarios was randomized for each participant.

The participants' task was to consider each scenario, and judge whether it did or did not contain a faux pas by pressing one of two buttons. For affirmative responses, participants additionally answered two questions regarding the amount of cognitive empathy (i.e., "How bad do you think [victim] felt from one (not bad) to seven (very bad)?") and affective empathy (i.e., "How bad do you feel for [victim] from one (not bad) to seven (very bad)?") they felt for the victim.

Interpersonal reactivity index

The IRI is a self-report scale assessing four main aspects of empathy. The "perspective taking" (PT) scale assesses the ability to adopt spontaneously the perspective of other people; the "fantasy" (F) scale assesses the tendency to identify with characters in movies, novels, and other fictional situations; the "empathic concern" (EC) scale assesses the tendency to experience feelings of warmth, compassion, and concern for others undergoing negative experiences; the "personal distress" (PD) scale assesses feelings of anxiety and distress for people going through sufferings and afflictions (Davis, 1980).

PROCEDURE

Each participant was scheduled for an individual experimental session. First, participants were asked to read the two life-stories and were informed that, after reading each story, they would have to recall it in as much detail as they could. The order of presentation of the two life-stories was counterbalanced across participants. There was no time limit to read and recall the life-stories, which took about 10 min in all cases. Participants' reports were recorded. All data were collected and scored by author FB. Scoring involved counting the number of conceptual units correctly recalled, a procedure similar to the one used for the Logical Memory subtest of the Wechsler Memory Scale (Wechsler, 1987). At the time of scoring, FB was blind to the results participants had attained in the faux pas recognition task. An additional rater, blind to the experimental hypotheses, rated 50% of the recall reports. Inter-rater agreement was high ($r = 0.96$).

Participants then underwent the faux pas recognition task. They were told that the task consisted in reading social scenarios, and deciding, for each scenario, whether it contained a faux pas, that is, a situation in which someone said something inconvenient or awkward that may hurt another person, and how they felt for the victim. Participants were encouraged to "put themselves in the victim's shoes" while considering the scenarios. They were also informed that the scenarios may involve the characters they had read about previously. After completing the faux pas recognition task, participants completed the IRI questionnaire.

RESULTS

FAUX PAS RECOGNITION ACCURACY

Table 1 reports participants' accuracy in detecting faux pas, by type of scenario and character. An analysis of variance (ANOVA) on accuracy scores with Scenario (Love scenarios, Work scenarios, Generic scenarios, and Neutral scenarios) and Character (unlucky in love, unlucky at work, unknown) as within-subject factors, and Set (A, B, C) as between-subject factor, revealed a significant effect of Scenario [$F(3,78) = 3.24$; $p < 0.05$, $\eta_p^2 = 0.11$]. *Post hoc* Duncan comparisons showed that subjects attained a lower recognition accuracy in detecting work-related faux pas compared to love-related faux pas, generic faux pas, or the absence of faux pas (Neutral scenarios; $p < 0.05$ in all cases). The effect of Set was significant [$F(2,26) = 4.32$; $p < 0.05$, $\eta_p^2 = 0.24$], such that a lower recognition accuracy was associated to Set A compared to Set C scenarios (0.79 vs. 0.94; $p < 0.05$). The factor Set, however, did not interact in a significant way with any of the other variables ($p > 0.47$, $\eta_p^2 < 0.06$) in all cases. The Scenario × Character interaction was not significant ($p = 0.79$, $\eta_p^2 = 0.01$), indicating that the identity of the victim did not influence participants' ability to detect faux pas in social interactions (or the lack thereof).

Table 1 | Mean faux pas recognition accuracy by type of scenario and character.

	Love scenarios	Work scenarios	Generic scenarios	Neutral scenarios
Unlucky in love	0.90 (0.03)	0.70 (0.04)	0.81 (0.04)	0.90 (0.02)
Unlucky at work	0.91 (0.02)	0.75 (0.04)	0.80 (0.04)	0.91 (0.03)
Unknown	0.88 (0.03)	0.69 (0.04)	0.80 (0.04)	0.90 (0.03)

Values in parentheses represent the standard error of the mean.

COGNITIVE AND AFFECTIVE EMPATHY

We next investigated whether individuals' empathy toward the victim of a faux pas depended on the identity (and story) of the victim. We first analyzed affective empathy scores. An ANOVA on affective empathy scores with Scenario (Love, Work, Generic), Character, and Set as factors revealed a significant effect of Scenario [$F(2,52) = 15.71$; $p < 0.0001$, $\eta_p^2 = 0.37$], and a significant effect of Character [$F(2,52) = 5.41$; $p < 0.01$, $\eta_p^2 = 0.17$], which were qualified by a significant Scenario × Character interaction [$F(4,104) = 6.40$; $p < 0.0001$, $\eta_p^2 = 0.19$]. *Post hoc* Duncan comparisons showed that affective empathy scores in Work scenarios were higher for the character unlucky at work than for the character unlucky in love ($p < 0.001$) or the unknown character ($p < 0.0005$), with no difference between the character unlucky at work and the unknown character ($p = 0.10$). Conversely, affective empathy scores in Love scenarios were higher for the character unlucky in love than for the character unlucky at work ($p < 0.05$), and, marginally, for the unknown character ($p = 0.07$), with no difference between the character unlucky at work and the unknown character ($p = 0.41$). In contrast, affective empathy scores were not modulated by the character's identity in Generic scenarios ($p > 0.09$ in all cases; see **Figure 1**). The factor Set was not significant, and did not interact in a significant way with any of the other variables ($p > 0.61$, $\eta_p^2 < 0.05$ in all cases).

Conceptually similar results were obtained on cognitive empathy scores. The ANOVA on cognitive empathy scores evinced a significant effect of Scenario [$F(2,44) = 12.14$; $p < 0.0001$, $\eta_p^2 = 0.35$], and a marginal effect of Character [$F(2,44) = 3.02$; $p = 0.058$, $\eta_p^2 = 0.12$]. The Scenario × Character interaction just failed to reach conventional levels of statistical significance [$F(4,88) = 2.45$; $p = 0.051$, $\eta_p^2 = 0.10$], likely due to the fact that this analysis was run on 25 subjects only. Because the effect size for the Scenario × Character interaction is in the medium range ($\eta_p^2 = 0.10$), and for completeness, we ran *post hoc* Duncan comparisons. Cognitive empathy scores in Work scenarios were higher for the character unlucky at work than for the character unlucky in love ($p < 0.05$) or the unknown character ($p < 0.01$), with no difference between the latter two ($p = 0.29$). Conversely, cognitive empathy scores in Love scenarios were higher for the character unlucky in love than for the character unlucky at work or the unknown character ($p < 0.05$ in both cases), with no difference between the latter two ($p = 0.76$). In contrast, cognitive empathy scores were not modulated by the character's identity in Generic scenarios ($p > 0.06$ in all cases; see **Figure 1**). Again, the factor Set was not significant, and did not interact in a significant way with any of the other variables ($p > 0.53$, $\eta_p^2 < 0.06$ in all cases).

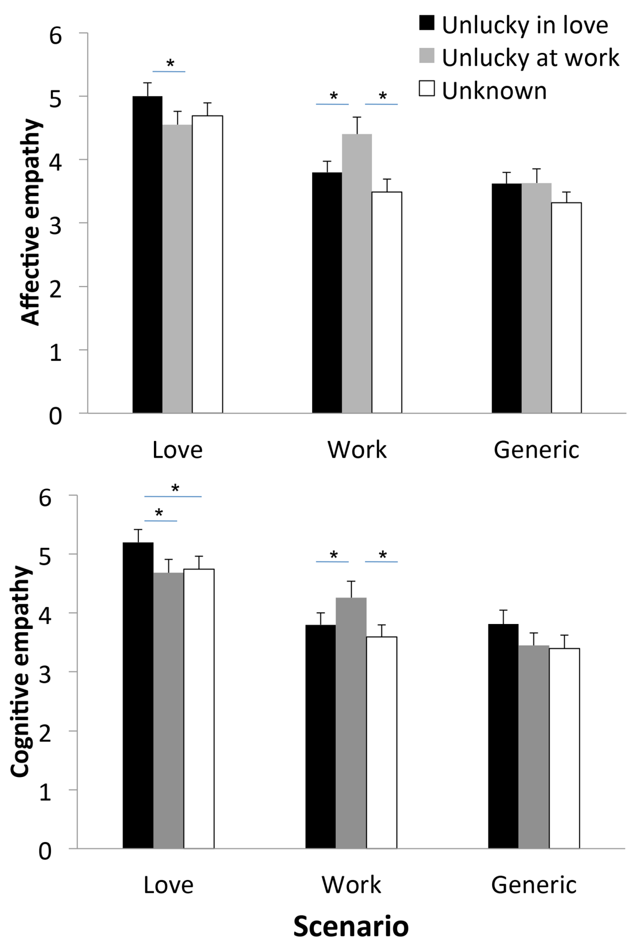

FIGURE 1 | Mean affective empathy scores (TOP panel) and cognitive empathy scores (BOTTOM panel) by type of scenario and character. Error bars indicate the standard error of the mean. $*p < 0.05$.

These findings indicate that empathic responses are influenced by the victim's identity and type of social violation s/he is facing, consistent with the hypothesis that retrieval of past episodes about others influences our appraisal of similar social situations involving the same individuals. This hypothesis is explored further in the next section.

EMPATHY MODULATION, EPISODIC MEMORY, AND EMPATHY SCALES

We next investigated whether the degree to which participants modulated their empathic responses depending on the victim's identity correlated with their ability to recall the victim's story in detail, and to standard self-report measures of empathy as assessed in the four subscales of the IRI (F, PT, EC, PD).

We calculated a recall accuracy score as the number of conceptual units recalled out of the total number of conceptual units (collapsed across the two life-stories). Recall accuracy was highly variable across participants, ranging from 0.07 for individuals who merely reported the gist of the stories to 0.36 for individuals who reported numerous vivid qualitative details (Mean = 0.21; SD = 0.08). We also calculated an index of memory-based empathy modulation. For Love scenarios, the index was calculated as $(\text{Empathy}_{\text{unlucky in love}} - \text{Empathy}_{\text{unlucky at work}})/\text{Empathy}_{\text{unknown}}$, and it indicated the difference between the amount of empathy felt in Love scenarios toward the victim unlucky in love minus that toward the victim unlucky at work, adjusted for the participant's general tendency to empathize, i.e., empathy toward the unknown victim. The same index was calculated for empathy scores in Work scenarios as $(\text{Empathy}_{\text{unlucky at work}} - \text{Empathy}_{\text{unlucky in love}})/\text{Empathy}_{\text{unknown}}$. The two indices were summed to get a general empathy modulation index. The empathy modulation index was calculated for cognitive empathy scores and affective empathy scores separately.

In order to investigate the relation between the empathy modulation indices and recall accuracy and self-report measures of empathy, while controlling for the effect of Set, we ran an Analysis of Covariance (ANCOVA) on affective and cognitive empathy modulation scores, with Set as between-subject factor, and recall accuracy, and the scores at the F, PT, EC, and PD subscales of the IRI as covariates. The ANCOVA on affective empathy modulation scores showed that the affective empathy modulation index correlated with recall accuracy [$\beta = 0.70$, $F(1,21) = 8.69$, $p < 0.01$, $\eta_p^2 = 0.29$; see **Figure 2**], but not with the scores at the IRI subscales ($p < 0.52$, $\eta_p^2 < 0.02$ in all cases). There was no significant effect of Set ($p = 0.27$, $\eta_p^2 = 0.11$). The same ANCOVA on cognitive empathy modulation scores showed that the cognitive empathy modulation index correlated positively with recall accuracy [$\beta = 0.79$, $F(1,17) = 10.69$, $p < 0.005$, $\eta_p^2 = 0.38$] (see **Figure 2**), but not with the scores at the IRI subscales ($p > 0.37$, $\eta_p^2 < 0.05$ in all cases). There was no significant effect of Set ($p = 0.14$, $\eta_p^2 = 0.20$).

FAUX PAS RECOGNITION ACCURACY, EPISODIC MEMORY, AND EMPATHY SCALES

Finally, we investigated whether the ability to detect faux pas was related to recall accuracy for the victims' life-stories, and to standard self-report measures of empathy. An ANCOVA on faux pas recognition accuracy with Set as between-subject factor, and recall accuracy and the scores at the F, PT, EC, and PD subscales of the IRI as covariates, yielded no significant effect of recall accuracy ($p = 0.52$; $\eta_p^2 = 0.02$), IRI scores ($p > 0.44$; $\eta_p^2 < 0.03$ in all cases), or Set ($p = 0.14$; $\eta_p^2 = 0.16$). Similar results were obtained if we focused on recognition accuracy for Work scenarios and Love scenarios, whose contents are related to the main themes of the victims' life-stories, and recognition accuracy for Generic and Neutral scenarios, whose contents are not related to memory contents ($p > 0.07$, $\eta_p^2 < 0.20$ in all cases).

DISCUSSION

Understanding other people's thoughts and feelings in a given situation is adaptive if we have a distinctive representation of who they are, and how they have behaved in similar situations. This enables us to anticipate their reactions to the current situation as accurately as possible. The present study shows that episodic memory for others' past experiences modulates significantly our appraisal of, and reaction to, what is happening to them currently.

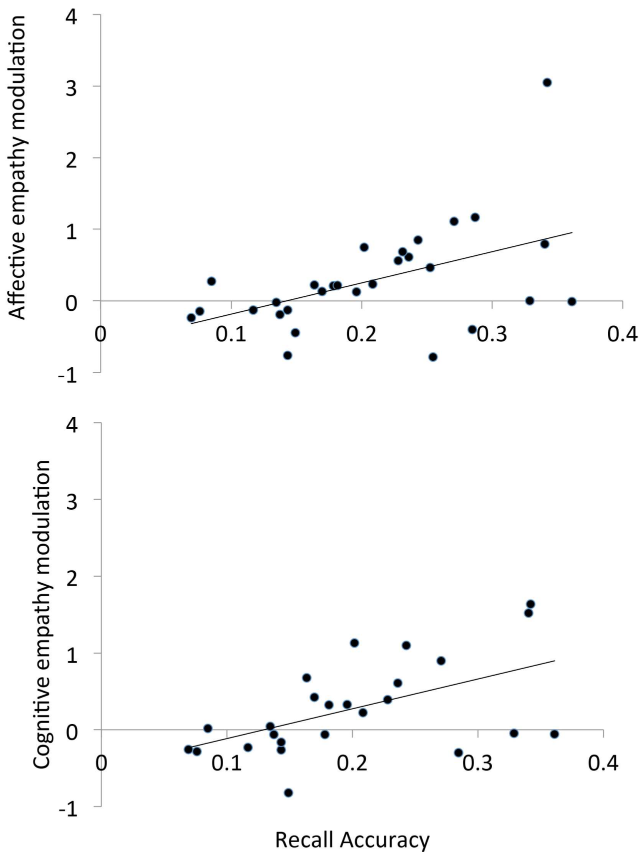

FIGURE 2 | Scatter plot of the bivariate correlation between recall accuracy for the life-stories and the affective empathy modulation index (TOP panel) and the cognitive empathy modulation index (BOTTOM panel).

Participants read the life-stories of two characters; one had experienced a long series of love-related failures, the other a long series of work-related failures. Consistent with the hypotheses, in a later faux pas recognition task, they reported more empathy for the character unlucky in love if she or he was the victim of an additional love-related faux pas than they did for the character unlucky at work or for an unknown character. Analogously, more empathy was reported for the character unlucky at work receiving yet another work-related social violation than it was reported for the character unlucky in love or an unknown character. It is worth emphasizing that participants did not appear to be generally more empathic toward the two familiar characters compared to the unknown character (e.g., Stinson and Ickes, 1992). The increase in empathy for the familiar characters, indeed, was highly situation-specific: participants felt more empathy toward the character unlucky in love in love-related scenarios, but treated this character normally in work-related scenarios, and vice versa for the character unlucky at work. Additionally, all characters attained comparable levels of empathy in Generic scenarios, whose contents were not relevant to the life story of either character. Rather, the present results suggest that while contemplating faux pas scenarios, individuals recollected previous episodes involving the victim analogous in content to the situation she currently faces, and how the victim had felt in those situations. Retrieval of past episodes involving the victim allowed a better simulation of how she felt in response to the current faux pas, or, in other words, the construction of an iToM, shaping individuals' empathic responses accordingly.

The present findings are in line with the "episodic simulation hypothesis" (Schacter et al., 2008; see also Buckner and Carroll, 2007), according to which retrieval of past experiences is needed to envisage fictitious events, and make decisions based on such simulations. In line with this, the amount of detail recalled from the victims' life-stories correlated positively with the degree to which individuals modulated their empathic responses depending of the identity of the victim, suggesting that a greater availability of episodic memories from the victims' life helped them to envisage their feelings in similar situations more vividly and faithfully (see also Spreng and Mar, 2012, for a Discussion). These results make contact with findings from a recent fMRI study (Perry et al., 2011), in which hippocampal activity was detected while subjects made emotional judgments about people deemed similar to themselves and facing events that had occurred in their own life (e.g., How would Joe feel about losing his wallet?), suggesting that individuals may resort to personal memories in order to understand other people better and empathize with them. Of course, different from Perry et al.'s (2011) paradigm, in ours subjects did not need to use the self (and personal memories) as a proxy to empathize with the victims (Mitchell et al., 2006), as they had the original memories of the victims' past experiences available.

Our findings fit nicely with the results of a recent fMRI study investigating the relation between autobiographical memory and ToM (i.e., imagining the thoughts and feelings of another person) for personally known versus unfamiliar others (Rabin and Rosenbaum, 2012). It was found that brain regions supporting ToM for personally known others overlapped more closely with those supporting autobiographical memory than did regions supporting ToM for unknown others, and the overlap was maximal in midline regions, including the hippocampus. This finding suggests that in order to imagine the mental states of known people individuals rely, to some extent, on shared past experience (Rabin and Rosenbaum, 2012; see also Rabin et al., 2012b). Consistently, a previous fMRI study had shown that the medial prefrontal cortex responded more strongly when participants made judgments about the personal preferences of friends and close others, which arguably are likely to trigger relevant past experiences, relative to strangers, regardless of whether the other person is perceived as similar to oneself (Krienen et al., 2010). On the other hand, ToM for unfamiliar others was associated with activity in more lateral frontal and temporal regions associated with accessing semantic knowledge (e.g., Martin and Chao, 2001), consistent with the idea that to infer strangers' mental states reliance on social scripts and general knowledge may be sufficient (Rosenbaum et al., 2007).

Previous research has shown that episodic memory retrieval is related to simulation of future events, and functional to social cognition. Amnesic patients with problems at remembering specific episodes from the past, indeed, may also exhibit problems at imagining specific episodes in the future (Tulving, 1985; Rosenbaum et al., 2005; Race et al., 2011; but see Squire et al., 2010), and their constructions of fictitious events appears significantly reduced in richness and content compared with those of controls (Hassabis et al., 2007). Crucially, it has been demonstrated that problems in simulating fictitious events has an impact on social problem solving. Sheldon et al. (2011) had patients with unilateral temporal lobe epilepsy and excisions (TLE), older adults, and control participants describe detailed solutions to various open-ended, social scenarios. TLE patients and older adults, both having deficits in episodic memory, provided fewer steps relevant to the given solution than their comparison group, and their descriptions of the step was made of fewer internal (episodic) details but a similar number of external (semantic) details compared to their control groups. Thus, even though amnesic patients can solve standardized ToM tasks normally (Rosenbaum et al., 2007), memory problems may in fact hinder performance in ill-defined, real world social situation that require evaluating the outcome of multiple, alternative mental simulations of the situation being considered, and integrating context-specific with person-specific information, tapping episodic simulation processes to a greater extent. Consistent with this interpretation, Levine et al. (1998) described a patient, ML, who had sustained damage to the right uncinate fasciculus, a band of fibers which connects the medial temporal lobe with ventral frontal cortex, and who had severe autobiographical memory deficits associated with problems in real world social interactions. Interestingly, ML had difficulty knowing how to behave around family members and friends and, despite being able to re-learn socially acceptable behavior under structured routines, he remained unable to self-regulate his behavior in unstructured situations (Levine et al., 1998).

It has been noted that both re-experiencing the past and inferring others' mental states require the ability to consider alternatives to events in the immediate environment, or self-projection (Buckner and Carroll, 2007; Mitchell, 2009), be this toward another time (for episodic memory) or another person's perspective (for ToM). One way to interpret the overlap in brain activity between episodic memory and ToM, therefore, is as structural in nature: both activities are supported by the same neural circuitry, the one that enables self-projection. Were the relation between episodic memory and ToM merely structural, however, one would expect a correlation between episodic memory and ToM performance. However, in the present study free recall (of the life-stories) was not related to faux pas recognition accuracy, and this held even if we focused on Love and Work scenarios, whose contents resonated with memory contents. This result is compatible with previous evidence showing that patients with significant episodic memory problems can attain normal accuracy in ToM tasks, including faux pas recognition tasks (Rosenbaum et al., 2007; Rabin et al., 2012a). Additionally, faux pas recognition accuracy was not related to "PT" scores in the IRI, as the self-projection hypothesis would predict. Our results, therefore, are more consistent with the view that ToM systems, though inherently sufficient to decipher social situation/violations, may co-opt episodic memory systems to integrate flexibly the characteristics of the situation with those of the victim, modulating empathic responses accordingly. This suggests a functional relation between episodic memory and ToM that is more in line with the episodic simulation hypothesis.

The "functional" (as opposed to "structural") interpretation proposed is also in line with the fact that we found largely parallel effect of episodic memory on cognitive empathy and affective empathy, while only the brain regions supporting cognitive empathy overlap with those supporting autobiographical memory (de Waal, 2008; Shamay-Tsoory et al., 2009; Zaki and Ochsner, 2012). In contrast, affective empathy is related to the ability to share others' emotional experiences through mirroring neural mechanisms (Preston and de Waal, 2002; Gallese et al., 2004; Singer and Lamm, 2009). Note, however, that mirroring occurs (and has been investigated) typically when perceivers make use of observable cues about what another person is feeling, whereas self-projection is mostly engaged when inferring the mental states of individuals that are not physically present (Zaki and Ochsner, 2012). Because in the present study participants made both cognitive and affective empathy judgments for individuals who were removed from their current experience, both judgments likely relied on, and were modulated by, the same type of (memory) cues (see de Vignemont and Singer, 2006, for other evidence for the contextual modulation of affective empathy). Indeed, the cognitive and the affective modulation indices were highly correlated in our sample ($r = 0.83$). An additional reason why cognitive empathy and affective empathy may have been aligned in our study is that participants were young individuals, likely struggling with similar love- and work-related issues as the protagonists in the two stories. Thus, while reading the faux pas stories, participants may not only have inferred what the characters unlucky in love and the character unlucky at work felt, but also shared their feelings because, to some extent, the saw bits of their own life in the lives of the fictitious characters. Future studies should investigate whether the degree to which memory for others' life resonates with one's own biography modulates the relation between cognitive and affective empathy (see also Batson et al., 1996).

A number of alternative interpretations to our data deserve consideration. Since in the present study recall accuracy was not experimentally manipulated, it is possible that a third variable, for example an initial empathic response while reading the life-stories, may have influenced both subsequent recall and empathic responses to social violations. In support to this hypothesis, recall accuracy correlated positively, though not significantly, with empathy scales (F scale: $r = 0.35$; $p = 0.056$; PD scale: $r = 0.36$; $p = 0.051$). However, the fact that the memory-based empathy modulation correlated with recall accuracy but not with measures of empathy suggests that it was episodic memory, not empathy, that drove the *situation-specific* adjustments in empathy for known individuals.

Another possibility is that, instead of episodic memory, a semantic labeling of the characters as "the unlucky in love" and "the unlucky at work," or implicit emotional associations (see Lieberman et al., 2001) supported situation-specific empathic responses in the current study. Lieberman et al. (2001), for example, have shown that, in a choice paradigm, amnesic patients show a normal tendency to revise their attitudes to fit a counter-attitudinal behavior, in the absence of explicit memory for that behavior. Although we cannot exclude that semantic or implicit memory contributed to our results, the fact that the modulation of empathic responses tracked the amount of detail in participants' recollection makes it unlikely that it derived merely from semantic or implicit memory.

This study has a number of limitations. First, our conclusions need to be confirmed with different materials. As Stone et al. (1998) noted, detecting a faux pas requires two things: (1) understanding that one person has knowledge that the other person is unaware of, or a mistaken belief, and (2) the empathic understanding of what kind of things someone (the victim) would find upsetting. In our experimental paradigm, episodic memory had an impact on this latter factor, tuning participants to the victims' inner motives. One may expect, then, that if the faux pas is subtle, or it depends relatively more on the victim's idiosyncrasies (point #2) rather then on "cold" aspects of ToM (point #1), then an impairment in episodic memory may prevent one from detecting a faux pas in the first place, having an impact on faux pas recognition accuracy. In the extreme case of the example we made in the Introduction, one would not call telling someone that he looks tremendously young for his age a faux pas without having memory for his life. Thus, future studies using more subtle social scenarios that cannot be deciphered completely within ToM systems or through abstract social knowledge would be important to test the relation between episodic memory and ToM accuracy further.

Moreover, it should be noted that the present results are limited to the healthy population we tested. In clinical populations (e.g., autistic patients, schizophrenic patients, patients with personality disorders), impairments in autobiographical memory, and ToM may co-occur and be related to each other (Corcoran and Frith, 2003; Adler et al., 2010; see Dimaggio et al., 2012 for a review). Interestingly, some therapeutic approaches for personality disorders and schizophrenia (e.g., Lysaker et al., 2007, 2011; Dimaggio and Attinà, 2012; Dimaggio et al., 2012) insist on the importance of eliciting patients' specific memories of relevant social interactions (as opposed to resorting to overgeneralized memories), to help patients appreciate psychological causalities, and track down the mental states of the individuals involved more accurately. For example, Dimaggio and Attinà (2012) described a patient with a narcissistic personality disorder who arrived demoralized at one session reporting that he had been socially rejected by two peers at a party. By re-exploring the original event with the therapist, he was able to recall additional contextual details ("There were more of us, and we were more familiar with each other. And to tell the truth, we weren't paying them much attention"), and consider the alternative possibility that his peers ignored him because they felt uncomfortable at the party, not because something was wrong with him (Dimaggio and Attinà, 2012, p. 931). The fact that, in clinical populations, the retrieval of past episodes promotes the explicit consideration of others' mental states is in line with the results of the present study. One question for future research is whether such memory-driven improvements in ToM depend on accessing specific contents about past episodes, or on the repeated activation of the neural network that supports both episodic memory and cognitive empathy.

Finally, we believe that an important step toward specifying the relation between autobiographical memory and ToM, would be to adopt both subjective and objective measures of ToM (see Zaki et al., 2008, for a measure of empathic accuracy). For example, most studies, including the present study, require participants to explicitly consider the mental states of other people, but do not assess whether participants did infer these mental states correctly (Rabin et al., 2010; Spreng and Grady, 2010; Rabin and Rosenbaum, 2012). As well, self-report measures of empathy may not track with the actual ability to read, and resonate with, others' mental states, especially in clinical populations (see Ritter et al., 2011; Dimaggio et al., 2012). This factor may also explain the lack of correlation between self-report empathy and ToM performance in the present experiment. Investigating the relation between episodic memory, and subjective as well as objective measure of ToM will reveal whether there is a causal relation between the two processes, or whether they represent two instances, not necessarily intertwined, of imagining a perspective removed from current experience.

To conclude, the present study shows that the retrieval of memories of previous episodes influences participants' current social processing significantly, such that empathy toward the victim of a social violation is modulated by memories involving the victim that bear a resemblance to the situation she or he is currently facing. These findings suggest that understanding others' thoughts and feelings entails integrating flexibly information about past experience and more contingent information, constructing detailed simulations of social targets and situations that preserve their uniqueness, a function we call individualized ToM.

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APPENDIX

LIFE-STORIES

Mike/Susan (unlucky in love; Toronto version)

My name is Mike/*Susan*|| and I am 30 years old.|| I was born in Dublin,|| but now I live in downtown Toronto||, in my own flat||. The flat is on Queen West,|| on the second floor|| of a Victorian house|| that is painted in red|| and with a blue ceiling.|| I still remember the moment I decided to rent this flat.|| I was wandering in Queen West when I bumped into this enchanted house for rent||. The landlord was there||, a funny|| Portuguese guy||. We talked for a while and the deal was done!|| I am so happy to live on Queen West||. I feel relieved that I can walk in my neighborhood||. It's like a breath of fresh air to me.|| Yet, I'm very close to my family|| and sometimes it's tough to be apart||. I spent such a pleasant childhood|| in Dublin||, mainly because we lived on a farm.|| I can still smell the cookies|| that my granny used to bake|| on Sunday mornings.||

I have always known I would leave, though||. When I was in sixth grade||, I got an award from my school|| for the best essay|| about organ donation||. I remember I was so proud of myself||. Even though I was really young, I was able to explain the pros and cons about organ donation.|| For example, I wrote about two parents that had lost their child||. They didn't want to donate their child's organs||, but the doctor told them that they would save|| three lives and||, somehow, their child would keep on living.|| So they allowed the donation||. I believe it was very simple for the readers to guess what my personal take on the topic was:|| I truly agree with people who accept to donate their organs,|| and I would do that myself.|| Indeed, even though I have little spare time,|| I still keep on promoting the cause for donation||. Also, I never forget about giving blood.|| Since I was very young, I have always been interested in the field of health.||

After graduating in Pharmacy|| at the University of Toronto,|| I found a job in the Pharmaceutical industry||. The name of the industry is "Atom"||, it is located downtown, between Dundas and Manning.|| You might have noticed the place, it is a colored building|| and there is a dog at the entrance||, Zac||, a very cute beagle|| that we all love||. I am fairly happy with the job|| and I especially enjoy working with my colleagues.|| They are fun,|| of my age,|| and collaborative||. I feel good there|| and it is important because, apart from them, I do not have many friends here in Toronto.||

I mean, I have a very small group of close friends||. We enjoy drinking beer while watching baseball games or planning trips/*We enjoy drinking coffee while watching TV or planning trips*||. Sometimes we go to our favorite club to hit on girls/*boys*||. Our favourite club is "Coca"||. It is on Queen street West||, very close to my place.|| One of my closest friends is Simon/*Kate*.|| He's a very good looking guy/*She's very pretty*,|| and, when we all hang out together, he always gets the cutest girls/*boys*.|| Simon/*Kate* doesn't need to try very hard to attract girls/*boys*||. He/*she* just starts talking about random topics and they listen to him/*her*||. I'm pretty sure that if I tried something like that, they would push me away with a lame excuse||. When I was younger and in High School||, girls/*boys* avoided talking to me.|| Some of them kindly avoided me; they would say that they had something urgent to do||. Others were totally upfront instead.|| For example, one day, I was walking down the street|| and I got near to a good looking girl/*boy* that I had noticed at school.|| I just asked her/*his* name|| and she/*he* answered: "I am sorry, I am very busy and cannot waste my time!"|| I remember she/*he* was looking at me as if she/*he* was thinking: "I can't even consider the idea of talking with you!"|| I felt very upset|| and frustrated|| and, as usual, I ran away and unburdened myself to my older sister|| Mary||.

It is difficult to describe in words how it feels to be rejected like that.|| It makes me feel like I am totally worthless||, like the skin of a banana on the corner of the street.|| But even that banana skin, I guess someone would care enough to throw it in the garbage. Me, not even that.|| Ok, now I am probably being too dramatic.|| It's just that sometimes I can feel like such a nothing||.

In fact, my private life has been being very calm lately||, too calm||. I don't have a girlfriend/*boyfriend*||. Women/*men* do not seem to be that into me||. I mean, I had two girlfriends/*boyfriends*|| but we split up badly||. My first girlfriend/*boyfriend*||, Ann/*David*,|| thought I was a bit apathetic||. She/*he* said she/*he* didn't have fun with me||. We were together for 5 months|| but I could see from her/*his* face that she/*he* was never enthusiastic||. She/*he* didn't talk to me about any relationship problems||, so I thought everything was normal.|| Then, one day, while wearing the yellow sweater|| I bought her/*him* for her/*his* birthday||, she/*he* said: "I am afraid you are not the man/*woman* for me"||. My latter girlfriend/*boyfriend*||, Lisa/*Simon*,|| she/*he* was super fun.|| I adored her/*him* at first||. After 3 months|| she/*he* dumped me|| for one of my best friends|| (not Simon/*Kate*, another one).|| Now, tell me that the banana skin metaphor is not appropriate||! But I'm optimistic,|| I think that I've just not found the right person yet.|| And I know that these things don't come easy.|| Lots of people say that they found their true love in their 30s.|| I strongly think that to find Miss/*Mr* Right, you have to be mature|| and also lucky.||

My ideal girlfriend/*boyfriend* should be very sensitive||. She/*he* must be interested in what I do,|| and remember what is going on in my life.|| For example, Ann/*David*,|| my former girlfriend/*boyfriend* forgot about my birthday||. I didn't want a big surprise or an amazing present, I just wanted to be told something||, or to receive a romantic birthday card||. But she/*he* completely forgot.|| This is what happened: she/*he* suggested to go out and spend a nice night together||. That night, she/*he* was holding a very big purse/*knapsack*,|| so I thought that maybe she/*he* put my gift inside it||, but at the end of the evening, we just went home|| and she/*he* didn't even say "happy birthday"||. It made me feel very sad|| and disappointed||. I happen to forget appointments|| or assignments too,|| but I never forget very important events,|| especially when they involve the person I love.|| But then again, maybe Ann/*David* did not love me.|| Maybe Ann/*David* remembers important events too.|| My birthday was just not an important event to her/*him*||. So I decided to get in my car and start driving||, listening to the radio loudly|| and blaming myself for allowing someone to hurt me.||

During the weekend I like doing some physical activity.|| I do some jogging|| in Bellwoods Park|| on Saturday||, but I know that is not enough|| and I want to start going to the gym||. A few days ago|| I went to a gym|| on Bloor & Bathurst|| to ask for information.|| The place was amazing!|| It had more machines|| and instruments you could imagine||, and a great team of trainers||. One of those trainers got close to me and explained to me how they work with their clients||: their principal aim is to make them feel at home||. It made me feel very comfortable||. Anyway, everybody knows that working out with a friend is more fun than alone||, so I think I will ask my friend|| Patrick/*Lisa*|| to join me||. When I was younger||, I used to go to the swimming-pool||. I liked that so much||, but I had to quit|| because my spare time got very limited||: homework||, friends||, etc. Moreover, I had long hair at the time||, so it was very uncomfortable to dry it each time,|| it took so long.|| But now I am committed to start working out seriously||. I've heard it's very healthy|| and cheers you up.||

I like watching movies||, in particular action movies;|| those ones have amazing special effects.|| One of my favorite movies is "The Day After Tomorrow."|| Even though the story is a little trivial,|| I was impressed by the director's ability to make everything appear so real!|| I remember that the first time I saw that movie I was with Patrick/*Lisa*.|| The theatre was really packed,|| but he/*she* managed to find two places|| right in the middle of the theatre||, the last two!|| The other people had to sit right in the front, destroying their neck||. I don't like watching a movie if I am not seated properly.||

Adam/Jean (unlucky at work; Toronto version)

My name is Adam|| and I am 30 years old||. I was born in Toronto,|| where I live with my family.|| My family is composed of four people||: my parents,|| my brother and I||. I'm having some problems with them, lately.|| Actually, I don't think I've ever been in a good relationship with my family,|| especially my parents.|| When I was in High school,|| they were very worried about me:|| I didn't study enough,|| and I loved to skip school.|| I still remember that day when my teacher||, Mrs. Brown,|| called my parents|| because I skipped school:|| when I got home, my mom asked me: "So what have you been up to at school?"|| And I answered: "Oh, Mrs. Brown didn't come this morning,|| so my classmates and I spent two hours chatting and stuff like that||." Well, my parent punished me|| and I couldn't go out for a very long week.||

Still I kept on skipping school occasionally||, and my friend and I|| used to go to the Islands instead||. It was fun!|| My friend had a house there||, a cute|| old|| little house|| painted in ochre|| with a hammock|| in the front||. We used to stay there||, safe||, talking about life||. It was a refuge for me.|| Truth is, I felt bad at school||. I had extreme difficulties concentrating||. For example, I could not stay concentrated on the lesson for more than 15 minutes.|| So I was often distracted,|| and I was never prepared||. I was one of the worst in my class||. Nobody believes me||, they all think I was lazy||, but I swear, I tried to study, but my head just flew somewhere else||. It was a frustrating feeling||. Like that day when I forgot my homework at home||: my teacher really believed that it was just one of my excuses||, but if I weren't that distracted, I would have remembered to bring them at school.||

I have a girlfriend/*boyfriend*||, Julia/*Jack*,|| who lives here in Toronto.|| It's a very serious relationship.|| I met her during a birthday party.|| I didn't feel like going there,|| because I was tired:|| I had spent all night with my friends||. But I decided to go there anyway.|| It was on May|| 28||, 2007||, I won't ever forget that day||. I was leaning against the wall||, thoughtfully drinking my "manhattan"|| and looking at people chatting and dancing||. Everybody looked like anyone else to me||. Suddenly, a girl/*boy* turned to me||: she/*he* had long black/*short blond* hair|| and was wearing a blue dress/*nice shirt*||, very simple||; I would say Armani style||, which fitted her/*him* so good||. Then we looked at each other and that was it: we've been together ever since.|| Now that I am older, I regretfully think that maybe, if I had done better at school, now I would have a good job|| and I could afford a house where I could live with Julia/*Jack*.|| We saw a place that would be perfect for us||. The rent is quite high:|| 1300$ per month, inclusive||. It's a big apartment|| in Markham||. The owners are two Italians|| who live in the apartment upstairs.|| The house is made of red small bricks|| and it has a big back-yard with a lot of vegetables||: cucumbers,|| tomatoes,|| fennels||. . . and even three|| fruit trees||. The apartment is very bright.|| But even thinking about it is a waste of time||: I can't afford any house at the moment|| and this makes me feel like a nobody.||

It will take a long time to get a good job||. Sometimes I think I won't ever have success in the future,|| because I often fail||, and that is very hard to deal with||. I couldn't even keep my job|| as shop assistant|| at Canada Tire||. Actually I didn't like the job||: I was forced to wear that stupid|| white t-shirt|| with the name of the store on.|| I used to get confused|| because of all the stuff they were selling||. There were 1000 different types of plugs||, and lamps,|| and I used to forget some of them||. Then they fired me.|| Now I'm attending Physical Education at University|| and I like it||, but I am slower than my classmates||, and I just took two exams|| in two years||. A few months ago||, my classmates and I were walking on College Street,|| in Little Italy,|| enjoying a very nice|| and warm afternoon.|| Even though it was a relaxing afternoon||, my classmates couldn't stop talking about exams and deadlines||. So, since I was getting very sick and tired||, I said: "Guys, why don't we just enjoy this nice weather and set aside our worries?"||. And Paul/*Miranda*,|| a guy/*girl* I don't like too much||, answered: "It's very easy to say so when you missed most of your deadlines!||" I felt very uncomfortable|| and I thought I shouldn't have talked at all||. Because of all these limitations, I am not positive about the house thing,|| and I feel guilty when I think about Julia/*Jack*.||

Once I made a plan||. I would get a job|| and try to make them notice me||. The point would be to become very indispensable||, so that they won't be able to go on without me.|| At that point, they'll pay me lots of money||. It's not that simple, I know.|| I had been hired recently,|| but I had a hard time with my boss||. He kept on saying that I had mistakenly filed some invoices|| and that was a disaster.|| I tried to answer that it wasn't my fault,|| because nobody had explained that to me,|| but he wasn't listening.|| Then he said: "You have no idea how many guys/*girls* are willing to be hired in place of you!"|| I felt so completely useless||. Can you imagine how unnecessary I felt at that time?|| And I tried to think more positively, but it didn't work.|| I still think I could do well in a job that does not require much attention and organization,|| but instead more imagination and creativity.|| For example, I love acting,|| and writing plays.|| I never leave home without my notebook||, so that I can write down hypothetical dialogues anytime I get the inspiration.|| Unfortunately, this kind of skill tends not to be valued.|| At least, my parents did not value them.||

Sometimes, in high school,|| I used to get good marks in acting class||. My parents used to say: "If you want to pursue this passion, at least you have to be the best in your class"||. I always answered to them: "If you truly believe in something, you can make it happen."|| But they used to look at me like they couldn't understand what I was saying.|| In these situations I usually feel so unappreciated.|| It's really tough.|| They probably wanted to discourage me from engaging in a very difficult career||, they wanted me to stop dreaming||. But in fact, the message I got was that I was never good enough.|| And that doesn't sound good at all.||

Besides that, my life goes on as usual.|| I hang out with my friends,|| I regularly go to the gym|| and I spend much time with my girlfriend/*boyfriend*.|| My friends and I would love to go to Ibiza|| next summer|| and we're saving money for that.|| If we go there, it will be fun,|| like last summer in Greece.|| Julia/*Jack* was there too,|| so it was fun and romantic at the same time.|| We visited the most famous places there|| and I loved the Acropolis of Athens.|| It is very charming|| because you can picture the ancient Greeks walking around|| and going to the temples to pray.||

I also enjoy watching movies|| with my friends|| and our girlfriends/*boyfriends*,|| at my place,|| where I have a very big TV||. I/*Jack* usually choose the movies,|| because I/*he* know/*s* what my friends like.|| But, sometimes, I/*he* rent/*s* some horror movies on purpose||, because I like to get scared and jumpy/*and this really bothers me*.|| Obviously, we all know that most girls don't like this kind of movie, because they/*we*'re chicks.|| So my friends and I/*the guys* make fun of them/*us*, when they/*we* scream during the scariest scenes.|| One night, Steven,|| one of our friends,|| turned the TV and the lights off,|| while we were watching "The Ring."|| The girls/*the girls and I* started screaming.|| But among their/*our* screams, we could hear a masculine voice|| and we couldn't figure out who it was.|| When I turned the light on,|| we found Steven,|| lying on the floor||, complaining,|| because he had hurt his ankle while fumbling in the dark.|| That time, the girls/*the girls and I* got their/*our* revenge,|| and the guys and I/*the guys* had one more reason to burst laughing.|| We were very mean,|| because we kept on making fun of him for a week||. But, the next night we spent together,|| Steven got his revenge||. He decided to buy popcorn for everyone||, because, as he told us, it was a very special event for him.|| So we started wondering that maybe he had found Miss Right, finally||. When we all gathered on the couch,|| I asked him: "Ok, tell us what's going on"||. And he answered: "Well, it's sad news||: I'm leaving the city tomorrow||, because I found a job in New York City."|| I got very sad|| and upset|| because he hadn't talked about that before||. So we quickly decided to have a party for him,|| to say goodbye.|| After that party||, we discovered that he made up this story to get revenge.|| I remember that, immediately after I realized that it was a joke||, I felt very mad at him||. But now I'm OK.||

Mike/Susan (unlucky in love; Chicago version)

My name is Mike/*Susan*|| and I am 25 years old.|| I was born in Dublin,|| but now I live in downtown Toronto,|| in my own flat||. The flat is on Queen West,|| on the second floor|| of a Victorian house|| that is painted in red|| and with a blue ceiling.|| I still remember the moment I decided to rent this flat.|| I was wandering in Queen West when I bumped into this enchanted house for rent.|| The landlord was there||, a funny|| Portuguese guy.|| We talked for a while and the deal was done!|| I am so happy to live on Queen West.|| Yet, I'm very close to my family|| and sometimes it's tough to be apart||. I spent such a pleasant childhood|| in Dublin||, mainly because we lived on a farm.|| I can still smell the cookies|| that my granny used to bake|| on Sunday mornings.||

I have always known I would leave though||. When I was in sixth grade||, I got an award from my school|| for the best essay|| about organ donation||. I remember I was so proud of myself||. Even though I was really young, I was able to explain the pros and cons about organ donation.|| Since I was very young, I have always been interested in the field of health||.

After graduating in Pharmacy|| at the University of Toronto,|| I found a job in the Pharmaceutical industry||. The name of the industry is "Atom"||, it is located downtown, between Dundas and Manning.|| You might have noticed the place, it is a colored building|| and there is a dog at the entrance||, Zac||, a very cute beagle||. I am fairly happy with the job|| and I especially enjoy working with my colleagues.|| They are of my age,|| and collaborative||. I feel good there|| and it is important because, apart from them, I do not have many friends here in Toronto.||

I mean, I have a very small group of close friends||. We enjoy drinking beer while watching baseball games or planning trips/*We enjoy drinking coffee while watching TV or planning trips*||. Sometimes we go to our favorite club to hit on girls/*boys*||. Our favorite club is "Coca"||. It is on Queen West||, very close to my place.|| One of my closest friends is Simon/*Kate*.|| He's a very good looking guy/*She's very pretty*,|| and, when we all hang out together, he/*she* always gets the cutest girls/*boys*.|| Simon/*Kate* doesn't need to try very hard to attract girls/*boys*||. He/*She* just starts talking about random topics and they listen to him/*her*.|| I'm pretty sure that if I tried something like that, they would push me away with a lame excuse||. When I was younger and in High School,|| girls/*boys* avoided talking to me.|| Some of them kindly avoided me; they would say that they had something urgent to do||. Others were totally upfront instead.|| For example, one day I got near to a good looking girl/*boy* that I had noticed at school.|| I just asked her/*his* name|| and she/*he* answered: "I am sorry, I am very busy and cannot waste my time!"|| I remember she/*he* was looking at me as if she/*he* was thinking: "I can't even consider the idea of talking with you!"|| I felt very upset|| and frustrated|| and, as usual, I ran away and unburdened myself to my older sister|| Mary.||

It is difficult to describe in words how it feels to be rejected like that.|| It makes me feel like I am totally worthless||, like the skin of a banana on the corner of the street.|| But even that banana skin, I guess someone would care enough to throw it in the garbage. Me, not even that.|| OK, now I am probably being too dramatic here.|| It's just that sometimes I can feel like such a nothing||.

In fact, my private life has been very calm lately||, too calm||. I don't have a girlfriend/*boyfriend*||. Women/*Men* do not seem to be that into me||. I mean, I had two girlfriends/*boyfriends*,|| but we split up badly||. My first girlfriend/*boyfriend*||, Ann/*Sam*,|| thought I was a bit apathetic||. She/*He* said she/*he* didn't have fun with me||. We were together for 5 months,|| but I could see from her/*his* face that she/*he* was never enthusiastic||. She/*He* didn't talk to me about any relationship problems||, so I thought everything was normal.|| Then, one day, while wearing the yellow sweater|| I bought her/*him* for her/*his* birthday||, she/*he* said: "I am afraid you are not the man/*woman* for me"||. My latter girlfriend/*boyfriend*||, Lisa/*Ramon*,|| was super fun.|| I adored her/*him* at first||. After 3 months|| she/*he* dumped me|| for one of my best friends|| (not Simon/*Kate*, another one).|| Now, tell me that the banana skin metaphor is not appropriate||! But I'm optimistic,|| I think that I've just not found the right person yet.||

My ideal girlfriend/*boyfriend* should be very sensitive||. She/*He* must be interested in what I do,|| and remember what is going on in my life.|| For example, Ann/*Sam*||, my former girlfriend/*boyfriend*, forgot about my birthday||. I didn't want a big surprise or an amazing present, I just wanted to be told something||, or to receive a romantic birthday card||. But she/*he* completely forgot.|| This is what happened: She/*he* suggested to go out and spend a nice night together||. That night, she/*he* was holding a very big purse/*knapsack*,|| so I thought that maybe she/*he* put my gift inside it||, but at the end of the evening, we just went home|| and she/*he* didn't say even "happy birthday"||. It made me feel very sad|| and disappointed||. I happen to forget appointments too,|| but I never forget very important events,|| especially when they involve the person I love.|| I don't like to say it,|| but maybe Ann/*Sam* did not love me.|| Maybe Ann/*Sam* remembers important events too.|| My birthday was just not an important event to her/*him*||. So that night I decided to get in my car and start driving||, listening to the radio loudly|| and blaming myself for allowing someone to hurt me.||

During the weekend I usually do some physical activity.|| A few days ago|| I went to a gym|| on Bloor & Bathurst|| to ask for information.|| The place was amazing!|| Also it has a great team of trainers||. One of those trainers,|| Ricky||, a very tall guy|| got close to me and explained to me how they work with their clients||: their principal aim is to make them feel at home|| and then they start asking you some questions|| in order to get to know you better||, because they really want to create the right working out schedule for your health||. It made me feel very comfortable||. When I was younger||, I used to go to the swimming-pool||, I loved it||, but I had to quit|| because my spare time got very limited.|| But now I am committed to start working out seriously||. I've heard it's very healthy|| and cheers you up.|| Rickie, the trainer,|| told me that people usually take nine months|| to see the first improvements,|| in terms of losing weight and becoming more tonic.||

I like watching movies||, in particular action movies||. One of my favorite movies is "The Day After Tomorrow."|| Even though the story is a little trivial,|| I think that the director was successfully able to make everything appear so real!|| I remember that the first time I saw that movie I was with my friend Patrick/*Kate*.|| The theatre was really packed,|| I truly wanted to leave and to come back another day||, but then Patrick/*Kate* managed to find two places|| right in the middle of the theatre||, the last two!|| The other people had to sit right in the front, destroying their neck||.

Adam/Jean (unlucky at work; Chicago version)

My name is Adam/Jean|| and I am 25 years old||. I was born in Toronto,|| where I live with my family.|| My family is composed of four people||: my parents,|| my brother and I||. I am really fond of my brother,|| Trevor,|| even though we sometimes fight||; it happens when you have to share your room with someone else.||

I think that my life hasn't always been easy||. For example, when I was at school, I immediately realized I could not stay concentrated on the lesson for more than 15 minutes.|| So I was often distracted,|| and never prepared||. I was one of the worst in my class||. My teachers didn't believe me||, they all thought I was lazy||, but I swear, I tried to study, but my head just flew somewhere else||. It was a frustrating feeling||. I remember the good students chatting with professors about topics of mutual interest, or even just about the lesson||. I would have loved to be able to feel part of that group||. But I just was not good enough for that,|| and I have always felt estranged because of this.||

In order to escape from those frustrating feelings of incompetence,|| I used to skip classes, as many students do||. I always smile by myself|| when I remember that day when my teacher,|| Mrs. Brown,|| called my parents|| because I skipped school.|| When I got home, my mom asked me: "So what have you been up to at school?"|| And I answered: "Oh, Mrs. Brown didn't come this morning,|| so my classmates and I spent two hours chatting and stuff like that||." Well, my parent punished me|| and I couldn't go out for a very long week.|| I remember I got very upset.|| I even remember what I did instead of going to school, that time: I went to the Islands||. It was fun!|| My friend had a house there||, a cute|| old|| little house,|| painted in ochre,|| with a hammock|| in the front||. We used to stay there||, safe||, talking about life||. It was a refuge for me.||

I am afraid it will take a long time for me to get a good job||. Sometimes I think I won't ever have success,|| because, let's face it, I often fail workwise||, and that is very hard to deal with||, because work is an important part of our lives.|| For example, I couldn't keep my job|| as shop assistant|| at Canada Tire||. The most exhausting thing about that job was that there were selling 1000 different types of plugs||, and lamps,|| and I used to forget some of them||. Then they fired me.|| At the moment I'm attending Physical Education at University|| and I like it||, but I am slower than my classmates||, and just took two exams|| in two years||. A few months ago||, my classmates and I were walking on College Street,|| in Little Italy,|| enjoying a warm afternoon.|| Even though it was a relaxing afternoon||, my classmates couldn't stop talking about exams and deadlines||. So, since I was getting very sick and tired|| – and defensive, I confess-||, I said: "Guys, why don't we just enjoy this nice weather and set aside our worries for a bit?"||. And Paul,|| a guy I don't even like||, answered: "It's very easy to say so when you missed most of your deadlines||." I felt very uncomfortable|| and thought I shouldn't have talked at all||.

Once I made a plan||. I would get a job|| and try to make them notice me.|| It's not that simple, I know.|| I have been hired recently,|| but I already had a hard time with my boss||. He said that I had mistakenly filed some invoices|| and that was a disaster||. Then he said: "You have no idea how many guys/*girls* are willing to be hired in place of you!"|| I felt so completely useless||. Can you imagine how unnecessary I felt at that time? || I keep thinking that if I had done better at school and gotten a good job,|| now I could afford a house to live by myself.|| I saw a place that would be perfect for me, the other day||. I liked it very much.|| The rent is quite high:|| 1300$ per month, inclusive||. It's a big apartment|| in Markham||. The owners are two Italians|| who live in the apartment upstairs.|| The house is made of red small bricks|| and it has a big back-yard with a lot of vegetables||: cucumbers,|| tomatoes,|| fennels||. . . and even three|| fruit trees||. The apartment is very bright.|| But I can't afford any house at the moment because of all my limitations,|| and this makes me feel like a nobody.|| And I feel guilty when I think about it:|| I think the reason I don't have a house is that I am not good enough.|| Sometimes I am more positive though,|| and think I could do well in a job that does not require much attention and organization,|| but instead more imagination and creativity.|| For example, I love acting||, and writing plays.|| I never leave home without my notebook||, so that I can write down hypothetical dialogues anytime I get the inspiration.|| Unfortunately, this kind of skill tends not to be valued.|| I took part in many competitions,|| during High School.|| They were a chance for me to show how good I was in acting||. When I didn't win, I used to feel terrible,|| because I had to see the arrogant look of the winner||, that seemed to say: "You won't be able to do better.|| You're a loser."|| And it's really tough,|| because it makes me feel like I don't have any chance to get better in the future.|| I would stay awake all night in those days.||

Besides that, my life goes OK.|| I hang out with my friends|| and I regularly go to the gym.|| My friends and I would love to go to Ibiza|| next summer|| and we're saving money for that.|| If we go there, it will be fun,|| like last summer in Greece: it was fun.|| We visited the most famous places there and|| I loved the Acropolis of Athens.|| It is very charming,|| because you can picture the ancient Greeks walking around|| and going to the temples to pray.|| I also enjoy watching movies|| with my friends,|| at my place||, where I have a very big TV||. I usually choose the movies,|| because I know what my friends like.|| But, sometimes, I rent some horror movies on purpose||, because I like to get scared and jumpy.|| Most girls don't like this kind of movies||, so my friends and I make fun of them, when they scream during the scariest scenes.|| One night, Steven,|| one of our friends,|| turned the TV and the light off,|| while we were watching "The Ring."|| The girls started screaming.|| But among their screams, we could hear a masculine voice|| and we couldn't figure out who it was.|| When I turned the lights back on,|| we found Steven,|| lying on the floor|| complaining,|| because he had hurt his ankle while fumbling in the dark.|| I laughed so much! || That time, the girls/*the girls and I* got their/*our* revenge,|| and the guys and I/*the guys* had one more reason to burst out of laughing.|| We kept on making fun of him for a whole week||.

FAUX PAS SCENARIOS

Love scenarios

1. "Tonight we'll go to the restaurant!" said [VICTIM] to his/*her* partner, who was singing in the shower. He/*She* had planned to have a nice evening with her/*him* because it was their anniversary. While he/*she* was secretly packing the present for her/*him*, he/*she* wondered whether his girlfriend/*her boyfriend* also remembered their anniversary. Then she/*he* came out of the shower. "What were you saying honey? I couldn't hear from the shower," asked the girl/*the boy*. [VICTIM] said: "I thought it would be nice to go out for dinner since today..." But she/*he* interrupted him/*her*: "Oh sorry honey, not today: I promised some colleagues I would join them for a drink! What about next Saturday?"
2. [VICTIM] was in Lisbon for a conference. He/*She* had met a lot of colleagues from abroad, who were working on similar topics as he/*she* was, but his favorite colleague was Valentina/*Luca*, an extroverted lawyer from Italy. On the last night in Lisbon, [VICTIM] and Valentina/*Luca* went for dinner together. After dinner, they took a nice walk through Bairro Alto. [VICTIM] said: "Lisbon is such a charming city." Valentina/*Luca* replied: "Yes, I agree, even though I think that visiting it with your partner would be a completely different story!" [VICTIM] replied: "I see."
3. [VICTIM] had shopped around all day and was very tired. He/*She* was looking for a seat, when he/*she* saw a bench in a park, with a very cute girl/*boy* sitting there. [VICTIM] thought that it would be great to sit by her/*him*. He/*She* got closer to the girl/*boy* and asked: Hi, do you mind if I have a seat here, or are you waiting for someone? The girl/*boy* replied: "No problem, I'm not waiting for anyone but, as you can see, the park is not too busy and there are a lot of empty seats."
4. [VICTIM] and his girlfriend/*boyfriend* met at a bar on the beach. They decided to take a walk close to the sea. [VICTIM] thought everything was very romantic: the sound of the waves, the moonlight, and the noise of the music that was now far away... "Hey," said [VICTIM], "Let's buy some red wine and come back here!" His girlfriend/*boyfriend* smiled. [VICTIM] asked: "Why are you smiling?" She/*He* replied: "Nothing important... It's that this place reminds me of my last boyfriend/girlfriend; we had such a great time last summer on this beach."
5. [VICTIM] was having problems with his new girlfriend/boyfriend. He was drinking a hot chocolate at a Café, thinking about his/her problems, when Peter, a guy he/she barely knew, came over and said: "Hi [VICTIM], how are you? You look so sad... Don't tell me it's a trivial love issue! Love is so overrated these days!" [VICTIM] answered: "Well, I guess the situation is more complicated than that..."
6. [VICTIM] and his girlfriend/*her boyfriend* went for an ice cream on College Street. [VICTIM]'s girlfriend/*boyfriend* had a double chocolate ice cream, whereas [VICTIM] tried the new blue flavor. His/*her* mouth went blue in less than 2 minutes. [VICTIM]'s girlfriend/*boyfriend*, looking for a Kleenex in her purse/*his bag*, took out a CD instead. "Hey, what is this CD?" asked [VICTIM]. "Oh nothing special, it's a compilation of my favorite love songs, answered [VICTIM]'s girlfriend/*boyfriend*. "Oh thank you!!! Finally, you made me a CD!" exclaimed [VICTIM]. "Actually, I made this for my friend from the acting school. Did I ever tell you about him/*her*?"
7. [VICTIM] and his girlfriend/*her boyfriend* had been together for 2 weeks. However, [VICTIM] had to fly to Europe for a holiday that he/*she* had planned before meeting her/*him*. During his/*her* stay in Paris, [VICTIM] thought a lot about his girlfriend/*her boyfriend*. He/*She* decided to buy her/*him* a little present. He/*She* bought a little depiction of the Eiffel Tower made by a street painter. The painting included a couple kissing each other. [VICTIM] thought it was so romantic. At the airport, [VICTIM] and his girlfriend/*her boyfriend* gave each other a huge hug. "Did you miss me?" asked his girlfriend/*her boyfriend*. "Oh, I missed you so much. I got you a present," replied [VICTIM]. She/*he* said: "That's so nice! I bet it's something high-tech and not some crappy souvenir."

8. [VICTIM] was talking on the phone with his girlfriend/*her boyfriend*. He/*she* was telling her/*him* about his/*her* frantic morning, and some problems he/*she* had at work with his PhD supervisor. "... and after I waited to talk to him for the entire day..." [VICTIM] said, "...guess what he told me? He told me to meet the next week! Can you believe that? I wasted so much time waiting!" His girlfriend/*her boyfriend* did not answer. "Hey, did you hear what I said?" [VICTIM] asked." Sure, sure," she/*he* answered, "it's just that I was trying to send an email, but it keeps bouncing back." "I see" said [VICTIM], "did you double-check the address?"

Work scenarios

1. [VICTIM] went to say bye to the director of his/*her* office, because he/*she* was planning to leave for the holidays. "Hi Dr. Henson," he/*she* said, "I wanted to say bye. I am heading to Italy. Should you need to contact me, please don't hesitate to do so by email." "Don't worry," answered the director "I don't think your absence will cause huge problems. Have fun!"
2. [VICTIM] was about to graduate. The same day that he/*she* was informed his/*her* thesis had been accepted by the committee, he/*she* met an old friend from high school, Antonio, with his new girlfriend. "Hi [VICTIM], how are you doing?" asked Antonio. "I am doing great! I just found out that I am going to graduate in a few weeks!" said [VICTIM]. "Wow," said Antonio, congratulations! By the way, let me introduce you my girlfriend, Tiffany. "Oh hi Tiffany, how are you doing?" asked [VICTIM]. Tiffany replied, "Not very well, actually. I am very busy. I am graduating too, but in Physics, which, as you can imagine, is among the most difficult studies..."
3. [VICTIM] was taking a walk, when he ran into his/*her* former professor of Psychology. "So, [VICTIM], did you finally manage to get a job?" the professor asked. "Yes, I found a job as a shop assistant on Queen street west. I was so happy when they hired me," he/*she* said. "How is that going?" asked the professor. "Oh it's not bad," said [VICTIM], casually.
4. [VICTIM] was very happy because he/*she* had obtained a B- in his/*her* favorite subject. Since he/*she* had been taking lessons for only 2 years, he/*she* was proud of his/*her* grade. He/*She* immediately called his/*her* father to tell him about the great news. "Dad," he/she said, "You know what happened? The instructor finally gave us the grades for the projects!" His/*Her* father exclaimed: "Oh my God! Are you trying to say you got an A???" [VICTIM] replied: "Oh, no, just a B-, but I will do better next time."
5. [VICTIM] was standing by the cashier in a restaurant, waiting to pay. A guy, seated at a table near [VICTIM], accidentally spilt some coffee on the floor. "I'll get you another cup of coffee," said the waiter to the guy. After a while nobody had come to clean the spilt coffee, so the guy went up to [VICTIM] and said, "I spilt some coffee over by my table. Could you please mop it up?"
6. [VICTIM] had taken a computer course for adults. He/*She* had studied lots of mathematics at school, and he/*she* thought he/*she* was one of the best at the course. He/*she* would have loved to get the highest grade in the final evaluation. The day the grades were made available, he/*she* found out that he/*she* only got B, whereas another guy from the class got A-. He/*She*, therefore, decided to go ask the professor what he/*she* did wrong. As soon as the professor saw him/*her*, he said, "Congratulation [VICTIM]! It is such a great grade for you, eh? You must be very happy!"
7. [VICTIM] was sick and tired of his/*her* current job. He/*She* needed something more challenging. He/*She* decided to make a change to his/*her* life and ask for a promotion to his/*her* boss. He/*She* told his mother about this decision. His/*her* mother was a very adventurous woman and she would have understood. But instead she appeared strangely cold. "What do you think, mom?" [VICTIM] asked. She said: "I was just thinking... are you sure that afterwards your new assignments won't be too difficult for you? Nevermind, you still have some time to think about it..."
8. [VICTIM] At Fernhaven school, there was a writing competition. Everyone was invited to enter. [VICTIM] loved the story he/*she* had entered in the competition. A few days later, the results were announced: [VICTIM]'s story had not won anything and a classmate, Jake, had won the first prize. The following day, [VICTIM] was talking to Jake. Jake said, "It was so easy to win that contest. All of the other stories in the competition were boring." "Where are you going to put your trophy?" asked [VICTIM].
9. [VICTIM] had been hired in a Canadian company. One day, he/*she* presented his/*her* first project to 50 people, including his/*her* boss. The presentation was very interesting and well-done. After that, [VICTIM] got closer to his/*her* boss and asked him: "What do you think about it?" His/*Her* boss answered: "I think that you look very good with this tie/*shirt*. Is it new?"

Generic scenarios

1. [VICTIM] had just started with his/*her* new job on Bay Street. He/*She* decided to join his/*her* new colleagues for a dinner, in order to get to know them better. He/*She* was drinking a cocktail when a man/*woman* asked: "You're the guy/*girl* who's just transferred here, aren't you? My name is Bob/*Sally*, nice to meet you." Yes, replied [VICTIM], "Actually I started at this office last week." "Last week?! That's really weird! I thought you just arrived. Nobody has noticed you yet..." said Bob/*Sally*. "Oh, I see," said [VICTIM].
2. [VICTIM]'s sister was throwing a surprise party for his/her birthday. She invited Sarah, a friend of [VICTIM]'s, and said: "Don't tell anyone, especially [VICTIM]." The day before the party, [VICTIM] was over at Sarah's and Sarah spilled some coffee on a new dress that was hanging over her chair. "Oh no!" said Sarah, "I was going to wear this at your party!" "What party?" said [VICTIM]. "Come on," said Sarah, "Let's go see if we can get the stain out."
3. [VICTIM] and Jennifer were attending the same Math class at College. One day, they took a walk on the sea-front. "I love hip-hop music so much," said [VICTIM]. "On Saturday nights I can't wait to hang out with my friends to dance in clubs." Jennifer said: "Oh, that's very interesting. I like reading in my spare time, instead. These days I'm reading a book by Oliver Sacks." "Who? Sorry, I didn't hear you," said [VICTIM]. Jennifer answered: "Never mind, I don't think you know him."

4. [VICTIM], during a break at work, asked his/*her* colleagues to come closer to him/*her*. "I have something to tell you," he/*she* said. "John Morehouse, one of our accountants, is very sick with cancer and he's in the hospital." Everyone was quiet, absorbing the news, when Robert arrived late. "Hey, I heard this great joke last night!" Robert said. "What did the terminally ill patient say to his doctor?" [VICTIM] said: "Okay, let's get back to work."
5. [VICTIM] had just met an Italian colleague, Fabio/*Paola*, who had joined their work group. [VICTIM] wanted to invite Fabio/*Paola* for dinner to get to know him/*her* better. He/*She* asked Fabio/*Paola*: "Hey Fabio/*Paola*, why don't you come over for dinner some time, we just bought a pasta machine and you could help us figure how to use it!" Fabio/*Paola* answered: "Oh why not. . . but I guess you should be able to get it to work. Was there an instruction manual?"
6. [VICTIM] bought his/*her* friend, Anne, a crystal bowl for a wedding gift. Anne had a big wedding and there were a lot of presents to keep track of. About a year later, [VICTIM] was over at Anne's for dinner. [VICTIM] accidentally dropped a wine bottle on the crystal bowl and the bowl shattered. I'm really sorry. I've broken the bowl, said [VICTIM]. "Don't worry," said Anne. "I never liked it anyway. Someone gave it to me for my wedding."
7. It was 9 p.m. and [VICTIM] was still doing his/*her* homework, because he/*she* had been watching TV all day long. He/*She* wasn't that good in Math and he/*she* couldn't go on with his/*her* homework. So he/*she* thought that his/*her* best friend could help him/*her,* and decided to call him/*her*, hoping he/*she* wouldn't mind. "Hi, it's [VICTIM], am I disturbing you?" asked [VICTIM]. "No, I really love being interrupted while I am watching my favorite TV program. . ." his/*her* friend replied.
8. [VICTIM] had just moved into a new apartment. [VICTIM] went shopping and bought some new curtains for his/*her* bedroom. When he/*she* had just finished decorating the apartment, his/*her* best friend came over. [VICTIM] gave her a tour of the apartment and asked, "How do you like my bedroom?" "Great, but those curtains are horrible," his/*her* best friend said. "I hope you're going to get some new ones!"
9. [VICTIM] had just started with his/*her* new job. One day, in the coffee room, he/*she* was talking to a new colleague, Andrew. "What does your father do?" Andrew asked. "He's a lawyer," answered [VICTIM]. A few minutes later, Claire came into the coffee room looking irritated. I just had the worst phone call ever, she said "Lawyers are all so arrogant and greedy. I can't stand them." "Do you want to come look over these reports?" Andrew asked Claire. "Not now," she replied, "I need my coffee."
10. [VICTIM] had won a first class flight to Las Vegas. He/*She* was enjoying his/*her* comfortable flight, when he/*she* heard two hostesses chatting in a very low voice: "Yes, I tried that lipstick too! But I think that it's not as smudge-proof as they told in the advertisement on TV. After drinking, it gets the glass dirty," said one of them. "Really?" answered the other, "Mine works perfectly. I think that something is wrong with yours." "Excuse me," said [VICTIM], "Can I have a glass of lemonade, please?" "Sure. But, I'm afraid that you'll have to wait a little bit because we're all busy at this moment," answered one of the hostesses.

Neutral scenarios

1. [VICTIM] met his neighbor Peter/*Joan*, who was taking his dog Zack out to the park. Peter/*Joan* had just thrown a stick for Zack to chase. Peter/*Joan* and [VICTIM] chatted for a few minutes and, after a while, [VICTIM] asked: "Are you heading home? Would you like to walk together?" "Sure," Peter/*Joan* said. He called Zack, but he was busy chasing pigeons and didn't come. "It looks like he's not ready to go," he/*she* said. "I think we'll stay." "OK," [VICTIM] said. "I'll see you later."
2. [VICTIM] went to the barber for a haircut. "How would you like it cut?" the barber asked. "I'd like the same style as I have now, only take about an inch off," [VICTIM] replied. The barber cut it a little uneven in the front, so he had to cut it shorter to even it out. "I'm afraid it's a bit shorter than you asked for," said the barber. "Oh well," [VICTIM] said, "it'll grow out."
3. [VICTIM] had had a major role in last year's school play and he/*she* really wanted the lead role this year. He/*She* took acting classes all year, and in the spring he/*she* auditioned for the play. The day the decisions were posted, he/*she* went before class to check the list of who had made the play. He/She hadn't made the lead but was cast in a minor role. He ran into his/*her* best friend in the hall and told him what had happened. "I'm sorry," he said. "You must be disappointed." "Yes," [VICTIM] answered, "I have to decide whether to take this role."
4. [VICTIM] was shopping for a shirt to match his/*her* suit. The salesman showed him/*her* several shirts. [VICTIM] looked at them and finally found one that was the right color. But when he/*she* went to the dressing room and tried it on, it didn't fit. "I'm afraid it's too small," he/*she* said to the salesman. Not to worry, the salesman said. "We'll get some in next week in a larger size." "Great. I'll just come back then," [VICTIM] said.
5. [VICTIM] stopped off at the gas station on the way home to fill up his/*her* car. He/*She* gave the cashier his/*her* credit card. The cashier ran it through the machine at the counter. "I'm sorry," said the cashier, "the machine won't accept your card." Hmmm, that's funny, [VICTIM] said. "Well, I'll just pay in cash." [VICTIM] gave the cashier 20 dollars and said, "I filled up the tank with regular gasoline."
6. [VICTIM] bought a new car, a red Peugeot. A few weeks later, he/*she* backed it into his/*her* neighbor Ted's car, an old beat-up Volvo. His/*her* new car wasn't damaged at all and he/*she* didn't do much damage to Ted's car either: just a scratch in the paint above the wheel. Still, he/*she* went up and knocked on the door. When Ted answered, [VICTIM] said, "I'm really sorry. I've just put a small scratch on your car." Ted looked at it and said: "Don't worry. It was only an accident."
7. [VICTIM] was at the library. He/*She* found the book he/*she* wanted about hiking in the Grand Canyon and went up to the front counter to check it out. When he/*she* looked in his/*her* wallet, he/*she* discovered he/*she* had left his/*her* library card at home. "I'm sorry," [VICTIM] said to the woman behind the counter. I seem to have left my library card at home." "That's OK," she answered. "Tell me your name, and if we have you in the computer, you can check out the book just by showing me your driver's license."
8. [VICTIM] went to the butcher to buy some meat. It was crowded and noisy in the shop. He/*She* asked the butcher: "Do

you have any free-range chickens?" He nodded and started to wrap up a roasted chicken for him. "Excuse me," [VICTIM] said, "I must not have spoken clearly. I asked if you had any free-range chickens." "Oh, sorry," the butcher said, "we're all out of them."

9. [VICTIM] was at a party at his/*her* friend Oliver's house. He/*She* was talking to Oliver when a woman came up to them. She was one of Oliver's neighbors. The woman said hello to Oliver then turned to [VICTIM] and said, "I don't think we've met. I'm Maria, what's your name?" "I'm [VICTIM]." "Would anyone like something to drink?" Oliver asked.
10. [VICTIM] was waiting at the bus stop. The bus was late and an old lady had been standing there a long time. She looked very tired. When the bus finally came, it was crowded and there were not many seats left. [VICTIM] managed to get a seat. The old lady saw a neighbor, standing in the aisle of the bus. "Hello, Ma'am," he said. "Were you waiting there long?" "About 20 minutes," the old lady replied. [VICTIM] got up and said: "Ma'am, would you like my seat?"

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Intrinsic default mode network connectivity predicts spontaneous verbal descriptions of autobiographical memories during social processing

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Neural systems activated in a coordinated way during rest, known as the default mode network (DMN), also support autobiographical memory (AM) retrieval and social processing/mentalizing. However, little is known about how individual variability in reliance on personal memories during social processing relates to individual differences in DMN functioning during rest (intrinsic functional connectivity). Here we examined 18 participants' spontaneous descriptions of autobiographical memories during a 2 h, private, open-ended interview in which they reacted to a series of true stories about real people's social situations and responded to the prompt, "how does this person's story make you feel?" We classified these descriptions as either containing factual information ("semantic" AMs) or more elaborate descriptions of emotionally meaningful events ("episodic" AMs). We also collected resting state fMRI scans from the participants and related individual differences in frequency of described AMs to participants' intrinsic functional connectivity within regions of the DMN. We found that producing more descriptions of either memory type correlated with stronger intrinsic connectivity in the parahippocampal and middle temporal gyri. Additionally, episodic AM descriptions correlated with connectivity in the bilateral hippocampi and medial prefrontal cortex, and semantic memory descriptions correlated with connectivity in right inferior lateral parietal cortex. These findings suggest that in individuals who naturally invoke more memories during social processing, brain regions involved in memory retrieval and self/social processing are more strongly coupled to the DMN during rest.

Keywords: autobiographical memory, default mode network, intrinsic connectivity, social emotion, admiration, compassion

INTRODUCTION

It is thought that people use their own memories to evaluate and relate to other people's social situations. Memories for personal experiences and self-relevant facts, known respectively as episodic and semantic autobiographical memories (AMs; Conway, 1992), often serve as bases from which to build mental models of others' experiences, in order to more effectively appreciate others' perspectives and emotional feelings (Robinson and Swanson, 1990; Ravenscroft, 1998; Frith and Frith, 2006).

Interestingly, converging evidence from neuroimaging studies reveals that many of the same neural systems that support autobiographical processing also support social processing (Svoboda et al., 2006; Schilbach et al., 2008; Mars et al., 2012; Spreng and Mar, 2012). For example, systems that support episodic autobiographical memory (Maguire, 2001) and semantic autobiographical processing, such as judgments of self-relevant traits (Kelley et al., 2002; Heatherton, 2011) and recollections of familiar, repeated experiences (Levine et al., 2004), are also involved in attributing mental states to others (Saxe and Kanwisher, 2003; Lieberman, 2007) and in feeling emotions about others' social situations (Immordino-Yang et al., 2009; Immordino-Yang and Singh, 2011; Bruneau et al., 2012). These distributed brain systems constitute the default mode network (DMN), a functionally interconnected set of regions most consistently activated during passive rest and deactivated during tasks requiring externally focused attention (Raichle and Snyder, 2007). These regions together are thought to support the self-referential and reflective processes that are common across memory-related and social processing tasks (Buckner and Carroll, 2007; Spreng et al., 2009; Spreng and Grady, 2010; Immordino-Yang et al., 2012).

Recently, interest has grown in understanding how individual differences in the functional integrity of the DMN at rest may relate to individuals' cognitive and emotional profiles. The distributed regions of the DMN exhibit characteristic, coherent patterns of low frequency BOLD fluctuation during awake and non-attentive task-free states (Fox et al., 2005). These intrinsic connectivity patterns are thought to reflect a fundamental property of the brain's functional organization and have been linked with structural (anatomical) neural connectivity (Greicius et al., 2009; Honey et al., 2009). These patterns also show considerable variability across individuals and research is beginning to link this variability to task-specific neural activation/deactivation patterns (Mennes et al., 2010), and to behavioral measures of general traits, such as intelligence (Song et al., 2009), and memory ability (Wang et al., 2010). Individual differences in DMN resting state connectivity have also been associated with socio-emotional and psychological symptoms in patients with mental disorders, including depression (Greicius et al., 2007), schizophrenia (Whitfield-Gabrieli et al., 2009), autism (Assaf et al., 2010), ADHD (Uddin et al., 2008), and others. However, relations between intrinsic DMN connectivity and natural social behavior in healthy participants have not been investigated.

Given that DMN regions are known to be centrally involved in social emotional and self-relevant processing as well as in autobiographical memory, here we investigate relations between DMN intrinsic functional connectivity and individual differences in spontaneous descriptions of autobiographical memories during a natural-feeling, open-ended social emotional interview in which experiment participants describe their feelings in relation to a set of true social stories. Of note, in relation to each story presented, participants were asked to discuss their reactions in an open-ended way, but were *not* specifically asked to describe personal memories and the experimenter did not probe for memories. In this way, the autobiographical memories spontaneously described by participants during the 2 h interview are likely to reflect participants' natural inclinations to call up memories for personal experiences in the context of social processing about unknown others' situations.

In analyzing the memories spontaneously described by participants, we examined both episodic and semantic autobiographical memories. Both types of memories are self-relevant and acquired through life experiences. However, these memory types differ in their content and in their associated qualities of recollective experience (Brewer, 1986; Conway, 1992). Episodic autobiographical memories are memories for specific events in one's past, and can be recalled with rich perceptual and emotional detail. Retrievals of such memories are often accompanied by a sense of reminiscence and can sometimes trigger strong emotional responses. For an example from our study, in describing how he felt after hearing a story about a young mother with cancer, one participant said, "...and I remembered how I felt when my mom got breast cancer..." and then went on to describe the details of his emotional experience.

By contrast, semantic autobiographical memories involve concepts and knowledge about one's self that are distilled from past experiences, and recalled independent of recalling any specific past event. Such memories are generally retrieved more quickly than episodic memories (Addis et al., 2004a) and in an emotionally neutral way. For instance, in reaction to a story about a man who dislocated his elbow during a weight-lifting competition, one participant in our study said, "I have never dislocated an elbow, but I've lifted weights."

Retrieval of episodic and semantic autobiographical memories is largely supported by overlapping systems that are also part of the DMN, including the hippocampi, parahippocampal gyri, medial prefrontal cortices, temporo-parietal and lateral temporal regions, and posteromedial cortices (an ensemble of cortices that includes portions of the posterior cingulate and precuneus; see Maguire, 2001; Svoboda et al., 2006; Cabeza and St. Jacques, 2007; for reviews). However, differential contributions of DMN regions to these two types of memory have also been found. Specifically, episodic autobiographical memory retrieval has been found to more heavily recruit the hippocampus, medial prefrontal, and posteromedial cortices when directly contrasted with retrieval of semantic autobiographical memories (Maguire and Mummery, 1999; Maguire and Frith, 2003; Levine et al., 2004), and the relative recruitment of these regions is thought to relate to the vividness, emotional poignancy, and self-significance of the memory (Maguire and Mummery, 1999; Piefke et al., 2003; Addis et al., 2004b; Gilboa et al., 2004; Oddo et al., 2010; see also Svoboda et al., 2006; Cabeza and St. Jacques, 2007).

In this study, we had two overarching aims: (1) to demonstrate variability across individuals in the proclivity toward describing autobiographical memories during social processing; (2) to relate this variability to individual differences in DMN regions' intrinsic functional connectivity during rest.

MATERIALS AND METHODS

PARTICIPANTS

Eighteen right-handed native English-speaking volunteers (10 females; mean age 21.2 years, SD 2.8 years; range 18–27 years), with no history of neurological or psychiatric illness, participated in the study. Participants were students or staff at a large private university on the U.S. west coast. All participants gave written consent and were compensated for taking part in the experiment. One participant identified as Latino-American, nine as Caucasian-American, six as Asian-American, and two as African-American. Data were collected as part of a larger study on neurobiological correlates of social emotions.

PROCEDURES

Social processing interview

Participants took part in a 2 h, one-on-one private video-taped interview session conducted by the same female interviewer (MHI-Y) in a quiet, dedicated room at the University of Southern California (following the method described in Immordino-Yang et al., 2009; note that the current dataset is new).

During the interview, the experimenter presented 50 narratives about true experiences of non-famous people (not actors or celebrities), some of which were meant to induce strong social emotional reactions in participants, and some of which were less emotionally evocative. The narratives unfolded like mini-documentaries, and were comprised of a scripted verbal description of 50 unique protagonists' stories recounted (live) by the experimenter, supplemented by video and audio clips of the protagonist shown on a laptop. The narratives fell into five categories, with 10 stimuli in each: (1) Narratives involving demonstrations of marked self-sacrifice and dedication to helping others, meant to elicit admiration for virtue; (2) Narratives involving demonstrations of exceptional talents in athletics, the arts, or other domains, meant to elicit admiration for skill; (3) Narratives involving situations of bereavement, social rejection, and other forms of psychological pain, meant to elicit compassion for social pain; (4) Narratives depicting accidental bodily injuries, e.g., sports accidents, meant to elicit compassion for physical pain; and (5) Narratives involving comparable living, mentally competent people engaged in or discussing how they felt about typical activities under commonplace social circumstances. Narratives in this category were piloted to be equally interesting but relatively less emotionally evocative.

Narratives in the different categories were equivalently complex and of similar length. The corpus of narratives had been extensively piloted for emotional evocativeness, interest, cultural relevance, and other dimensions; see Immordino-Yang et al., 2009 and Immordino-Yang and Singh, 2011 for details.

The narratives were presented to each participant in one of two pseudo-random orders that counterbalanced one-back presentation history, with no more than two narratives from the same category presented in a row. After each narrative presentation, participants were asked the open-ended question, "How does this person's story make you feel?" and were given time to answer openly. Participants were not told the emotion categories represented in the narratives, and were encouraged to talk freely and honestly about their reactions and thoughts in relation to each story. (Participants almost universally reported in a post-experiment debriefing interview that they felt comfortable and genuinely engaged during the interview, and all participants reported feeling emotional during the experiment; see Saxbe et al., 2012). Participants were not prompted for personal memories or any other information beyond the initial question.

Transcript coding

Videotaped interview sessions were transcribed by native American English speakers, and transcriptions were independently verified. Verified interview transcripts were edited to remove the experimenter's speech and transcription notes, so that only participants' responses remained for coding. Independent coders who were blind to the hypotheses judged participants' responses to each narrative for the presence (score of 1) or absence (score of 0) of references to episodic or semantic autobiographical memories.

Episodic autobiographical memories. Descriptions of episodic AMs were defined as any reference to a specific event from one's past, and the perceptual or emotional details associated with this event.

Examples:

"...this makes me especially sad just because I'm [also] gay and I'm looking for a roommate right now..."

"So I just thought of a friend of mine who committed suicide. No one had any idea because he was just incredibly successful and talented and I just wondered if he thought that... people were gonna be better off without him."

Semantic autobiographical memories. Descriptions of semantic AMs were defined as any reference to autobiographical concepts or self-relevant factual knowledge that was not associated any specific event and did not contain perceptual or emotional details.

Examples:

"My family is Italian and I bake bread for a hobby myself."

"I used to do that [skateboarding] when I was a little kid but I never had anything [any injury] like that."

To establish coding reliability, three raters first worked together to code six transcripts from participants who were part of an earlier study, whose data were not included in this study. After this initial training period, the three raters independently coded transcripts from six participants included in this study (Fleiss' kappa = 0.75); discrepancies were resolved by three-way discussion. The remaining 12 transcripts were independently coded by one rater; 20% of those data were randomly selected for blind verification by a second rater (Cohen's kappa = 0.97). Because inter-rater reliability was very high for these transcripts, analyses were performed on the original rater's codes.

Because the focus of the current study was individuals' trait-level differences in reliance on these two types of memories, participants' responses to narratives from the five narrative types were combined. For each participant, we calculated the number of narrative responses (out of 50) in which at least one memory was reported. Frequencies were calculated separately for episodic and semantic autobiographical memories.

Functional neuroimaging data acquisition and preprocessing

Approximately 50 min after the interview ended, participants underwent a 5 min resting state MRI scan, during which they were asked to "relax and rest as we take pictures of your brain." (The data for this study were acquired as part of a larger functional study on social emotions. The resting state scan analyzed here was acquired after we acquired two 9-min functional runs in which participants viewed again the narratives they had discussed during the interview. There was a 30 min lapse between the end of the interview and the start of scanning.). Whole brain images were acquired using a Siemens 3 Tesla MAGNETON TIM Trio scanner with a 12-channel matrix head coil. Resting state scans were acquired using a T2∗ weighted Echo Planar (EPI) sequence (TR = 1.5 s, TE = 30 ms, flip angle = 90°) with a voxel resolution of 3 mm × 3 mm × 4.5 mm. Thirty-two continuous transverse slices were continuously acquired to cover the whole brain. Anatomical images were acquired using a magnetization prepared rapid acquisition gradient (MPRAGE) sequence (TI = 900 ms, TR = 1950 ms, TE = 2.26 ms, flip angle = 7°) with an isotropic voxel resolution of 1 mm.

Data were preprocessed using SPM8 (Wellcome Department of Cognitive Neurology, London, UK) in MATLAB 2011b (MathWorks, Inc.). Functional images were slice-timing corrected, motion corrected, and co-registered to the anatomical image. Anatomical images were segmented and normalized to MNI space (Montreal Neurological Institute) using tissue probabilistic maps (segmentation, SPM8). The same normalization transformation was applied to the functional images, which were then resampled into a resolution of 2 mm × 2 mm × 2 mm and smoothed using a 4 mm full-width, half-maximum Gaussian kernel.

Identifying the default mode network for each participant

The DMN was separately identified for each individual using spatial independent component analysis (ICA) carried out via the

Infomax algorithm (Bell and Sejnowski, 1995) from the GIFT toolbox[1]. This software separates each participant's fMRI data into independent (uncorrelated, non-Gaussian) spatial components and their corresponding time courses (McKeown et al., 1998). We allowed the software to estimate the optimal number of components (using minimum description length criteria; Li et al., 2007), which ranged across participants from 15 to 25.

A two-stage procedure was performed to identify the component for each participant that best corresponded to the DMN. First, we excluded components whose high frequency power (>0.1 Hz) constituted more than 50% of the total power of the component. Then, a spatial correlation was performed between each of the remaining components and a binary DMN template (mask) provided in the GIFT toolbox. (This template covers regions previously reported to be part of the DMN, e.g., Raichle et al., 2001; Buckner et al., 2008). The component that was most strongly correlated with the template was chosen as the DMN component. Visual inspection confirmed that the identified component for each participant did include the brain regions associated with the DMN. (Note that this method effectively removes from the analysis components corresponding to global signal and noise, making it unnecessary to implement band-pass filtering or to regress out global signal; see De Luca et al., 2006; Seeley et al., 2007. In addition, the connectivity of each voxel to the overall network was not affected by application of the mask or by the selection process.)

We performed spatial normalization on the component map identified as corresponding to the DMN, in essence adjusting the overall strength of each participant's DMN component in order to perform a group-level analysis. This procedure transformed each voxel's value to a z-score that represents the degree to which the voxel's time course is modulated by the time course of the participant's overall DMN component (McKeown et al., 1998). **Figure 1** depicts the conjunction of the 18 participants' DMN component maps.

We implemented the ICA method rather than a seed-based analysis for two reasons. First, recent analyses comparing seed-based and ICA calculations of functional connectivity show that connectivity strength obtained using seed-based calculations is equivalent to the sum of within-network ICA-derived connectivity and between-network ICA-derived connectivity for a given region (Joel et al., 2011). We were interested in isolating connectivity associated only with the DMN. Second, a seed-based analysis would require that we choose *a priori* regions of interest, which would bias the results depending on the precise size and location of the ROI.

Correlating memory scores with DMN intrinsic connectivity

We separately regressed on the z-score maps participants' scores for frequency of episodic and of semantic AM descriptions. We then anatomically masked the whole-brain results to increase statistical power by reducing multiple comparisons. The mask was pre-defined using the Automated Anatomical Labeling Atlas (Tzourio-Mazoyer et al., 2002) to include precuneus, posterior cingulate cortices, medial prefrontal cortices, inferior parietal lobules, angular gyri, middle temporal gyri, temporal poles, hippocampi, parahippocampal gyri, and fusiform gyri; see **Figure 2**.

We imposed on the group-level results a statistical threshold of $p < 0.005$ and a cluster extent threshold of 23 voxels, which corresponds to $p < 0.05$ controlling for multiple comparisons. The cluster extent threshold was determined by 10,000 Monte Carlo simulation iterations conducted using the AlphaSim program in AFNI[2]. The criteria input to AlphaSim were: uncorrected p-value of 0.005, voxel size of $2 \times 2 \times 2$, spatial smoothing kernel of 4 mm, and the number of voxels in the mask (48420 voxels).

Using bootstrapping to validate the robustness of the results

For each cluster that survived thresholding, z-scores from included voxels were extracted and averaged for each participant using the MarsBar toolbox in SPM (Brett et al., 2002). The averaged z-score

[1]http://mialab.mrn.org/software/#gica

[2]http://afni.nimh.nih.gov/afni/

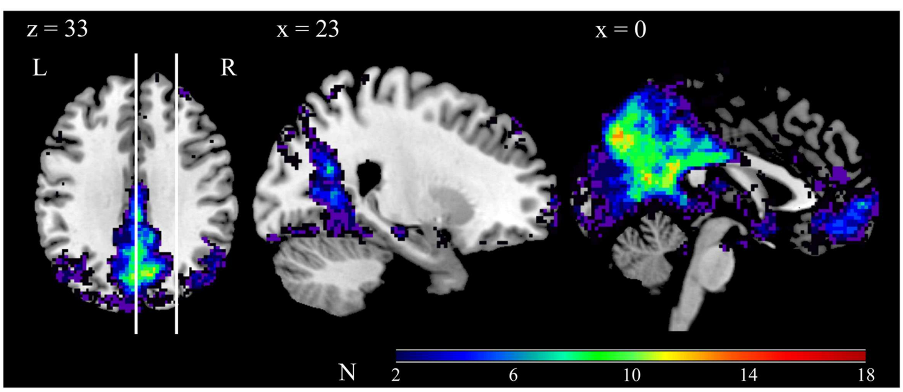

FIGURE 1 | Conjunction of the 18 participants' DMN component maps. Each participant's DMN component map was thresholded at z-score ≥ 2, and then converted into a binary map (1 for above threshold, 0 for below threshold). Color codes indicate the degree of overlap, as per the scale depicted in the bar. The vertical lines in the left panel indicate the position of the sagittal slices. Note that the views depicted are taken from the same slice position as the views depicted in **Figure 2**.

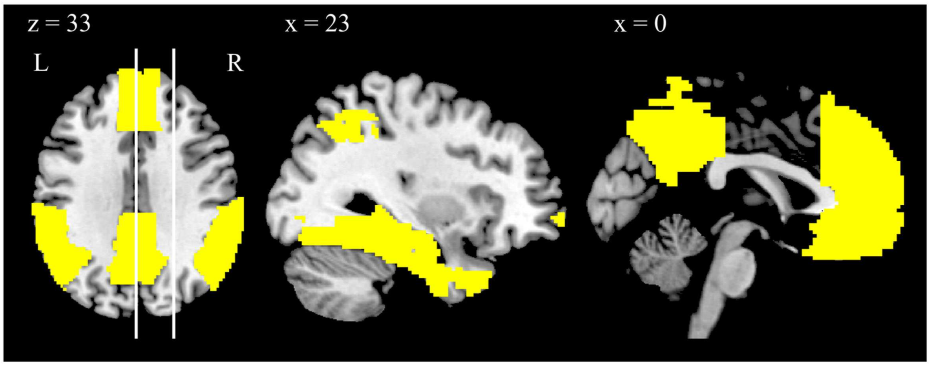

FIGURE 2 | Depiction of the anatomically defined DMN mask, displayed on a template brain. The vertical lines in the left panel indicate the position of the sagittal slices. Note that the views depicted are taken from the same slice position as the views depicted in **Figure 1**.

and corresponding memory frequency score from each participant were paired. These pairs were randomly resampled with replacement to generate 10,000 bootstrapped samples of 18 pairs of values each, corresponding to the number of participants in the experiment. A correlation coefficient for each bootstrapped sample was calculated, and from the distribution of coefficients a 99% confidence interval was derived (Matlab version 2011b; MathWorks, Inc; see Yarkoni, 2009). For none of the identified clusters did the 99% confidence interval cross zero; hence all are reported as results.

RESULTS

BEHAVIORAL RESULTS

All participants spontaneously reported semantic AMs to at least one narrative out of 50 ($M = 6.6$, Range: 2–16, $SD = 3.3$); 14 participants (77.8%) reported episodic AMs to at least one narrative ($M = 2.5$, Range: 0–8, $SD = 2.4$). Frequency of episodic and semantic AMs were uncorrelated [$r(16) = 0.11$, $p = 0.67$]. There were no effects of gender or age (lowest $p > 0.17$). Participants' responses averaged 77 words ($SD = 27$; individuals' averages ranged from 29 to 121 words).

CORRELATIONS BETWEEN AM FREQUENCIES AND INTRINSIC DMN CONNECTIVITY

Higher frequencies of episodic and semantic AMs were linked to higher DMN intrinsic functional connectivity in middle temporal and parahippocampal gyri. Frequency of episodic AMs was additionally related to connectivity in the hippocampi bilaterally, and to connectivity in the dorsal, anterior, and ventral sectors of the medial prefrontal cortex. Frequency of semantic AMs correlated with connectivity in the right inferior parietal lobule. Neither memory type was correlated with connectivity in the posteromedial cortices (medial parietal or posterior cingulate cortices). See also **Table 1** and **Figure 3**.

Table 1 | Voxel clusters whose intrinsic connectivity correlates with frequency of reported episodic (A) and semantic (B) autobiographical memories.

Brain region	Coordinates			Cluster size	*z*-Score	99% CI of rho
	x	*y*	*z*			
A. EPISODIC AM						
dMPFC	−10	40	50	55**	4.36	[0.52, 0.97]
aMPFC	10	66	10	337**	3.76	[0.21, 0.96]
vMPFC	14	44	−8	86**	3.68	[0.26, 0.96]
MTG	−64	−6	−8	24	3.82	[0.30, 0.98]
	−60	−14	−20	28	3.20	[0.17, 0.94]
	64	−8	−26	58**	4.32	[0.04, 0.95]
PHG/Hippocampus	−30	−22	−20	24	3.85	[0.24, 0.97]
PHG	36	−34	−18	52**	3.68	[0.35, 0.98]
Hippocampus	20	−10	−20	56**	3.65	[0.42, 0.96]
B. SEMANTIC AM						
pIPL	48	−70	36	57**	3.85	[0.13, 0.99]
MTG	−64	−26	−8	69**	3.34	[0.37, 0.97]
	58	10	−26	23	3.49	[0.10, 0.97]
PHG	26	−36	−10	79**	3.46	[0.33, 0.99]

*dMPFC, dorsal medial prefrontal cortex; aMPFC, anterior medial prefrontal cortex; vMPFC, ventral medial prefrontal cortex; MTG, middle temporal gyrus; PHG, parahippocampal gyrus; pIPL, posterior inferior parietal lobule. Coordinates of the peak voxel are given in MNI space. Clusters are significant at $p < 0.05$, corrected for multiple comparisons; those significant at $p < 0.001$ are marked**. Corresponding 99% confidence intervals are given (CI of rho) and do not cross zero.*

DISCUSSION

Autobiographical memories play an important role in our social lives by allowing us to cognitively and emotionally relate to others' situations based on simulations we build from our own memories for similar experiences and feelings. Autobiographical memories and social processing are supported by a largely shared set of neural systems (Lieberman, 2007; Buckner et al., 2008; Spreng et al., 2009), whose activity is most reliably heightened and shows functional coordination during passive rest (the DMN; Raichle and Snyder, 2007). Although there is strong interest in probing the psychological correlates of interpersonal variability in these regions' coupling during rest, relations to individual differences in natural social

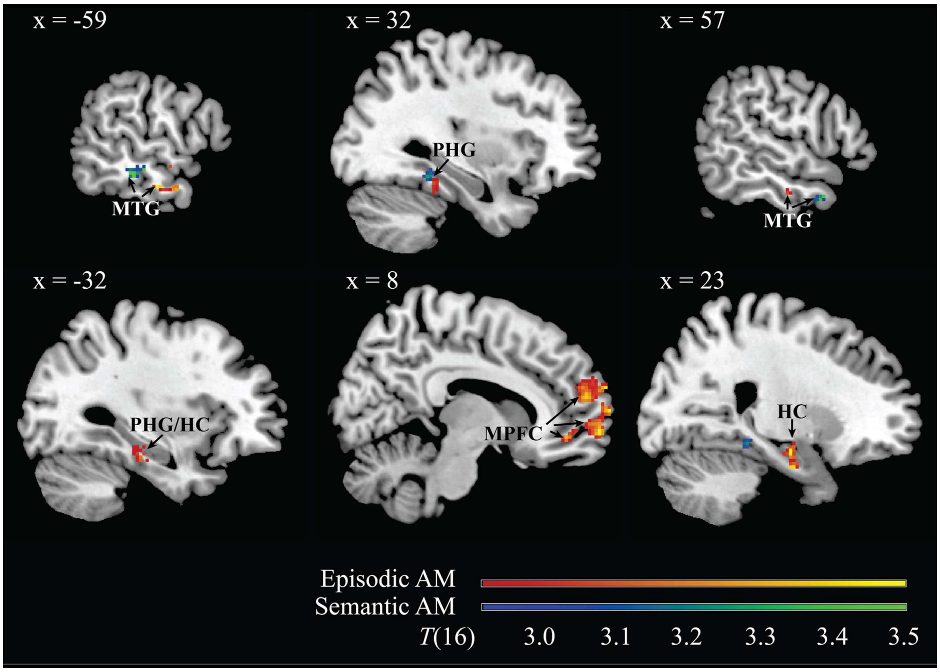

FIGURE 3 | Representative images of neural regions from within the DMN whose intrinsic functional connectivity to the overall DMN component correlated with individual differences in frequency of spontaneous verbal descriptions of episodic (red → yellow) and semantic (blue → green) autobiographical memories during the social processing interview. Results are thresholded at $p < 0.05$, corrected for multiple comparisons. The 99% confidence interval for all depicted clusters does not cross zero. MNI coordinate of the sagittal plane is given. Note: MTG, middle temporal gyrus; PHG, parahippocampal gyrus; MPFC, medial prefrontal cortex; HC, hippocampus.

behavior have not been studied. Here we provide data supporting a relationship between intrinsic connectivity in regions of the DMN known to especially support memory processing (Maguire, 2001; Svoboda et al., 2006; Cabeza and St. Jacques, 2007), self-related processing (Heatherton, 2011), and simulation of hypothetical and future scenarios (Gilbert and Wilson, 2007), and individuals' tendencies to spontaneously describe autobiographical memories as they react to unknown others' social situations in an open-ended interview. The results provide modest evidence that correspondences exist between natural social behavior and resting brain function.

Critical to our study design is the natural feel of the interview, and the fact that we did not probe for memories or prompt participants to describe personal experiences. We made this methodological decision to maximize the chances that our findings would reflect participants' natural behavioral inclinations, and would relate to individual differences in social behavior outside of the lab. Indeed, over the course of the interview all participants reported feeling genuinely emotional, and outside researchers who have viewed the videotaped interviews in the context of other analyses have been struck by participants' comfort and openness, and by their genuine reflectiveness and engagement with the narratives (S. Schnall, personal communication, June 2012), many of which recount quite extraordinary circumstances and accomplishments.

Every participant spontaneously reported at least one AM during the 2 h interview. However, there was a considerable amount of variability in the frequency with which participants described these memories, and descriptions of episodic memories were comparatively rare. Frequencies of semantic and episodic autobiographical memory descriptions were uncorrelated, and we found that these types of AM were associated with connectivity in some shared and some distinct DMN regions. Both types of AMs were associated with connectivity in middle temporal regions, which are critically involved in semantic processing, and important in the storage and retrieval of personal knowledge about the world (Martin and Chao, 2001; Binder et al., 2009). Both were also associated with connectivity in the parahippocampal gyrus. However, only episodic AMs were related to connectivity in the hippocampus, perhaps due to this structure's role in more complex scene reconstruction (Hassabis and Maguire, 2007, 2009), and to its increased involvement in processing of memories with greater personal significance and vividness (Addis et al., 2004b; Gilboa et al., 2004; Moscovitch et al., 2005).

In addition to finding correlations between memory descriptions in the interview and connectivity in canonical memory-related regions in the brain, i.e., the hippocampus and parahippocampal gyrus, our most prominent, extensive results are in the medial prefrontal cortex. Descriptions of episodic autobiographical memories were strongly associated with connectivity in the dorsal, anterior, and ventral MPFC sectors. This region is especially involved in self-referential processing (Heatherton, 2011) and in mentalizing (Frith and Frith, 2006), and its involvement in functional studies has been shown to differentiate episodic autobiographical memories from other laboratory memory tasks without personal relevance (e.g., remembering a list of objects; Gilboa, 2004). More recently, activity in this region has been shown to be load-dependent during tasks involving working memory for social information (Meyer et al., 2012). In another experiment, MPFC activity as participants' viewed entertaining video clips (TV pilots) predicted participants' subsequent recall of the videos' details when attempting to persuade another person of the videos' entertainment value (Falk et al., in press). Analyses of the dynamic interactions between the MPFC and the medial temporal lobe system during experimentally induced episodic autobiographical recall reveal that activation in MPFC initiates and maintains activation in the medial temporal lobe (St. Jacques et al., 2011). These findings together suggest that the MPFC has an important role in strategically encoding and recalling memories with a social purpose. Our findings accord well with this interpretation, and extend previous work by demonstrating that resting connectivity in MPFC is related to the prominence of episodic memories in participants' social processing.

Notably, we did not have significant results in the posterior cingulate or precuneus, both regions with important roles in AM retrieval (Wagner et al., 2005; Svoboda et al., 2006). It has been shown that during episodic autobiographical recall, MPFC and hippocampus were more active during the initial search and construction of the memory, whereas precuneus was more active during the elaboration phase, after the memory was successfully accessed (Cabeza and St. Jacques, 2007; Daselaar et al., 2008). It is possible that because our coding system identified the initiation of memories but did not code for the memories' elaboration or vividness of imagery, that we did not pick up on individual variability in these dimensions that might have corresponded to medial parietal connectivity strength at rest. In a related study in progress, we find that participants who engage higher level cognitive construals of social situations, in effect more abstract, elaborated conceptualizations (Liberman and Trope, 2008), show stronger activation in posteromedial cortices during subsequent social emotion processing (Pavarini et al., under review). Future studies could investigate possible relations between individuals' tendencies to recall autobiographical memories more vividly and elaborately, and intrinsic connectivity of posterior medial nodes of the DMN.

Our findings do seem to be specific to the DMN component of intrinsic connectivity, and are not explainable by differences in the strength of emotion participants reported experiencing in relation to our narrative stimuli. To test the specificity of the results to the component identified as the DMN, we identified the component corresponding to the salience network (anchored by orbital frontoinsular cortices and dorsal anterior cingulate, extending into ventral tegmental area; Seeley et al., 2007; Menon and Uddin, 2010) and repeated the analysis. We found no relationships between AM scores and strength of salience network connectivity in the regions in which we report DMN findings. (That analysis did reveal that a region in the superior-most portion of the precuneus showed correlation between semantic AM score and connectivity to the salience network.)

To test the relation between AM score and participants' reported strength of experienced emotion, we utilized participants' reports of the strength of their experienced emotion during the scanning experiment (i.e., during the functional runs that preceded the resting state scan). During the functional runs, participants viewed short versions of the video narratives they had discussed during the interview, and reported for each narrative the strength of their real-time reaction from 1 (no strong reaction) to 4 (overwhelmingly strong reaction). We correlated participants' average reported strength of emotion with their total AM score, and found no relationship ($p = 0.42$).

Although our study, in addition to several others, have now reported correlations between individuals' resting state connectivity and psychological traits, it is unclear at this stage how these differences should be interpreted. Our behavioral (interview) study shows a trait-level effect (tendency to spontaneously describe AMs) that is expressed in the context of a particular state (social processing). But in the neural data, trait-level and state-level effects cannot be disentangled (and may, in fact, be co-dependent). It is possible that the relations to resting DMN connectivity revealed in our study reflect differences in the resting properties of the brain that are invariant within a person. It is also possible that they may reflect either residual influences of the prior social processing task ("state" residue), or differences in the quality of thoughts individuals spontaneously engage during rest. (That is, for our study, it is possible that people who described more memories in the interview also reminisced more during the resting state scan; revealing a mind-level "trait."). Given that individuals better at remembering past experiences also show greater intrinsic DMN connectivity (Wang et al., 2010), and given our finding that greater production of descriptions of episodic memories during social processing is related to greater connectivity at rest in neural regions supporting memory and self-relevant processing, future studies should investigate DMN intrinsic connectivity in different experimental contexts, and relations to individual differences in content of resting thought, as well as relations to social skillfulness.

Although the present analysis investigated trait-level differences among participants across emotion states, we note that the five narrative conditions did not produce equivalent descriptions of memories. Instead, although AMs were described in response to all five narrative types, disproportionately more (33%) AMs were described in response to the narratives that involved relatively commonplace, less emotionally potent social circumstances. This finding suggests that participants may have called up personal memories more often in response to stories that described situations they (arguably) would have been more likely to have personally experienced.

We also note that the quality of autobiographical memories participants recounted was aligned with an important dimension of the narrative protagonists' situation. Our narratives had been designed to engage processing about concrete, physical circumstances separately from processing about abstract, inferred aspects of the protagonists' psychological situation. That is, feeling compassion for another's physical pain or admiration for another's skill relies on straightforward perceptions of bodily actions whose emotional consequences are immediately apparent. (For example, one needs only to see the narrative protagonists' leg break to appreciate that he is experiencing noxious physical pain). By contrast, feeling compassion for social pain or admiration for virtue requires making complex inferences about the protagonists' hidden qualities of mind that may not be apparent from outward, observable behavior (Immordino-Yang, 2010, 2011). Interestingly, we find in the current analysis that participants recounted more semantic AMs when responding to narratives about protagonists' physical actions or abilities (i.e., narratives meant to induce compassion for physical pain or admiration for skill; $t = 4.6$, $p < 0.001$), and trended toward producing more episodic AMs when responding to narratives about protagonists' mental qualities, predicaments, or accomplishments (i.e., narratives meant to induce compassion for social pain or admiration for virtue; $t = -1.72$, $p = 0.10$). There were no differences in the number of AMs described in response to compassion-inducing narratives as compared to admiration-inducing narratives (approximately 33% of total memories in each case). In relation to research on experimentally induced recall of AM via interviews (e.g., Maguire and Mummery, 1999; Levine et al., 2002) or responses to word prompts (e.g., Bayley et al., 2003), this finding suggests that differences in the framing of social contexts (i.e., concrete, action-oriented versus abstract, psychologically oriented) may be an important factor shifting participants' memories between semantic and episodic varieties.

Our study demonstrates the viability of relating natural behavior during social processing to individual differences in resting brain function, and suggests a promising future avenue for research on the neural correlates of psychological traits (see also Saxbe et al., 2012). However, our attempt to attain real-world validity also comes at a cost: participants' verbal reports of memories may only be a subset of the memories that actually occurred to them. Reports of personal memories were relatively rare in our study. However, we believe that the number of memories participants reported would be in proportion to the total memories that occurred to them, and therefore that these numbers would reflect real individual differences in reliance on memories during social processing. As we develop a better understanding of individual differences in the contribution of memories to social processing, future research could control for the possibility that some people may be more inclined to verbally report their memories while others keep them private. Nonetheless, our findings corroborate the idea that AM is involved in social cognition during natural behavior, and extend the current literature by demonstrating that individual differences in reliance on memory processing are related to the intrinsic organization of the DMN.

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Memory as social glue: close interpersonal relationships in amnesic patients

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Memory may be crucial for establishing and/or maintaining social bonds. Using the National Social life, Health, and Aging Project questionnaire, we examined close interpersonal relationships in three amnesic people: K.C. and D.A. (who are adult-onset cases) and H.C. (who has developmental amnesia). All three patients were less involved than demographically matched controls with neighbors and religious and community groups. A higher-than-normal percentage of the adult-onset (K.C. and D.A.) cases' close relationships were with family members, and they had made few new close friends in the decades since the onset of their amnesia. On the other hand, the patient with developmental amnesia (H.C.) had forged a couple of close relationships, including one with her fiancé. Social networks appear to be winnowed, but not obliterated, by amnesia. The obvious explanation for the patients' reduced social functioning stems from their memory impairment, but we discuss other potentially important factors for future study.

Keywords: amnesia, memory, hippocampus, medial temporal lobe, friendship, social networks

INTRODUCTION

What is memory for? Episodic memory enables one to capture the precise details of an experience, and then to recollect this information rapidly whenever and wherever needed. Typical examples of its evolutionary value focus on the individual navigating the world, but the advantages conferred by episodic memory may be more far-reaching than often appreciated. For example, interactions with other people are important for our survival and wellbeing (Eisenberger and Cole, 2012). Might episodic memory be crucial for establishing and/or maintaining interpersonal relationships?

To address this question, we examined social relationships in three amnesic patients. In such patients, damage to medial temporal, diencephalic, and/or basal forebrain structures yields a profound and relatively specific impairment in episodic memory, with other faculties (i.e., sensory-perceptual, cognitive, and motor) remaining essentially intact (for recent reviews, see Squire and Wixted, 2011; Rosenbaum et al., 2012). On the one hand, many of the psychological functions necessary for interpersonal relationships are preserved in amnesia. For example, amnesic patients usually are able to hold a simple conversation, as long as they are not distracted. Their semantic knowledge about the basic rules of social interaction and friendship is intact; many retain exemplary social graces (Corkin, 1984; Rosenbaum et al., 2005). Many also retain considerable semantic knowledge about their family members and friends from their pre-morbid lives. Amnesic patients are even capable of learning whether new people are associated with positive versus negative outcomes (e.g., Tranel and Damasio, 1993; Claparède, 1995; Turnbull and Evans, 2006), and often seem to grow more comfortable with people and objects following repeated exposure to them (Johnson et al., 1985). Their ability to infer other people's thoughts, feelings, and intentions is normal, at least under many circumstances (Rabin et al., in press; Rosenbaum et al., 2007).

On the other hand, several psychological functions that would appear to be crucial for social bonding are impaired in amnesic patients. The most obvious is episodic memory itself: the ability to consciously recollect experiences (including the often arbitrary associations among their elements, such as people, names, places, times, and things) and to use these memories flexibly and update them when necessary (Rosenbaum et al., 2012). Thus, amnesic patients often fail to learn who new people are, even after hundreds of encounters. Even when they can accrue bits of information, they may be unable to bind these together into coherent entities, instead retrieving only fragments of previous events. In addition, difficulty updating their memories means that even when they *can* remember something about old friends' and family members' lives, they may fail to keep track of changes and consequently commit social faux pas errors (e.g., Patient: *How's your father?* Friend: *Remember – He died last year*; Klein et al., 2009). Amnesic patients' inability to discuss current events (even momentous ones; Davidson et al., 2005; Ogden, 2005; Rosenbaum et al., 2005) and to share warm reminiscences with others may hamper social bonding (Alea and Bluck, 2003). Episodic memory (and the medial temporal lobe memory system) also appears to support other potentially important abilities, including aspects of discourse (Duff and Brown-Schmidt, 2012), thinking about one's future to help plan social interactions (Rosenbaum et al., 2005; Hassabis et al., 2007; Squire et al., 2010), empathy (Ciaramelli et al., submitted), and social problem-solving (Sheldon et al., 2011). For these reasons, amnesic patients have been described as ending up "interactionally marooned"[1] (Ogden, 2005; Duff et al., 2009). In converging evidence from healthy people, individual differences in social network size are predicted by episodic memory (among other cognitive functions; Stiller and Dunbar, 2007; Dunbar, 2008).

Although there already exists a literature on the negative consequences of brain injuries and dementia for social functioning (e.g., Finset et al., 1995; Morton and Wehman, 1995; Dijkers, 2004; Andrew et al., 2011; Henry et al., 2012), relatively few of these studies have examined the potential influence of memory impairment *per se*, and, regardless, these patients often have other important cognitive and behavioral problems, including disorganized thinking and behavior, emotional lability, poor inhibition, poor insight, anxiety, and depression. As far as we are aware, there exist only a few reports on social functioning in amnesia. The most recent one was surprising: Duff et al. (2008) described Angie, a densely amnesic woman who established several new close interpersonal relationships post-injury, including a new marriage (see also Wilson, 1999)! This report seemed at odds with our anecdotal observations of other patients, as well as with other case reports (Kaushall et al., 1981; Tate, 2002; Warren et al., 2012). The existing literature, however, is based primarily on clinical observations and qualitative descriptions. Thus, to examine close friendships in amnesia in a more systematic way, we administered a formal questionnaire.

MATERIALS AND METHODS

PARTICIPANTS

Patient K.C. is a 60-year-old right-handed man with 14 years of education. He sustained a head injury in a motorcycle accident in 1981 (for more detail, see Rosenbaum et al., 2005). His brain lesions are widespread; most notable is near-complete loss of the hippocampus, septal area, and posterior thalamus bilaterally, and damage to the parahippocampal cortices, amygdala, mammillary bodies, and anterior thalamus that is greater in the left than right hemisphere. Despite the extent of K.C.'s brain damage and resulting anterograde amnesia, his retrograde amnesia is relatively limited to episodic memory, affecting his ability to re-experience, and imagine personal events from across his lifetime (Rosenbaum et al., 2009). In contrast, K.C.'s semantic memory for personal and world facts learned prior to his head injury is relatively spared (Westmacott et al., 2001). His overall intellectual ability, language, visual perception, short-term and working memory, and executive function are also intact, though he exhibits some psychomotor slowing that may account for low average verbal fluency.

With respect to personality and social function, K.C. is very polite, cooperative, and friendly, though somewhat tranquil and reserved. The latter characteristic represents a change from his premorbid personality, which he and others describe as thrill-seeking and extroverted. He rarely initiates conversation but otherwise interacts well with others. Formal testing of K.C.'s theory of mind indicates that he is able to take other people's perspectives and infer their thoughts and feelings without difficulty (Rosenbaum et al., 2007).

Patient D.A. is a 60-year-old right-handed man with 17 years of education. He contracted herpes encephalitis in 1993, which produced a pattern of volume loss most prominent in the anterior and medial temporal lobe, including the hippocampus, amygdala, and parahippocampal cortex, and orbitofrontal cortex bilaterally, with overall more extensive damage in the right hemisphere (shown in Rosenbaum et al., 2008). D.A.'s ensuing memory problems required him to leave his professional career. Neuropsychological assessment revealed marked anterograde amnesia but intact performance on tests of intellectual function, language, visual perception, short-term and working memory, and executive function. A temporal gradient in remote autobiographical memory and semantic memory was also characterized, with poorer performance for events experienced in the 30 years prior to his injury (Rosenbaum et al., 2008), and for names and words that became well known in the 5 years prior to his injury (Westmacott and Moscovitch, 2002).

D.A. behaves appropriately in a social context and values his relationships with his wife, children, and friends. He has retained a warm-hearted, amicable, and gregarious personality, with a keen sense of humor that he uses to compensate for his memory loss.

Patient H.C. is a 23-year-old right-handed woman with developmental amnesia resulting from a probable hypoxic event at the age of 1 week. MRI has revealed significant bilateral reduction in hippocampal volumes, with the remaining tissue at least 2 SD smaller than that of age-matched healthy controls. When H.C. was included in a group of developmental amnesic patients, the group showed additional reduced volumes in the thalamus and basal ganglia bilaterally and in retrosplenial cortex in the right hemisphere (see Vargha-Khadem et al., 2003, patient E6, for additional neuroanatomical details).

H.C.'s cognitive profile features average IQ and normal fluency and semantic memory. She completed regular-stream high school and a year of community college. In contrast to her generally preserved cognitive functioning, H.C. has not developed normal episodic memory, based on reports from family members and as seen on clinical and experimental measures (Vargha-Khadem et al., 2003; Kwan et al., 2010). Her episodic memory impairment extends to memory for public events (Rosenbaum et al., 2011) and to imagination of future experiences in response to cue words (Kwan et al., 2010) but not to cues that are more elaborative/detailed or that depict commonplace scenes (Hurley et al., 2011; see Rosenbaum et al., 2011 for detailed neuropsychological profile).

H.C. has a bubbly, agreeable, and generally positive disposition. She is aware of having a memory problem, but approaches her impairment with light-hearted humor and acceptance. She is even-tempered, friendly, and talkative, often telling jokes and stories with great animation and detail in between testing (although these stories are typically the same as she has told in the past). When alone, H.C. passes the time by reading fiction, watching television, and browsing online social media/sharing sites such as Facebook and Pinterest.

[1]We are grateful to an anonymous reviewer for this suggestion.

Demographic and neuropsychological data for the patients are presented in **Table 1**.

To ensure that the patients' memory problems would not confound their answers on our questionnaire, we administered it to patients' family members: K.C.'s mother, D.A.'s wife, and H.C.'s mother and fiancé. We used the ratings from K.C.'s mother and D.A.'s wife, and from H.C. herself (we corroborated H.C.'s answers with her mother's and fiancé's, and found that their answers were similar to hers). Although these family members know the patients very well and the patients' interactions with others are relatively limited (making us confident that their answers on behalf of the patients were *reasonably* accurate), we acknowledge that it is possible that these informants are not fully aware of the individuals with whom the patients may discuss problems or concerns.

Twenty healthy older men (age $M = 66$ years, range = 57–72 years; education $M = 17$ years; range = 13–23 years) served as controls for K.C. and D.A. Eighteen healthy young women (age $M = 20$ years, range = 17–26 years; education $M = 13$ years; range = 12–16 years) served as controls for H.C.

QUESTIONNAIRE AND PROCEDURE

We administered the National Social Life, Health, and Aging Project's Social Network Module (Cornwell et al., 2009) to close relatives of each amnesic patient (see Participants), to patient H.C. herself, and to controls. This questionnaire assesses social network size and composition by collecting egocentric network data: the respondent identifies a set of people in his or her network and comments on the emotional closeness and connectedness of the relationship(s) linking them. The questionnaire uses *name generator* questions to prompt participants to enumerate relevant family and friends. With this method, it is possible to identify several different types of network members: core confidantes (Roster A), other potentially important network members (Rosters B and C), and any remaining household members (Roster D). We combined these four rosters in our analyses of social network size and density.

In keeping with the standard procedure, we introduced the questionnaire with: "From time to time, most people discuss things that are important to them with others. For example, these may include good or bad things that happen to you, problems you are having, or important concerns you may have. Looking back over the last 12 months, who are the people with whom you most often discussed things that were important to you?" If participants did not give an answer, we prompted them with: "This could be a person you tend to talk to about things that are important to you." After participants finished naming an initial group of close family and friends in Roster A, we asked: "Is there anyone else?" Any names listed after this prompt were included in Roster B. Then we asked: "Is there anyone else that you haven't named, perhaps someone with whom you feel especially close?" Any additional names were added to Roster C. Finally, we asked: "Is there anyone that you haven't named yet that lives in the same house as you?" Any names elicited at this point were added to Roster D. We altered the standard administration in only one way: whereas the standard procedure involves eliciting details regarding a maximum of five names, we asked for details on as many names as each participant was able to provide.

Table 1 | Neuropsychological profiles of the amnesic patients.

	K.C.	D.A.	H.C.
WAIS-R (STANDARD SCORE)			
FSIQ	88 (99)[1]	117	106
VIQ	96 (99)	121	104
PIQ	79 (99)	106	106
AM-NART (standard score)	102	117	101.28
WAIS-R vocab (scaled score)	9	12	–
Boston naming (/60)	57	56	58
Semantic fluency[2] (scaled score)	10	12	>14
WMS-R			
General memory (standard score)	61	74	49*
Verbal memory (standard score)	67	74	46*
Visual memory (standard score)	69	81	59*
LP I (%ile)	5th	15th	2nd
LP II (%ile)	<1st	<1st	<1st
VR I (%ile)	13th	19th	–
VR II (%ile)	<1st	<1st	–
WRMT (/50)			
Words	26	21	–
Faces	25	25	–
CVLT			
Acquisition (*T*-score)	12	9	38
Short delay free (*Z*-score)	−4	−4	−4
Long delay free (*Z*-score)	−4	−4	−3
Recog. discrim. (*Z*-score)	−3	−4	−2
ROCF (/36)			
Copy	36	35	36
Immediate recall	4	–	<20 (*Z*-score)
Delayed recall	0	0	<20 (*Z*-score)
AMI Autobiographical (/9)			
Childhood	2	7	–
Early adult life	3	6	–
Recent life	1	3	–
AMI personal semantics (/21)			
Childhood	16	17.5	–
Early adult life	13.5	21	–
Recent life	8	16	–
Judgment of line orientation (/30)	23	26	24
Benton visual discrimination test (%ile)	>95th	–	–
Benton face recognition test (%ile)	1st	–	33rd–59th
Letter fluency[3] (scaled score)	6	8	11–12
WAIS-R digits (scaled score)	12	13	–
WCST			
Categories (/6)	–	6	6
Persev. resp. (*Z*-score)	–	−0.5	–

WAIS-R, Wechsler Adult Intelligence Scale – Revised; AM-NART, American National Adult Reading Test; WMS-R, Wechsler Memory Scale – Revised; LP, logical passages; VR, visual reproduction; CVLT, California Verbal Learning Test; ROCF, Rey Osterrieth complex figure; AMI, Autobiographical memory interview; WCST, Wisconsin Card Sorting Test.

[1] Number in parentheses represents standard score on the Wechsler Abbreviated Scale of Intelligence (WASI) from a 2003 re-assessment of general intellectual function.

[2] Score is based on the number of animal names produced in 1 min.

[3] Score is based on the total number of words produced for the letters F, A, and S when given 1 min for each.

**WMS-III (Hurley et al., 2011).*

For each named person, participants specified (1) their relationship (e.g., spouse, mother, neighbor, etc.), (2) their age and gender, (3) whether they live in the same household, (4) for how long they've known each other, (5) how often they speak (on an eight-point scale ranging from 1 = *daily* to 8 = being *less than once a year*), (6) how close they are (on a four-point scale ranging from 1 = *not very close* to 4 = *extremely close*), and (7) their likelihood of sharing important concerns (on a three-point scale ranging from 1 = *very likely* to 3 = *not very likely*). Given the lack of sensitivity in this last scale we did not analyze it.

In order to obtain information on the density of their networks, we asked participants to specify the frequency of contact between each possible pairing among the identified family and friends (with the highest frequency being *daily* and the lowest frequency being *never*). If participants asked, they were told that communications via the internet or telephone were to be counted. We entered these data into a social network plotting program, Social Networks Visualizer (http://socnetv.sourceforge.net), to create social network maps for each individual, shown in **Figure 1**.

Finally, participants rated how frequently (on a seven-point scale ranging from 1 = *several times a week* to 7 = *never*) they have engaged in social activities (visiting neighbors, volunteering, and attending religious or social groups) in the past year. Because these four social activity scores were positively correlated across individuals, we combined them into a composite. For all questions, participants could also select "*don't know*" or "*refuse to answer*" as response options, although everyone used the scales without difficulty.

All participants provided informed consent before beginning, and the project was approved by the Research Ethics Boards of the University of Ottawa, York University, and Baycrest.

RESULTS

We performed one-tailed single case t-tests to compare each amnesic patient to his or her control group (Crawford and Howell, 1998). Given the similarities between patients K.C. and D.A. (in terms of both their demographic characteristics and their data), we present their results together first, followed by results for patient H.C.

PATIENTS K.C. AND D.A.

Although K.C. and D.A. do get out for weekly routine social activities through local brain injury programs (K.C. swims and plays pool, and D.A. plays poker), both were reported to be much less involved in social activities than normal (each scoring 7 on the aggregate social activity scale from 1 = *several times a week* to 7 = *never*; control $M = 3.43$, SD = 1.29, range = 1.25–6; ts = 2.70, ps = 0.007). Closer to home, both K.C. and D.A. have a normal number of close relationships (K.C. = 5 and D.A. = 6; control $M = 9.70$, SD = 5.69, range = 2–22; ts < 1), as shown in **Figure 1A**. The median closeness of these relationships, estimated using a scale from 1 = *not very close* to 4 = *extremely close*, is normal for K.C. (score = 3; control $M = 2.98$, SD = 0.64, range = 2–4; $t < 1$), but marginally reduced in D.A. (score = 2, $t = 1.49$, $p = 0.08$). The median amount of contact between these patients and their close others, using a scale from 1 = *every day* to 8 = *less than once a year*, is comparable to controls for both patients (K.C. = 4 and D.A. = 3; control $M = 2.95$, SD = 1.21, range = 1–5; ts < 1).

K.C.'s and D.A.'s relationships tend to have been established pre-morbidly and to stay within the family. For example, K.C. has made no new close friends in the three decades since the onset of his amnesia, and D.A. has made just one new friend in the two decades since his. This is below average (for K.C., control number of friends made since 1981 $M = 5.11$, SD = 4.21, range = 0–16; $t = 1.18$; for D.A., control number of friends made since 1993 $M = 3.42$, SD = 4.02, range = 0–15; $t < 1$), albeit not significantly. A somewhat higher-than-normal percentage of their relationships are with nuclear family members (K.C. = 80% and D.A. = 83%; control $M = 49\%$, SD = 25%, range = 13–83%; for K.C., $t = 1.21$, $p = 0.12$; for D.A., $t = 1.33$, $p = 0.10$). The density of K.C.'s social network (i.e., the ratio of existing links to all possible links) is a little higher than average, and D.A.'s is a little lower than average, but both are within the normal range (K.C. = 1.00 and D.A. = 0.48; control $M = 0.70$, SD = 0.23, range = 0.30–1.00; for K.C., $t = 1.27$, $p = 0.11$; for D.A., $t < 1$). In the past, K.C. has volunteered at a local library and participated in outpatient programs, including organized social outings to a community center. Now, however, other than an annual visit from an old friend and the occasional outing, his social interactions have become more limited, to his parents, siblings, and his parents' friends. After his encephalitis, D.A. used to volunteer at a school and community group, but he has recently ceased both these activities and now focuses on visiting occasionally with family and friends.

PATIENT H.C.

Throughout her life, H.C. has been provided with opportunities to make and keep up social links: she attended regular schooling, and uses her smartphone for organizing her social life and her computer for social networking. Yet, she and her family still estimate that she is less involved in social activities than normal (7 on a scale from 1 to 7; control $M = 4.53$, SD = 1.44, range = 1.5–6.5; $t = 1.67$, $p = 0.06$).

Despite this, and despite her lifelong memory impairment, H.C. has established a normal number of close relationships (7; control $M = 8.06$, SD = 2.71, range = 4–12; $t < 1$). Two of these relationships are with people outside of her family, which is within the range of normal (control $M = 4.89$; SD = 2.68, range = 2–11; $t = 1.05$). One of these relationships is particularly notable: she is engaged to be married. The estimated closeness of her relationships is normal, with a median score of 4 on a scale from 1 to 7 (control $M = 3.31$, SD = 0.55, range = 2–4; $t = 1.22$), and so is her degree of contact with these people (3 on a scale from 1 = *every day* to 8 = *less than once a year*; control $M = 2.08$, SD = 1.05, range = 1–5; $t < 1$). The density of her network is normal (0.75; control $M = 0.73$, SD = 0.23, range = 0.36–1.00; $t < 1$) H.C. spends most of her time with her family, her fiancé, and a small group of friends from high school. The majority of her socializing takes place at the movies, at her friend's house, and occasionally at a restaurant or bar, although when she goes out to these places she usually only does so with one person or a small group (i.e., her fiancé, sister, mother, and/or friend). H.C.'s mother describes her lifestyle as becoming increasingly sedentary and routine in recent years.

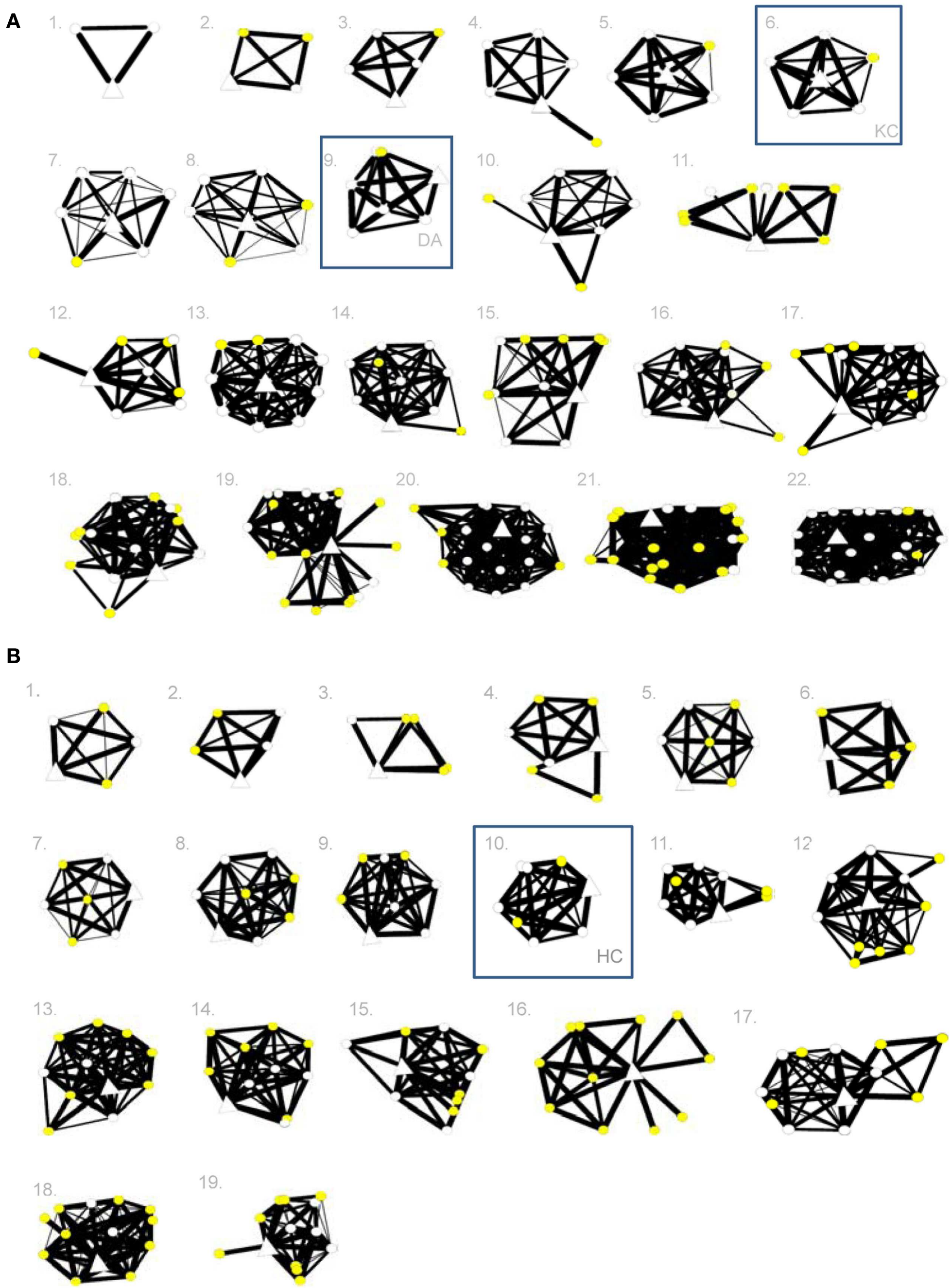

FIGURE 1 | (A,B) Social network maps for amnesic patients K.C. and D.A. **(A)** and H.C. **(B)** and their individual controls. In each person's network, the open triangle represents the individual participant, open circles represent family members, and yellow circles represent friends. A higher degree of relationship "closeness" between two nodes is shown by a thicker line between them. Individuals' maps are presented in ascending order from less dense to more dense social networks.

DISCUSSION

We examined the potential significance of memory to close interpersonal relationships. Overall, the picture presented by our three amnesic patients is of social networks being winnowed, although not necessarily obliterated, by amnesia. Cases K.C. and D.A. are less involved than normal with neighbors and religious and community groups. The confluence of quantitative and qualitative data suggests that K.C.'s and D.A.'s close relationships tend to be with family members. K.C. has made no new close friends in the 30 years since the onset of his amnesia, and D.A. has made just one in the 20 years since the onset of his. Like the adult-onset cases, H.C. is involved little with neighbors and religious and community groups. On the other hand, she has perhaps been more socially successful than our two adult-onset cases: despite being memory-impaired all her life, she has forged a couple of close relationships outside of her family, including one with her fiancé. This is a notable accomplishment. A marriage is perhaps the most difficult kind of interpersonal relationship for *anyone* to establish and to maintain, let alone someone with a severe memory impairment.

The reduced but not eliminated social functioning exhibited by our patients, along with the potential subtle differences from patient to patient, are consistent with the literature: after patient H. M. underwent his bilateral temporal lobectomy in 1953, his friends appear to have fallen away. He lived with various family members, and after they could no longer care for him he ended up in a nursing home. Nonetheless, even in his later years he was still capable of establishing what might best be described as quasi-friendships, in which he and certain other residents preferred each others' company (Corkin, 1984; Suzanne Corkin, personal communication, March 23, 2012). Another well-known case, N. A., lost his friends after the onset of his amnesia, but remained close to his mother, learned to get along with her new romantic partner, and became popular at the day treatment center he attended (Kaushall et al., 1981). The amnesic patient Clive Wearing may be the most socially isolated case. A newspaper report on him and his wife Deborah notes that they:

> live in a closed, insular world of two. Clive has no friends for the simple reason that he would forget who they are. "We don't mix," explains Deborah. "Clive lives in his unit and goes out accompanied by members of staff. Occasionally when he's out with me he will say strange things to people in cafes like, 'Are you the Prime Minister?,' [or] 'Are you the Queen of England?' It's because they are the first person he has seen since waking from 'unconsciousness' that minute, so they must, he presumes, be important." (France, 1995)

Taken together, our data and the descriptions of these other amnesic patients (see also Tate, 2002; Gupta et al., 2009; Warren et al., 2012; but see Wilson, 1999; Duff et al., 2008) suggest that episodic memory may serve as a kind of "social glue," enabling people to form social bonds more rapidly and easily, and to maintain them over the years. Even with considerable effort from family members, many amnesic patients get out less often than normal, and participate less often in community events and activities, giving them fewer opportunities to make new friends (see text footnote 1). Even if they do meet new people, the inability to consciously recollect those people, their names, the places and times they have met, and what happened (and difficulty using these memories flexibly and updating them when necessary) likely further hampers social functioning. Consistent with this idea, an initial report suggests that in healthy people episodic memory abilities predict social network size (Stiller and Dunbar, 2007). In fact, Dunbar has argued that our social networks have an upper limit in size ("Dunbar's number"; Dunbar, 1992) partly because we can only recollect in detail a certain number of people. However, what is intriguing is that not all amnesic patients appear to be hindered to the same degree (e.g., Wilson, 1999; Duff et al., 2008). We consider potentially important factors below.

FACTORS TO CONSIDER IN FUTURE WORK

The accumulating data on episodic memory and social functioning are intriguing, and set the stage for further research. However, several other factors might help to explain the variability among amnesic patients (and among healthy people, for that matter) and should be included explicitly in future work, including:

Developmental and sex differences

Might developmental amnesic patients (such as case H.C., described here) be more socially resilient than adult-onset patients? If so, it could be due to their memory and other cognitive impairments often being less severe than those of adult-onset cases (Cooper et al., 2011). Another possibility is that developmental amnesic patients' family and friends have never known them to be different, and are not required to adjust to the sudden appearance of a memory impairment. It is interesting to note that, like H.C., many of the adult patients with developmental amnesia studied by Faraneh Vargha-Khadem and colleagues are involved in serious relationships (personal communication, August 17, 2012). A formal comparison of adult-onset and developmental cases would be informative.

It might also be that women are better able than men to deal with the consequences of memory impairment. Warren et al. (2012; see also Duff et al., 2008) raised this intriguing possibility in discussing two of their more socially successful amnesic patients (cases 1846 and Angie), who, like our case H.C., are women.

Emotional functioning

Close relationships require us to experience, understand, communicate, and occasionally control our own emotions, and to interpret others' and then behave appropriately. Two brain regions particularly crucial to these functions are the frontal cortex and the amygdala. Might amnesic patients' social problems be attributable to concomitant frontal and/or amygdalar damage? Among our patients, K.C. and D.A. do have amygdalar involvement and D.A. has orbitofrontal damage too (Rosenbaum et al., 2005, 2008), whereas, as far as we can tell, H.C. does not. The literature is mixed, though: on the one hand, structural neuroimaging studies of these regions in healthy people suggest that smaller volumes are associated with smaller and/or less complex social networks (Powell et al., 2010, 2012; Bickart et al., 2011; Lewis et al., 2011; Kanai et al., 2012). On the other hand, some patients with damage to these regions show only subtle, if any, impairments. For example, when Becker et al. (2012) examined the social networks of identical twins with focal amygdalar damage, one twin had a smaller than normal network but the other was better connected socially than many controls.

Personality and motivation

People who are less neurotic and more extraverted, open, agreeable, and conscientious are more likely to make and keep friends (e.g., Pollet et al., 2011). Amnesic patients vary in their personalities, and, what is more, adult-onset cases' personalities can subsequently change. For example, among our patients, K.C. was a gregarious thrill-seeker before his brain injury and by all accounts had a large social network. He is quiet and reserved now and undoubtedly has a smaller network. In contrast, developmental case H.C. has always had a vivacious personality, which may be the reason for her relative social success. D.A. falls somewhere in between the other two patients: he has a personality that is similar to H.C.'s but not as much social success (in fact, his social relationships seem to be limited to couples and depend on his wife).

A related question is that of motivation: many of the more socially successful amnesic patients have been described as particularly motivated to recover (and/or to not appear to be impaired). Duff et al.'s (2008) successful case Angie worked hard to conceal her memory impairment from others; Wilson (1999) described two similar cases (Jay and Alex). Among our patients, D.A. appears to be the most similar to Angie in this regard.

Opportunities to socialize

No matter how motivated one might be, myriad contextual factors (as varied as family size, neighborhood density and services, available transportation, local crime rates, and family and cultural norms) affect one's chances of making and keeping up social bonds. Some amnesic patients follow regimented routines and stay close to home. In these cases opportunities to socialize (especially with new people, but also with old friends and family) are limited. In contrast, our most socially successful patient, H.C., had normal schooling and has been steadfastly supported by her family in exploring new venues, including summer camps, part-time jobs, trips to the movies, and social networking on the computer. These opportunities may have been the crucial factor allowing her to forge a few relationships outside of her family. (Note: of course, these opportunities may have been more available to H.C. because of the young age at which she exhibited episodic memory impairment.)

Other aspects of memory and cognition

Although all amnesic patients share a profound anterograde episodic memory impairment, the severity of this impairment can vary somewhat from case to case (as can the locus and extent of damage in the brain). At present, we have too few data to know whether the degree of anterograde amnesia is what separates the more socially successful patients from the less successful ones, although the initial data from healthy people would support this prediction (Stiller and Dunbar, 2007). However, other aspects of declarative memory (including retrograde episodic memory, and anterograde and retrograde semantic memory abilities) can also vary from patient to patient and may be important. Might those patients who are more capable of new semantic learning be more successful in forging new friendships? Might those who are able to draw on intact pre-morbid memories be more likely to retain old friendships? Might those who can develop a vague sense of familiarity (despite no recollection) grow more comfortable with someone over repeated encounters with him or her? These are interesting questions for future work, while bearing in mind the potential importance of other cognitive faculties, including problem-solving, theory of mind, executive function, future thinking, processing speed, meta-cognition, attention, language, and overall intelligence.

The variables outlined above (among others) must be taken into account in future research. A multi-factorial study on how memory impairment fits in with these other potential influences would be quite useful. Because individuals with selective episodic memory impairment are so rare, it might be fruitful to also use this approach with other groups with memory problems (e.g., normal aging). Another potentially productive avenue is experimental work with animal models, in which each of the potentially important factors outlined above can be better-controlled. Even though non-human primate social interactions are not as sophisticated as human ones, it is possible to make discrete lesions to particular brain areas, and to control the animals' social contexts (e.g., Bauman et al., 2004, 2006; Machado and Bachevalier, 2006; Goursaud and Bachevalier, 2007; Machado et al., 2009; Toscano et al., 2009).

OTHER FUTURE QUESTIONS

A useful future project would be to differentiate pre-morbid social networks from post-morbid ones. As mentioned above, K.C. was the "life of the party" before his amnesia, but now has relatively few social links. How do social networks *change* following the onset of amnesia? K.C.'s and D.A.'s family members were willing to try to reconstruct their pre-morbid social lives from decades ago, but when we explored this idea with controls it became apparent that it would be very difficult to obtain reliable data with this method. A more informative approach might be to track how recent-onset cases' social networks change longitudinally after the onset of amnesia. Other future methods might be to verify with nominated friends that their feelings are mutual, and to probe what these friends see as the strengths and deficiencies of the patients.

In future work, incorporating other kinds of patients would be beneficial. First, it would be useful to know what the similarities and differences are between amnesia and other severe cognitive deficits (for example, aphasia: Davidson et al., 2008; Northcott and Hilari, 2011). Second, such work might help us learn the degree to which the mere *stigma* associated with brain injury and cognitive deficits might hamper social bonding. That is, in comparison to other patients with similarly limited opportunities for social engagement and who have been labeled as "brain damaged" or "mentally impaired," are memory-impaired people less likely to establish and maintain good social links? (See text footnote 1). Finally, in the present study, we did not explore patients' subjective feelings. Are they lonely? In the past, one of us (R. S. R.) has asked K.C. about this, and he has responded "no." A report from Gupta et al. (2009) suggests that other amnesic patients might be lonely (depending on their degree of insight into their memory impairments), and a recent study of older adults with amnestic-type Mild Cognitive Impairment (Parikh et al., 2012) suggests that this group too experience feelings of loneliness and isolation.

Our social lives are inherently complex, and memory may be more important for establishing and maintaining some kinds of relationships than others. Whatever close relationships remain in amnesic patients are often familial, in which the bonds are supported by kinship or social norms, such as marriage vows. Indeed, one of the most poignant consequences of memory impairment is the heavy weight it places on these family ties. It is heartening that so often, under such tremendous strain, these ties bend but do not break.

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Empathy in hippocampal amnesia

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Empathy is critical to the quality of our relationships with others and plays an important role in life satisfaction and well-being. The scientific investigation of empathy has focused on characterizing its cognitive and neural substrates, and has pointed to the importance of a network of brain regions involved in emotional experience and perspective taking (e.g., ventromedial prefrontal cortex, amygdala, anterior insula, cingulate). While the hippocampus has rarely been the focus of empathy research, the hallmark properties of the hippocampal declarative memory system (e.g., representational flexibility, relational binding, on-line processing capacity) make it well-suited to meet some of the crucial demands of empathy, and a careful investigation of this possibility could make a significant contribution to the neuroscientific understanding of empathy. The present study is a preliminary investigation of the role of the hippocampal declarative memory system in empathy. Participants were three patients (1 female) with focal, bilateral hippocampal (HC) damage and severe declarative memory impairments and three healthy demographically matched comparison participants. Empathy was measured as a trait through a battery of gold standard questionnaires and through on-line ratings and prosocial behavior in response to a series of empathy inductions. Patients with hippocampal amnesia reported lower cognitive and emotional trait empathy than healthy comparison participants. Unlike healthy comparison participants, in response to the empathy inductions hippocampal patients reported no increase in empathy ratings or prosocial behavior. The results provide preliminary evidence for a role for hippocampal declarative memory in empathy.

Keywords: hippocampus, declarative memory, social cognition, empathy

INTRODUCTION

The scientific investigation of empathy has become a cornerstone of the study of social cognition (Preston and de Waal, 2002; Adolphs, 2003). Indeed, empathy, or the ability to understand and share the feelings of others, is integral to the quality of our relationships with others and plays an important role in relationship satisfaction and subjective well-being (Davis and Oathout, 1987; Wei et al., 2011). Converging methods point to a network of structures that contribute to empathy including the bilateral orbitofrontal and ventromedial prefrontal cortices (vmPFC), anterior cingulate, anterior insula, and amygdala (Eslinger, 1998; Mesulam, 2000; Hornak et al., 2003; Shamay-Tsoory et al., 2003, 2009; Singer et al., 2004; Anderson et al., 2006; Lamm et al., 2007; Beadle, 2011).

The purpose of the current study is to investigate the contribution of the hippocampus to empathy. Whereas the hippocampus and its core processing features have not previously been a focus of empathy research, our motivation for their inclusion is based on the role of the hippocampus in declarative (relational) memory (Cohen and Eichenbaum, 1993; Eichenbaum and Cohen, 2001) and a set of empirical findings with neurological patients with hippocampal amnesia pointing to deficits in various aspects of social behavior. In addition, we have heard anecdotal reports from the family members of patients with amnesia that these individuals have post-morbid changes in the ability to understand or predict the thoughts and feelings of others, and to display compassion or offer help to others in need, suggesting there may be disruptions in empathy and prosocial behavior. Our overarching hypothesis, elaborated below, is that the hippocampus is intimately tied to a set of cognitive processes, and is a critical component of the network of brain structures that supports aspects of social cognition. Here we extend this proposal to examine the contribution of the hippocampus to empathy.

HIPPOCAMPAL DECLARATIVE MEMORY AND EMPATHY

The role of the hippocampus (and related medial temporal lobe structures) in the formation of new long-term memories and their subsequent retrieval is well established. The hippocampus also plays a critical role in support of declarative memory *use*. The hippocampal declarative memory system has two processing features or properties that are critical to our hypothesis for its role in social cognition. First, declarative memory supports the flexible expression of memory (O'Keefe and Nadel, 1978; Cohen, 1984; Squire, 1992; Cohen and Eichenbaum, 1993; Bunsey and Eichenbaum, 1996; Dusek and Eichenbaum, 1997; Eichenbaum and Cohen, 2001). The *representational flexibility* of this form of memory permits it to be accessible across processing systems (as when a rich, multisensory autobiographical memory is evoked by the sight of a familiar face or the sound of a familiar song) and to be used in novel situations. This flexibility permits memory to be called upon promiscuously in supporting diverse and complex cognitive and social capabilities. The second property of the hippocampal declarative memory system is its support of *relational memory binding* (Cohen and Eichenbaum, 1993; Cohen et al., 1997; Ryan et al., 2000; Eichenbaum and Cohen, 2001; Davachi, 2006), which permits the encoding of memories of (even arbitrary) co-occurrences of people, places, and things along with the spatial, temporal, and interactional relations among them (see Konkel et al., 2008), that constitute events, as well as representations of relationships among events, providing the basis for the larger record of one's experience.

Recent evidence has also emerged that the hippocampus plays a role in on-line processing. Although most research on hippocampal declarative memory, as with other forms of long-term memory, has been on its role in the formation of new memories and subsequent recollection, recent work by our lab and others (Hannula et al., 2006; Olson et al., 2006; Barense et al., 2007; Hannula and Ranganath, 2008; Warren et al., 2010) show that it is also critical for on-line processing, i.e., for *acting on the present for the present*. The declarative memory system, via hippocampal-cortical connections, is in ongoing interaction with various cortical processing areas, as new information is perceived, as old information is retrieved, and as processing outcomes are held on-line to be evaluated, manipulated, and used in service of behavioral performance. Taken together, the representational flexibility, relational memory binding, and on-line processing afforded by the hippocampus in support of declarative memory use may also support the capability to manage the very complex social relationships and social interactions that are a necessary part of successful social functioning in the world.

Indeed, a growing body of research points to the hippocampus and the declarative memory system as being important for various types of social behavior. For instance, we have shown that hippocampal amnesia impairs decision-making (Gupta et al., 2009a), character judgments (Croft et al., 2010), and various aspects of language and social discourse (Duff and Brown-Schmidt, 2012). Patients with amnesia may also have difficulty establishing and maintaining interpersonal relationships as they have smaller social networks than age and sex matched healthy comparison participants (Gupta et al., 2009b; Davidson et al., 2012). These studies suggest that deficits in the cognitive processes supported by the hippocampus (e.g., representational flexibility, relational binding, on-line processing) disrupt a core set of abilities necessary for recognizing the shifting and changing status of friends and foes, thinking about ourselves and other people, and communicating events in the moment from time frames that stretch from the distant past to possible futures. The extent to which these same hippocampal dependent processes are also important for empathy is an open question.

Empathy is defined by its cognitive and emotional components (Davis, 1980, 1983; Batson, 1991; Eisenberg et al., 1994; Preston and de Waal, 2002). The cognitive component of empathy supports our ability to understand the mental states of another person, including their thoughts, intentions, and feelings. This involves *perspective-taking* which entails imagining or simulating another person's mental state. Perspective taking is thought to involve the flexible re-experiencing of relevant autobiographical memories or semantic social knowledge about the situation or individual. The emotional component of empathy supports our ability to feel sympathy or compassion for another individual in need and has been termed *empathic concern*. Empathic concern may involve the processes of *emotion contagion* and *emotional responsiveness*, enabling individuals to vicariously experience the emotions of another person. Importantly, individuals often employ emotion regulation in order to dampen their negative emotional arousal due to experiencing others' vicarious emotions (i.e., *personal distress*) ultimately leading to the experience of *empathic concern*.

While we are agnostic regarding the main theories of empathy, we speculate that the hippocampus and its related processes could play a role in each. There are three main theories of empathy: (1) theory–theory, (2) simulation theory, and an (3) adapted simulation theory. Theory–theory purports that we discern others' mental states by developing a theory about their behavior (Gopnik and Wellman, 1992, 1994; Gopnik and Meltzoff, 1997). The development of a theory about others' mental states may involve the hippocampus to bind together social and emotional information about the other person, the scenario, and the environmental location and to hold this information on-line to make judgments and comparisons. Such a role for the hippocampus would, in part, be consistent with neuroimaging evidence suggesting hippocampal recruitment in theory of mind, or the cognitive domain of empathy (Buckner and Carroll, 2007; Spreng et al., 2009; Spreng and Mar, 2012). Whereas theory of mind is often linked to the frontal lobes, Buckner and Carroll (2007) proposed that the processes by which we project ourselves into a different time and place to remember our past are the same processes by which we project ourselves into the future or into the mental states of others and this process may involve the hippocampus. This projection of self into another person's mental state may reflect the process of *perspective-taking* that occurs in the cognitive component of empathy. Additional evidence that the hippocampus is important for self-projection comes from a study that showed that patients with hippocampal amnesia have difficulty imagining future events (Hassabis et al., 2007). Other studies show that the hippocampus is involved in tasks that require the flexible re-construction of previous memories or imagination of either new events in the future or others' mental states (Spreng et al., 2009; Spreng and Grady, 2010; Spreng and Mar, 2012).

Simulation theory suggests that the way in which we are able to understand another person's mental state is through internal simulation that occurs after we first comprehend their mental state (Gordon, 1986; Heal, 1986). This pre-requisite understanding of others' mental states may recruit the hippocampus in a manner similar to that for theory-theory. However, in order for an individual to feel *empathic concern* for others who are suffering rather than *personal distress*, individuals must regulate their emotions and distinguish others' emotions from one's own. This process may recruit the hippocampus as individuals must maintain on-line their shared emotional experience, distinguish the relational emotion-individual pairings experienced by the self and other, and flexibly use personal memories to guide behavior in the moment. It is also possible that certain social demands disproportionately engage the hippocampus. Rabin and Rosenbaum (2012) demonstrated that imagining or simulating the mental state of familiar or known individuals recruits the hippocampus to a greater degree than for unknown individuals. The adaptation of simulation theory defines the internal simulation process to be unconscious and automatic rather than a conscious process requiring knowledge about the mental state of the other person (Gallese, 2003; Goldman and Sripada, 2005; Gazzaniga, 2008). Considering this theory in the context of emotional empathy and its subdomains would suggest that the process by which individuals vicariously adopt the emotions of others (i.e., *emotion contagion* and *emotional responsiveness*) would occur automatically and would not require intact theory of mind. The hippocampus may be recruited to maintain on-line and flexibly use emotional information about one's own emotional state and that of the other person to experience empathy toward them. Previous research has demonstrated that the hippocampus is involved in unconscious processing of relational information (Ryan et al., 2000; Hannula and Ranganath, 2009; Hannula and Green, 2012).

THE CURRENT STUDY

The current study extends our proposal about the role of the hippocampus in social cognition to empathy. We conducted a preliminary investigation of cognitive and emotional empathy in patients with hippocampal damage and severe declarative memory impairment. This consisted of an assessment of the subdomains of empathy including *perspective-taking*, *emotion contagion*, *emotional responsiveness*, and *empathic concern*. As a first pass at measuring empathy in amnesia, we used the gold standard tools from the field of social neuroscience, i.e., self-report questionnaires. Building on our success using an emotion induction paradigm in this same group of hippocampal patients (Feinstein et al., 2010), we investigated the induction of empathy through two methods adapted from standard empathy methodology (Batson et al., 1995; Batson and Moran, 1999). We hypothesized that patients with hippocampal amnesia would report lower empathy on trait questionnaires and measures of empathy after undergoing an empathy induction than healthy comparison subjects.

MATERIALS AND METHODS

EXPERIMENT 1

Participants

Participants were three patients (one female) with bilateral damage to the hippocampus and severe declarative memory impairment and three healthy comparison participants matched pair-wise to the amnesic patients on age, sex, handedness, and education (see **Table 1**). The etiology for the patients was an anoxic/hypoxic event (e.g., cardiac arrest, status epilepticus).

For patients 2363 and 1846, structural magnetic resonance image (MRI) examination was completed confirming bilateral hippocampal damage and significantly reduced hippocampal volumes [studentized residual differences in hippocampal volume relative to a matched comparison group were −2.6 and −4.24 *z*-scores, respectively; (Allen et al., 2006)]. There was no evidence of damage to the structure of the amygdala in either 1846 or 2363 (Allen et al., 2006; Warren et al., 2012). We do not have functional connectivity data on these patients so we cannot comment on the integrity of the functional connectivity between the hippocampus and related structures. For patient 2563, anatomical analysis was based on computerized tomography (he wears a pacemaker and was unable to undergo MRI) and only damage in the hippocampal region was visible.

Neuropsychological testing confirmed a selective and severe memory impairment disproportionate to any deficits in general cognitive or intellectual functioning (see **Table 1**). Performance on the Wechsler Memory Scale-III (General Memory Index) was at least 25 points lower than performance on the Wechsler Adult Intelligence Scale-III (Full Scale IQ; M=92.0), with an average delay score on the memory scale (64.3) that was nearly 3 standard deviations below population means. Basic speech and language abilities were intact and all patients performed within normal limits on standardized measures of language. Patients 2363 and 2563 indicated no evidence of depression on the Beck Depression Inventory (BDI). Responses on the BDI from 1846, the only female participant, were interpreted as mild depression (see Warren et al., 2012 for more information about 1846's case).

Measures

Empathy is multidimensional in nature and includes cognitive and emotional components. Empathy was assessed using four self-report, trait measures including the Interpersonal Reactivity Index (IRI; Davis, 1980), the Questionnaire Measure of Empathic Tendency (QMET; Mehrabian and Epstein, 1972), the Empathy Quotient (EQ; Baron-Cohen and Wheelwright, 2004), and the Emotion Contagion Scale (EC; Doherty, 1997). While the IRI and EQ assess both components of empathy, the QMET and EC focus on the emotional component of empathy. These questionnaires have demonstrated high validity and reliability in healthy adult

Table 1 | Demographic and neuropsychological characteristics of hippocampal patients.

Patient	Sex	Onset age (years)	Testing age (years)	Edu (years)	Chronicity (years)	WAIS-III FSIQ	WMS-III GMI	Token test	Boston naming test	BDI
1846	F	30	46	14	16	84	57	41	43	9
2563	M	45	54	16	9	94	63	44	52	0
2363	M	42	53	18	11	98	73	44	58	0
Mean (SD)		39.0 (7.9)	51.0 (4.4)	16.0 (2.0)	12.0 (3.6)	92.0 (7.2)	64.3 (7.2)	43.0 (1.7)	51.0 (7.5)	3 (5.2)

M, male; F, female; Edu, education; WAIS-III, Wechsler Adult Intelligence Scale-III; FSIQ, Full Scale Intelligence Quotient; WMS-III, Wechsler Memory Scale-III; GMI, General Memory Index; BDI, Beck Depression Inventory.

samples (for questionnaire details see below). Two of the patients (1846 and 2363) were available to complete the questionnaires for a second time at least 6 months after the initial testing session allowing an assessment of test reliability. In general, this revealed adequate reliability across testing sessions (see **Table 2**).

Participant data on the trait questionnaires was compared to the healthy comparison participants from the present study (see **Table 3**). As a secondary comparison, the participant data was also compared with healthy control normative data available in the literature. A standardized *z* score was computed for each participant that compared their raw score on the questionnaire to the mean and standard deviation of the normative data set. Normative data sets for these questionnaires consisted of individuals in the young adulthood age range and participants were compared based upon gender-specific norms. A *z* score was computed for the patient with hippocampal damage as well as the family member and healthy comparison participant. This is particularly important in the case of our dataset because our present sample is somewhat older than the young adulthood range found in most normative studies. The comparison data sets included: (Davis, 1980; IRI), (Lawrence et al., 2004; EQ sum score), (Lawrence et al., 2007; EQ factor scores), (Mehrabian and Epstein, 1972; QMET), and (Doherty, 1997; EC). When available, a qualitative comparison of the participant data was made with an older adult sample that was similar in age to the participants.

Interpersonal Reactivity Index. The IRI (Davis, 1980) is one of the few empathy questionnaires designed to measure empathy as a multidimensional construct in healthy adults. The IRI has four subscales measuring an individual's perception of their ability in each of these domains: Perspective Taking (PT-adopting the mental perspective of another person), Empathic Concern (EC-experiencing feelings of compassion for others), Fantasy (FS-adopting the perspective of a fictional character in a book or movie), and Personal Distress (PD-feeling unease or distress in the face of the physical or emotional harm of another person). Each subscale contains 7 items that are summed to create a total score for each subscale with ranges from 0 to 28 points, with higher scores indicating greater empathy. The IRI has adequate test/re-test reliability across its four subscales in healthy adults (range: r=.61 to .81; test/re-test interval: 60–75 days) and the subscales have adequate internal consistency (PT: Cronbach's α: males = .71, females = .75; EC: Cronbach's α: males = .68, females = .73; FS: Cronbach's α: males = .78, females = .79; PD: Cronbach's α: males = .77, females = .75.)

Cognitive empathy is measured by the PT subscale through such items as, "When I'm upset at someone, I usually try to 'put myself in his shoes' for awhile." An example item from the FS subscale includes, "When I am reading an interesting story or novel, I imagine how I would feel if the events in the story were happening to me." For the EC subscale an example item includes, "I often have tender, concerned feelings for people less fortunate than me." The PD subscale measures vicarious negative arousal resulting from viewing another person's emotional or physical distress, for example, "I sometimes feel helpless when I am in the middle of a very emotional situation."

Table 2 | Trait empathy: reliability.

Measures	1846	1846 Re-test	Diff score	2363	2363 Re-test	Diff score
IRI-PT	16	15	1	17	21	−4
IRI-EC	19	23	−4	19	19	0
IRI-FS	7	11	−4	21	19	2
IRI-PD	19	17	2	12	12	0
EQ-sum	47	46	1	42	50	−8
EQ-cog	11	10	1	11	11	0
EQ-emot	14	13	1	7	11	−4
EQ-soc	6	5	1	5	7	−2
QMET	36	54	−18	17	19	−2
EC	2.93	3.33	−.40	2.53	2.73	−.20

IRI-PT, Interpersonal Reactivity Index (IRI)-Perspective-Taking Subscale; IRI-EC, IRI Empathic Concern subscale; IRI-FS, IRI Fantasy subscale; IRI-PD, IRI Personal Distress Subscale; EQ, Empathy Quotient (EQ); EQ-Sum, total score on EQ; EQ-Cog, EQ Cognitive Empathy Factor; EQ-Emot, EQ Emotional Reactivity Factor; EQ-Soc, EQ Social Skills Factor; QMET, Questionnaire Measure of Empathic Tendency; EC, Emotion Contagion Scale; Diff score, Initial testing – Re-test score.

Empathy Quotient. The Empathy Quotient (EQ) was developed to assess dispositional empathy in individuals with Asperger's Syndrome/High Functioning Autism and in healthy adults (Baron-Cohen and Wheelwright, 2004). The scale has sufficient test/re-test reliability in healthy adults (r=.84; test/re-test interval: 10–12 months; Lawrence et al., 2004) and adequate internal validity (Cronbach's α=.92; Baron-Cohen and Wheelwright, 2004). Although originally designed to measure empathy as a unidimensional construct, a recent factor analysis has revealed that it may measure three factors: Cognitive Empathy, Emotional Reactivity, and Social Skills (Lawrence et al., 2004). Total scores are computed by summing responses to all of the items, while factor scores involve summing items that measure a particular factor. The range of total scores is from 0 to 80 points, with higher scores indicating greater empathy. While cognitive empathy is assessed by the Cognitive Empathy Factor and includes such items as, "I am good at predicting how someone will feel," emotional empathy is measured by the Emotional Reactivity factor through items such as, "I get upset if I see people suffering on news programs." Emotional empathy as measured by this scale is more similar to the construct of emotion contagion than sympathy. The Social Skills factor does not measure empathy but rather assesses individuals' perceptions of their ability to interact socially with others, for example, "I find it hard to know what to do in a social situation" (which is a reverse-scored item).

Questionnaire Measure of Empathic Tendency. The Questionnaire Measure of Empathic Tendency (QMET) was designed to measure dispositional emotional empathy in healthy adults (Mehrabian and Epstein, 1972). The split-half reliability for this scale in healthy adults is .84. The QMET has demonstrated good construct validity in healthy adults through its association with other measures of empathy such as the IRI-EC [males: $r(225)$=.63, p<.05, females: $r(235)$=.56, p<.05] and the IRI-PT [males: $r(225)$=.22, p<.05; females: $r(235)$=.17, p<.05; Davis,

Table 3 | Trait empathy.

Participant			Measure									
			IRI				EQ				QMET	EC
			PT	EC	FS	PD	Total	Cog	Emot	Soc	Total	Total
1846	Patient	Raw	16	19	7	19	47	11	14	6	36	2.93
		z	−.40	−.70	−2.27	1.34	−.39	2.33	3.95	−.16	−.38	−1.46
	Family	Raw	7	16	2	19	25	2	5	4	16	2.47
		z	−2.26	−1.48	−3.24	1.34	−2.78	−2.67	−.79	−.96	−1.33	−2.31
	NC	Raw	24	22	14	16	51	13	10	9	83	3.00
		Z	1.25	.09	−.92	.74	.04	3.44	1.84	1.04	1.86	−1.33
	P–F score		9	3	5	0	22	9	9	2	20	.46
2363	Patient	Raw	17	19	21	12	42	11	7	5	17	2.53
		z	.05	−.01	.94	.56	.07	3.39	.72	−.40	−.27	−1.60
	Family	Raw	16	25	13	16	29	4	9	3	20	2.20
		z	−.17	1.42	−.49	1.44	−1.22	−.50	1.41	−1.20	−.14	−2.23
	NC	Raw	21	24	19	11	55	10	14	5	86	3.53
		z	.89	1.18	.58	.34	1.36	2.83	3.14	−.40	2.86	.33
	P–F score		1	−6	8	−4	13	7	−2	2	−3	.33
2563	Patient	Raw	11	23	7	1	51	9	12	10	14	2.13
		z	−1.22	.94	−1.56	−1.86	.96	2.28	2.45	1.60	−.41	−2.37
	NC	Raw	21	23	25	22	59	12	16	8	53	2.93
		z	.89	.94	1.66	2.76	1.75	3.94	3.83	.80	1.36	−.83
HC		M	14.67	20.33	11.67	10.67	46.67	10.33	11.00	7.00	22.33	2.53
GRP		SD	3.21	2.31	8.08	9.07	4.51	1.15	3.61	2.65	11.93	.40
NC		M	22.00	23.00	19.33	16.33	55.00	11.67	13.33	7.33	74.00	3.15
GRP		SD	1.73	1.00	5.51	5.51	4.00	1.53	3.06	2.08	18.25	.33

HC GRP, group of patients with hippocampal damage; NC GRP, group of normal healthy comparison participants; NC, each normal, healthy comparison participant matched to a particular patient; Raw, raw sum score on each questionnaire; Z, standardized score on each questionnaire based upon the mean and standard deviation of a normative control sample from the literature; P–F score, Patient–Family member raw score on questionnaire; IRI, Interpersonal Reactivity Index (IRI); PT, Perspective-Taking Subscale of IRI; EC, Empathic Concern subscale of IRI; FS, Fantasy subscale of IRI; PD, Personal Distress Subscale of IRI; EQ, Empathy Quotient; Sum, total score on EQ; Cog, Cognitive Empathy Factor of EQ; Emot, Emotional Reactivity Factor of EQ; Soc, Social Skills Factor of EQ; QMET, Questionnaire Measure of Empathic Tendency; EC, Emotion Contagion Scale.

1983]. Because the scale measures vicarious emotional responsiveness to others, it is more similar to the emotion contagion construct than to sympathy. Emotional empathy is assessed by computing a total sum score on the thirty-three items on the questionnaire, some of which are negatively worded and thus reverse scored. The response scale ranges from −4 ("I strongly disagree") to +4 ("I strongly agree") and is anchored at 0 with a range of scores from −132 (lowest empathy) to +132 points (highest empathy). Although initially designed to be separated into subscales, it was shown that the best fit is a uni-dimensional measure of emotional empathy. A couple of example items include: "I tend to get emotionally involved with a friend's problems," and, "Seeing people cry upsets me."

Emotion Contagion Scale. The Emotion Contagion Scale (EC) measures one's tendency to vicariously experience the emotions of others in daily life and measures emotion contagion (Doherty, 1997). In healthy adults, this scale has shown adequate test-retest reliability [$r(41)=.84$, $p<.001$, over a three week interval] and high internal consistency (Cronbach's $\alpha=.90$). The EC scale shows moderate associations with other measures of emotional empathy, such as the IRI-EC [$r(119)=.37$, $p<.05$] and the QMET [$r(80)=.47$, $p<.05$]. The EC scale measures emotion contagion as a uni-dimensional construct through fifteen positively scored items. The response choices range from 1 ("Never"), 2 ("Rarely"), 3 ("Often"), and 4 ("Always"), and the average score of the items is computed, with higher scores indicating greater emotion contagion. A few example items from the scale are, "If someone I'm talking with begins to cry, I get teary-eyed" and, "I get filled with sorrow when people talk about the death of their loved ones."

RESULTS

TRAIT COGNITIVE EMPATHY

On the Perspective Taking subscale of the IRI (IRI-PT), which assesses one's ability to adopt the mental perspective of others, all three hippocampal participants (1846, 2363, 2563) reported lower scores on this measure than healthy comparison participants (see **Table 3**). In fact, the patients' ratings were 3 standard deviations (SD) or more below that of the three demographically matched healthy comparison participants (1846: 3.47 SD; 2363: 2.89 SD; 2563: 6.35 SD). The group of hippocampal patients were significantly different from the healthy comparison group on this measure [Mann–Whitney: $z(4)=1.99$, $p<.05$]. The family members of two of the amnesic patients (1846 and 2363) reported the patients as having even lower PT scores than the patients themselves reported (difference score: patient score – family member score: 1846 = 9 points; 2363 = 1 point). We were unable to obtain family member ratings for patient 2563.

Next, we compared the participants' scores on the IRI-PT to a normative dataset of healthy adults (Davis, 1980). All of the matched comparison participants had positive *z* scores ranging from approximately +1 SD to +1.25. In comparison, the patients' *z* scores were negative in 2 out of 3 cases (1846: −.40, 2563: −1.22, 2363: .05). Furthermore, where family member scores were available, their *z* scores were more negative than the reports of the patients (1846: −2.26, 2363: −.17). In an effort to also compare the patients to a more similar age cohort, the patients' responses were compared to a previous paper examining trait empathy in older adults (age: $M=66.2$, $SD=7.6$; range = 55–81 years; Beadle et al., 2012). The patients with hippocampal damage in the present study were slightly younger ($M=51$, $SD=4.4$ years). This previous paper demonstrated that older adults report lower cognitive empathy than younger adults (Beadle et al., 2012). For this comparison, the hippocampal group was approximately 1 SD below the group of older adults, suggesting that their reported scores are not simply an effect of age (hippocampal patients: $M=14.7$; older control group: $N=20$, $M=17.7$, $SD=3.4$).

The EQ cognitive empathy scale measures one's ability to accurately predict others' mental states. Two out of three patients with hippocampal amnesia reported lower scores (1846, 2563) than the demographically matched healthy comparison participants on this scale. Relative to the mean of the healthy comparison participants, 2563 was 1.7 SD lower, while 1846's score was within 1 SD from the comparison group mean. As a group, however, the amnesic patients did not differ from healthy participants on the EQ cognitive empathy factor [$z(4)=1.11$, $p=.27$]. Because the family members of patients 1846 and 2363 reported the patients as having much lower cognitive empathy than the patients' own ratings (difference score: 1846=9 points; 2363=7 points), it suggests that the patients' own ratings may not be completely accurate in this case. In comparison to standard normative data (Lawrence et al., 2007), healthy comparison participants had positive *z* scores ranging from +2.83 to +3.94 SD, while the family member ratings of the patients were both negative (1846F:−2.67, 2363F:−.50).

TRAIT EMOTIONAL EMPATHY

Emotional responsiveness to others, one domain of emotional empathy, was reported to be low in all three amnesic participants relative to the healthy comparison participants on the Questionnaire Measure of Empathic Tendency (QMET; see **Table 3**). The amnesic patients were at least 2 SD lower than the healthy comparison participants' mean (1846: 2.10 SD, 2363: 3.10 SD, 2563: 3.30 SD), a difference that was marginally significant [$z(4)=1.96$, $p=.05$]. Family members rated the patients as slightly higher than the patients' own ratings in one case (2363: patient=17, family member=20), and quite a bit lower in another case (1846: patient=36, family member=16). In comparison to a normative data set (Mehrabian and Epstein, 1972), the patients and the family member reports resulted in negative *z* scores (range: patient=−.41 to −.27; family member=−1.33 to −.14). In contrast, healthy comparison participants all had positive *z* scores (range: 1.36 to 2.86).

For the EQ Emotional Reactivity Factor, which also measures emotional responsiveness to others, two out of three amnesic participants were lower than the healthy comparison participants. Of the two hippocampal amnesic participants, one had a score 2 SD away from the mean of the demographically matched healthy comparison participant group (2363) and the other patient was .4 SD lower (2563). As a group, the hippocampal patients did not significantly differ from the demographically matched healthy comparison participants on the EQ Emotional Reactivity Factor [$z(4)=.89$, $p=.38$]. The family member of 2363 rated the patient 2 points higher than the patient's own rating, while the family member for 1846 rated the patient 9 points lower. Relative to a normative dataset (Lawrence et al., 2007), 2363 and 2563 had qualitatively lower *z* scores than their matched comparison participants (2363=.72, 2363C=3.14; 2563=2.45, 2563C=3.83).

Two out of three participants with amnesia were also low relative to the healthy comparison participants on another measure of emotional responsiveness that assesses primitive emotional contagion toward others (Emotion Contagion Scale), with scores approximately 2 SD or more lower than the healthy comparison participant mean (2363: 1.90 SD; 2563: 3.10 SD). Hippocampal patients as a group did not differ significantly from the demographically matched healthy comparison participants on the EC [$z(4)=1.77$, $p=.08$]. For both 1846 and 2363, the family members of these patients rated them as having lower levels of emotion contagion than the patients themselves reported (1846: patient=2.93, family member=2.47; 2363: patient=2.53, family member=2.20). In terms of the patients' scores relative to normative data (Doherty, 1997), patients had lower *z* scores than the matched comparison participants (1846=−1.46, 1846C=−1.33, 2363=−1.6, 2363C=.33, 2563=−2.37, 2563C=−.83). Furthermore, patients' family members *z* scores were even lower than the patients' (1846F=−2.31, 2363F=−2.23).

Sympathy or compassion toward others in need was measured by the IRI Empathic Concern subscale. On this subscale, two out of three participants with amnesia reported lower scores (1846, 2363) than the healthy comparison participants. The scores of 1846 and 2363 were 4 SD lower than the healthy comparison participants mean. When comparing the group of hippocampal patients to the healthy comparison participants, there were no significant differences [$z(4)=1.35$, $p=.18$]. In terms of the family member ratings from the present study, 1846's family member reported slightly lower scores than the patient (1846=19, family member=16), while 2363's family member reported slightly higher scores than the patient (2363=19, family member=25). A comparison to a normative dataset of younger adults (Davis, 1980) revealed that 1846, based upon self and family member ratings, had *z* scores that were lower than that of their matched comparison participant (1846=−.70, 1846F=−1.48, 1846C=.09). The z scores for 2363 and 2563 did not show a consistent pattern (2363=−.01, 2363F=1.42, 2363C=1.18; 2563=.94, 2563C=.94). Compared to data from a group of older adults, the mean of the hippocampal group was similar to that of the older adult control mean (hippocampal amnesic: M=20.30, healthy older adult control mean: M=20.78, SD=2.64; Beadle et al., 2012).

INTERIM DISCUSSION

These results provide preliminary evidence for lower trait cognitive and emotional empathy on some measures in patients with hippocampal amnesia than in healthy comparison participants, both matched to the patients and group norms in the literature. However, given that all of these measures rely on self-report, we were concerned that the extent of the patients' memory impairment may have influenced their ability to accurately report their experience of cognitive and emotional empathy. These questionnaires likely require some degree of declarative memory to recall how one responded in a particular situation in the past or to imagine how one might respond in the future. The consistency of the patients' reports alleviate some of these concerns, as do the family member reports of the patients' empathy. The reports from the patients' family members were largely consistent with the patients' own reports of lower empathy. In fact, in line with their anecdotal reports, the family member reports were actually slightly lower than those of the patients in several cases, suggesting an observable deficit in empathy. Furthermore, in addition to age-matched comparison data, we also compared the amnesic patients' ratings to norms from healthy older adults who are assumed to have experienced age-related changes to hippocampal function. The amnesic patients had even lower levels of empathy than these older adults in the case of cognitive empathy. That said, we were still concerned about the limitations of the questionnaires as well as our low number of participants and the variability across measures (i.e., not all patients were lower on all questionnaires) and sought a more objective measure of empathy.

In a second experiment, we conducted a behavioral study that assessed the induction of empathy and measurement of prosocial behavior in hippocampal amnesia. In previous work in our lab, these same amnesic patients underwent an emotion (happiness, sadness) induction procedure (using affectively-laden film clips) to ascertain whether their experience of a basic emotion would persist beyond their memory for the sadness-inducing films (Feinstein et al., 2010). The induction procedures were successful as the patients reported higher levels of the target emotion long after they were able to recall any information about the film clips. Building upon this previous study, we measured the level of empathy participants reported after undergoing an empathic induction and the prosocial behavior they demonstrated after experiencing the induction.

MATERIALS AND METHODS

EXPERIMENT 2

Participants

Two participants with hippocampal amnesia from Experiment 1 (1846 and 2363) were available to complete Experiment 2A and B over two separate testing sessions. In Experiment 2A, the behavior of these patients was compared to healthy comparison participants matched to the patients on age, sex, handedness, and education[1]. For Experiment 2B, the performance of the hippocampal amnesic participants was compared to a separate group of 7 healthy comparison participants (4 females, 3 males) matched to the hippocampal patients on age and education.

EXPERIMENT 2A

Measures

Empathy induction through audio recording. We adapted an empathy induction procedure from Beadle (2011) where participants listened to two audio recordings that included a neutral condition and an empathy condition. In the original version of the procedure, participants were told they were overhearing a conversation between their opponents in an economic game and a research assistant over a speakerphone. Here, participants listened to the exact same recording but were told that they were in fact listening to an audio recording. In pilot studies of these two versions of the task (overhearing vs. recording), we found the two versions to be comparable in their effectiveness in inducing empathy in 12 healthy adults (25–62 years; see Beadle, 2011 for details).

The premise of the audio recordings were that they were taped conversations between a female Research Assistant in her 20's interacting with a series of two participants in a previously conducted experiment and each of the participants were men of approximately 55 years of age. The Research Assistant made "small-talk" with participants and asked about their day as they were preparing to begin the experiment. In reality, these audio recordings were performed in a sound studio by a series of community theater actors and a graduate student serving in the role of the Research Assistant. In the neutral conversation, a man talks about the events that occurred in his day thus far which included reading the newspaper over breakfast and talking with his wife. The empathy-inducing conversation begins with a man talking about his day and describing how he played a card game, when he reveals that it is the anniversary of his son's death and demonstrates his deep anguish and grief over his loss.

Empathy ratings. Immediately before and after listening to each audio recording, participants completed a self-report questionnaire consisting of items that assessed participants' current level of empathy, as well as other positive and negative emotions (Beadle, 2011). Adapted from the instructions for the Positive and Negative Affective Schedule (PANAS; Watson and Clark, 1994), participants were asked to perform ratings based upon a series of items following the prompt, "Indicate to what extent you feel this way right now, that is, at the present moment" on a rating scale that ranged from 1 ("very slightly or not at all") to 5 ("extremely.") The empathy items on this questionnaire were derived from the emotional response scale that has been used to measure empathic concern in a variety of empathy induction studies in young adults (Batson, 1987,

[1]The healthy comparison participant matched to 2363 in Experiment 1 was no longer available at the time of Experiment 2, and thus a different healthy comparison participant that was matched to 2363 on demographic characteristics completed Experiment 2A.

1991). The specific items that measured empathy in the present study included "sympathetic" and "compassionate." Also drawn from Batson and colleagues emotional response scale were items measuring the social emotion of personal distress. In addition, items were drawn from the PANAS that assessed sadness, hostility, and joviality (Watson and Clark, 1994). Two items were used to measure each domain of emotion (empathy, sadness, joviality, hostility, and personal distress), and then within each individual the two responses were averaged. To determine the level of empathy specifically produced by the empathy induction, a change score was calculated that accounted for baseline ratings prior to each induction as well as due to the neutral condition [Empathy Change Score = (After – Before Empathy Induction) – (After – Before Neutral Induction)].

EXPERIMENT 2B

Measures

Empathy induction through note. The second experiment (Part B) also involved an empathy induction, but in this case empathy was induced in participants through a written note rather than an audio recording. In addition, participants' prosocial behavior was measured in response to the empathy induction. Participants were told that the purpose of the study was to play an economic game against two other participants, one at a time. This paradigm was employed in a previous study of healthy younger and older adults (Beadle et al, under review). Out of the three participants, two would serve in the role of the "Sender," meaning that they would be asked to write a note about something interesting that recently happened to them, and one of them would be in the role of the "Receiver" who would read the notes from the opponents immediately prior to playing them in a series of economic games. The use of notes to induce empathy in an economic game context was adapted from methodology by Batson and colleagues (Batson et al., 1995; Batson and Moran, 1999), while the specific content of the notes used in this experiment was the same as that used by Beadle and colleagues (Beadle et al, under review). The content of the empathy induction note consisted of the participant describing that they recently found out they have a potentially fatal form of skin cancer, and their thoughts and feelings as they attempted to cope with this news. In the neutral note, the participant describes a series of errands they completed in the downtown area, and then in order to make the arousal level more similar to that of the empathy note, the participant discusses being followed on the freeway by another car that eventually drives away. The participants performed empathy ratings immediately prior to reading each note and immediately afterward. The self-report scale used in this experiment was the same as the one described in Experiment 2A.

Empathy and prosocial behavior. Prosocial behavior was measured as the amount of money ($) given to a game opponent on a standard economic game, the Dictator Game, in response to the neutral condition and the empathy condition. In the Dictator Game, the participant must decide how they would like to split $10 with their game opponent, and their opponent must accept any offer amount. The participant who is splitting the money must follow a few rules: (1) the split must add up to $10; (2) the offer must be in dollar increments; and (3) the offer must range between $1–9. Behavior on the dictator game due to the empathy condition was compared to the control neutral condition.

RESULTS

EMPATHY RATINGS

Empathy induction through audio recording

In comparing the empathy ratings in response to the neutral and empathy conditions, 2363 and 1846 had an empathy change score of 0, indicating that the empathy condition did not produce greater empathy ratings than the neutral condition in these patients (see **Table 4**). The healthy comparison participant matched to 1846 showed an empathy change score of a 2 point increase due to the empathy induction (vs. the neutral induction) and the healthy comparison participant for 2363 showed an increase in empathy of 1 point.

Empathy induction through note

Participants with hippocampal amnesia reported experiencing lower empathy after undergoing an empathy induction (see **Table 4**) than a group of healthy comparison participants. Specifically, 1846 had a change score of 0 from her ratings on the empathy condition vs. the neutral condition, and this was less than 1 SD away from the healthy comparison group mean (M=1.43, SD=1.59, Median=1). Participant 2363's change score included a decrease of 1.5 points in empathy in comparison to the neutral condition and this was approximately 2 SD's away from the healthy comparison group mean.

EMPATHY AND PROSOCIAL BEHAVIOR

Hippocampal amnesic participants gave no more money to their game opponent in the neutral condition than in the empathy condition, and this differed from the group of healthy comparison participants who gave more money in the empathy condition than the neutral condition. 1846 gave $4 in the neutral condition and $4 in the empathy condition, while 2363 offered $6 in the neutral condition and $6 in the empathy condition. The healthy comparison participants gave on average $4.14 in the neutral condition (SD=1.68) and $5.71 in the empathy condition (SD=1.25). 1846 and 2363 showed no difference between the amount of money they gave in the neutral and empathy conditions ($0 change score), while the healthy comparison group gave on average $1.57 ($SD$=1.62, Median=$2) more in the empathy condition than in the neutral condition. The hippocampal amnesic participants' responses were about 1 SD away from the healthy comparison group mean.

DISCUSSION

We propose that the hippocampus is intimately tied to a set of cognitive processes, and is a critical component of the network of brain structures, that supports aspects of social cognition. Here, we extended this proposal to test a hypothesis about the role of the hippocampus in empathy. We found preliminary evidence that hippocampal amnesia is associated with reduced cognitive and emotional empathy relative to healthy comparison participants. Patients with hippocampal amnesia had lower ratings of trait empathy on self-report questionnaires of both cognitive and emotional empathy when compared to healthy demographically

Table 4 | Empathy inductions: ratings.

Rating	Exp. type	Neutral condition					Empathy condition				
		1846	1846C	2363	2363C	NC M (SD)	1846	1846C	2363	2363C	NC M (SD)
EC	Recording	.50	.00	.00	.00	.00 (.00)	.50	2.00	.00	1.00	1.50 (.71)
	Note	−.50	NA	.50	NA	−.36 (1.21)	−.50	NA	−1.00	NA	1.07 (.67)
HOS	Recording	.00	.00	.00	.00	.00 (.00)	.50	.00	.00	.00	.00 (.00)
	Note	.00	NA	.00	NA	.50 (1.12)	.00	NA	.00	NA	.14 (.38)
JOV	Recording	−1.00	.00	.00	.00	.00 (.00)	−1.50	−.50	−3.00	−.50	−.50 (.00)
	Note	.00	NA	.00	NA	−.64 (1.14)	−.50	NA	.00	NA	−1.00 (.96)
PD	Recording	−1.00	.00	.00	.00	.00 (.00)	−.50	.00	1.00	.00	.00 (.00)
	Note	.00	NA	.00	NA	.50 (1.00)	−1.00	NA	.00	NA	1.21 (1.58)
SAD	Recording	−.50	.00	.00	.00	.00 (.00)	1.00	1.00	1.00	.50	.75 (.35)
	Note	.00	NA	.00	NA	−.07 (.73)	−1.00	NA	.00	NA	1.29 (1.11)

Values represent change scores of participants' self-report ratings completed immediately before and immediately after each type of induction. Change score, Rating After – Before Condition (Neutral or Empathy); EC, empathic concern subscale; HOS, hostility subscale; JOV, joviality subscale; PD, personal distress subscale; SAD, sadness subscale; Exp., Experiment; C, healthy matched comparison participant rating; NC, for recording study: represents the mean of the normal, healthy matched comparison participants (N=2). For note study: represents the mean of the healthy comparison group (N=7). NA, not applicable.

matched participants, normative data of healthy younger adults, and to older adults who are assumed to have experienced age-related changes to hippocampal function. These self-ratings were consistent with family member ratings, which were either equal to or lower than that of the patients themselves in the majority of cases. Results from the behavioral empathy studies corroborate the self-report data providing preliminary evidence that the hippocampus may be necessary for some aspects of healthy empathy.

A growing body of work suggests that hippocampal memory processes contribute to a variety of other cognitive domains. At the heart of proposals regarding how the hippocampus contributes to capabilities as diverse as visual perception, problem solving, and language processing, to name a few, is the functionality and core processing features of the hippocampus. Here we have expanded the reach of the hippocampus to the neural network that supports social cognition and empathy. Linking disruptions in empathy to the hippocampus demonstrates how promiscuously the hallmark processing features of the hippocampus are used in service of a variety of cognitive domains.

Like other complex behaviors, empathy requires the coordination and orchestration of cognitive and neural systems. Empathy is characterized by the fact that its diverse components must function together in a relational, flexible, and on-line manner in order for effective empathic responding to occur. For instance, in terms of cognitive empathy, the process of perspective-taking necessitates the flexible integration and retrieval of previously acquired memories and social knowledge relevant to the situation in order to imagine and predict the mental state of another person. For emotional empathy, an important interplay must occur between an individual's vicarious emotional response to another person's emotional state and adequate emotion regulation of that state in order to experience empathic concern for the other person. This process is likely to require on-line monitoring and updating of one's own and others' emotional states. We have argued that the functionality of the hippocampus, in its support of relational binding, representational flexibility, and on-line processing, is well suited to meeting the demands of some aspects of empathy.

While the inclusion of the hippocampus to the neural network of social cognition is supported by our preliminary results on empathy disruptions in patients with hippocampal amnesia, it also raises a number of interesting and open questions about the nature and timing of hippocampal contributions and the interactions with the rest of the network. It will be informative in future work to differentiate the contributions of distinct neural and cognitive systems to empathy and the patterns of impairments in patients with selective damage across the empathy network. For example, with respect to hippocampal contributions, the ability to recognize, process, and experience basic emotions appears to be independent of the hippocampus and instead would be the purview of other neural systems (e.g., amygdala). However, once the processing demands of empathy require the binding of this information to a person and a context, the continuous updating of information, and the flexible deployment of this information in dynamic and evolving situations, patients with hippocampal amnesia are particularly challenged.

While it makes good sense that hippocampal damage and profound amnesia would significantly impair the acquisition and updating of new social information, can the patients rely on their remote episodic and semantic knowledge, that is often judged to be intact, to produce an appropriate empathic response in some contexts? The patients would certainly be in a better position to marshal information from their remote autobiographical memory in service of producing an appropriate empathic response than if they had to rely exclusively on information acquired in the recent past, in the window of their anterograde amnesia. The question, however, is would that remote knowledge be sufficient? And, would the result be the same as someone without hippocampal damage?

While we are unaware of any evidence that directly addresses this, we would speculate that the patients with hippocampal amnesia would still be disadvantaged and would not produce a fully normal empathic response relying on remote autobiographical memory alone. One reason for this line of thinking is that the hippocampus plays a role in the flexible manipulation and use of declarative memory. That is, even if representations of a previous empathic response were retrieved from memory, there are still hippocampal contributions, as the use of the reconstructed episode would require the active maintenance of relational information as judgments and comparisons are made between the previous and current situation. These are certainly interesting and open questions for future work on empathy and on the nature of preserved episodic memory more broadly.

Recent literature has suggested that during the process of perspective-taking the hippocampus may show greater recruitment when thinking about the mental states of others who are more similar to us (or known) or in situations that we have encountered (Perry et al., 2011; Rabin and Rosenbaum, 2012). It is thought that the hippocampus may show greater recruitment because the individual may have more relevant personal memories that can serve as a guide in predicting the mental state of a known other (Rabin and Rosenbaum, 2012). On the other hand, there is some evidence for a reduced role for the hippocampus in understanding the mental states of strangers (Rosenbaum et al., 2007). While this question was not addressed specifically in our study, there is some evidence for disruption in thinking about the mental states of close others (as measured by the questionnaires) and strangers (as measured by the empathy induction). Anecdotal reports by the family members about their ability to detect others' mental states, suggest that they have difficulty detecting the thoughts and feelings of their family members. Given the nature of the measures and the limited amount of data, of course, we cannot say if there is a disproportional contribution of the hippocampus to thinking about strangers or close others, but this remains an interesting question for future research.

It is likely that non-declarative forms of memory contribute to some aspects of empathy. Indeed, non-declarative forms of memory such as priming have been evoked to account for a range of social phenomena (Chartrand and Bargh, 1999; Milne and Grafman, 2001; Garrod and Pickering, 2009) and may contribute at some level to the complex set of processes that result in an empathic response. Understanding the interaction and time course of memory systems with other neural systems critical for social behavior will further our conceptualization of the network supporting the social brain.

While this study offers preliminary support for the notion that the hippocampus contributes to the neural network supporting empathy, there are certain caveats and limitations of the study that should be noted. The hippocampal patients did not report elevated levels of empathy following the induction protocol using two separate methods of empathy induction conducted on two separate occasions. However, these same induction procedures were successful in inducing empathy in healthy comparison participants (Beadle, 2011; Beadle et al, under review) and in individuals with frontal lobe damage in another study (Beadle, 2011). This result is also in contrast to our previous work inducing happiness and sadness in patients with hippocampal amnesia (Feinstein et al., 2010). Nevertheless, the amnesic patients did not report elevated empathy and thus we did not see an increase in prosocial behavior. While methodological differences in the induction protocols should be considered further, we are intrigued by the possibility that the hippocampus may not be required for the experience (and induction) of basic emotions but that it is required for social emotions such as empathy. Already there is some evidence that social emotions may recruit a different neural system than basic emotions (Moll et al., 2002). The hippocampus may be recruited for the processing of social information and emotions due to its role in relational thinking, i.e., thinking about others' mental states and retrieving relevant autobiographical memories to understand others. Future work to explore this idea is warranted. The small sample size and the lack of familiar partner ratings of empathy from the healthy comparison participants are also limitations. Future replication and extension of this work is needed.

The goal of the current work was to argue for the inclusion of the hippocampus in the larger neural network supporting social behavior and empathy. Our preliminary results suggesting that hippocampal damage produces a deficit in empathy have implications for studying empathy in other populations where hippocampal pathology and declarative memory impairments are common (e.g., normal aging, Alzheimer's Disease and other dementias, schizophrenia, and Traumatic Brain Injury). Indeed, because the hippocampus has not routinely been considered to be a significant part of the network critical for social behavior, such deficits are seldom attributed to the impairments in declarative memory that are a hallmark in so many patients that also have deficits in empathy.

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Imagining other people's experiences in a person with impaired episodic memory: the role of personal familiarity

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Difficulties remembering one's own experiences via episodic memory may affect the ability to imagine other people's experiences during theory of mind (ToM). Previous work shows that the same set of brain regions recruited during tests of episodic memory and future imagining are also engaged during standard laboratory tests of ToM. However, hippocampal amnesic patients who show deficits in past and future thinking, show intact performance on ToM tests, which involve unknown people or fictional characters. Here we present data from a developmental amnesic person (H.C.) and a group of demographically matched controls, who were tested on a naturalistic test of ToM that involved describing other people's experiences in response to photos of personally familiar others ("pToM" condition) and unfamiliar others ("ToM" condition). We also included a condition that involved recollecting past experiences in response to personal photos ("EM" condition). Narratives were scored using an adapted Autobiographical Interview scoring procedure. Due to the visually rich stimuli, internal details were further classified as either descriptive (i.e., details that describe the visual content of the photo) or elaborative (i.e., details that go beyond what is visually depicted in the photo). Relative to controls, H.C. generated significantly fewer elaborative details in response to the pToM and EM photos and an equivalent number of elaborative details in response to the ToM photos. These data converge with previous neuroimaging results showing that the brain regions underlying pToM and episodic memory overlap to a greater extent than those supporting ToM. Taken together, these results suggest that detailed episodic representations supported by the hippocampus may be pivotal for imagining the experiences of personally familiar, but not unfamiliar, others.

Keywords: episodic memory, theory of mind, hippocampus, amnesia, social cognition

INTRODUCTION

Amnesia following damage to the hippocampus has been characterized by impaired episodic memory for personally experienced events. However, there is growing evidence that other, non-mnemonic processes may be compromised in amnesia as well. These findings have led researchers to suggest a broader role for the hippocampus and episodic memory that goes beyond recalling past personal experiences. Much of this work has focused on the idea that episodic memory is necessary for imagining possible future scenarios (Tulving, 1985; Klein et al., 2002; Okuda et al., 2003; Rosenbaum et al., 2005; Addis et al., 2007; Szpunar et al., 2007; Andelman et al., 2010), whereas much less attention has been paid to the role that episodic memory plays in social behavior. In the current study, we examined if, and under what conditions, the ability to remember and imagine one's own experiences serves a social function in facilitating the ability to imagine other people's experiences.

An impressive body of research has shown that episodic memory, supported by the hippocampus, is closely related to the ability to imagine one's own personal future. Amnesic individuals with hippocampal damage who are unable to recollect past events also have difficulty imagining themselves in future events (Tulving, 1985; Klein et al., 2002; Rosenbaum et al., 2005; Andelman et al., 2010). Consistent with this finding, neuroimaging studies have revealed that both abilities recruit a similar set of brain regions that include the hippocampus and adjacent medial temporal lobe (MTL) regions as well as medial frontal, medial parietal, and lateral temporal cortex (Okuda et al., 2003; Addis et al., 2007; Szpunar et al., 2007). Some of these studies have included a control condition in which participants are asked to imagine the experiences of an "average" person or a famous person, which appears to engage regions within the MTL as well, albeit to a lesser extent (Szpunar et al., 2007; see also Gilboa et al., 2004). However, it may be the case that episodic memory and associated MTL function play an important role in imagining other people's experiences, as suggested by qualitative reviews and meta-analyses of the neuroimaging literature. These studies show that the same set of brain regions activated during tests of episodic memory and future imagining are also engaged during standard tests of theory of mind (ToM; Buckner and Carroll, 2007; Hassabis and Maguire, 2007; Spreng et al., 2009).

In addition to an overlapping set of brain regions, episodic memory, future imagining, and ToM emerge close in time in ontogenetic development (Perner and Ruffman, 1995; Atance and O'Neil, 2001; Perner et al., 2007) and tend to be impaired in patients with schizophrenia (Corcoran and Frith, 2003; D'Argembeau et al., 2008) and high functioning autism and Asperger's syndrome (Adler et al., 2010; Lind and Bowler, 2010). These findings lend support to an influential theoretical perspective that individuals draw on past experiences via episodic memory to simulate future personal experiences and to imagine other people's experiences during ToM (Gordon, 1986; Goldman, 1992; Corcoran, 2000, 2001; Gallagher and Frith, 2003; Buckner and Carroll, 2007; Schacter and Addis, 2007; Spreng and Mar, 2012). However, work with hippocampal amnesic patients shows preserved performance on standard tests of ToM despite impaired episodic memory and future imagining (Rosenbaum et al., 2007; Rabin et al., 2012). Standard ToM tests included in these studies ranged from predicting a character's false belief (Stone et al., 1998) and identifying a faux pas (Stone et al., 1998) based on narratives, to inferring others' thoughts and emotions based on viewing the eye region of faces (Baron-Cohen et al., 2001). The amnesic patients' successful performance on these tests may have been achieved via semantic memory, which remains relatively intact in these patients (Rosenbaum et al., 2007). This might include reliance on social knowledge of the average person's thoughts, feelings, and intentions in different circumstances (Lieberman, 2012).

More recent neuroimaging studies have directly compared episodic memory with ToM in the same individuals using more naturalistic stimuli (Rabin et al., 2010; Spreng and Grady, 2010; St. Jacques et al., 2011; see also Gilboa et al., 2004; Szpunar et al., 2007). These studies revealed that relative to recalling past episodes, imagining the experiences of other people elicited less activity within MTL and midline regions. However, the "other" targets in these studies were not intimately known by participants (i.e., strangers or public figures). It is possible that when the target person is personally known, shared past experiences can influence participants' current social processing. Indeed, knowing someone for a long period of time and observing that person's behavior in different situations provides a rich source of information from which one can draw when imagining his/her mental states in specific situations. Consistent with this idea, Rabin and Rosenbaum (2012) recently showed that imagining the experiences of personally familiar versus unfamiliar others preferentially engaged regions known to support episodic memory, suggesting a strategy of relying on past personal experiences when the target person is personally known. In another study, Krienen et al. (2010) focused exclusively on midline frontal regions and found greater anterior medial prefrontal cortex and rostral anterior cingulate cortex activity for judgments relating to participants' friends versus strangers. In fact, participants in that study indicated that they relied on a specific memory or anecdote significantly more often for judgments relating to friends than strangers. Perry et al. (2011) showed that hippocampal activity during judgments of others' emotional states was specific to conditions in which the protagonist was deemed similar to the self and when the event had occurred in the participant's own life. Taken together, these studies suggest that episodic memory may serve a social role in imagining other people's experiences, but only when intimacy or closeness exists between the participant and the perceived other.

In the current study, we test the idea that episodic memory is necessary for imagining events from the perspective of personally known others. One way to address this question is to assess whether a person with hippocampal amnesia and impaired episodic memory is able to imagine events experienced by well-known others, including reconstructing others' thoughts and feelings. Here, we test H.C., a unique young woman with normal intellectual function despite impaired development of her episodic memory due to selective hippocampal damage 1 week after birth (Vargha-Khadem et al., 2003; Rosenbaum et al., 2011; see also Kwan et al., 2010; Hurley et al., 2011). Importantly, as was the case for the adult-onset hippocampal amnesic cases described above, we recently found that H.C.'s performance on a wide range of standard ToM tests was indistinguishable from that of controls (Rabin et al., 2012). We believe that her preserved ToM performance is due to reliance on her semantic memory and general knowledge abilities, which remain relatively intact (Rabin et al., 2012). In the current study we employed a naturalistic test of ToM that involved describing the experiences of other people in response to photos of personally known others (i.e., relatives and close friends; "pToM" condition) and unknown others ("ToM" condition) engaging in specific events. We also included a condition that involved recollecting past experiences in response to personal photos ("EM" condition). This naturalistic task was selected because it is less constrained than most standard tests of ToM and therefore better captures ToM as it occurs in everyday life. Findings of impaired pToM that parallel H.C.'s episodic memory deficit would suggest that pToM relies on episodic memory or that a common process mediates both abilities. Alternatively, it may be the case that intact aspects of H.C.'s semantic memory are sufficient to support mental state inferences involving pToM and ToM, and therefore H.C. would show intact performance on both tasks, similar to her performance on standard ToM tests.

MATERIALS AND METHODS

PARTICIPANTS

H.C. is a right-handed woman who was 20 years old at the time of testing. A second testing session was performed when H.C. was 23 years old for reliability purposes. She was born prematurely and suffered hypoxic damage, which led to reduced bilateral hippocampal volume by approximately 50% relative to healthy controls (Vargha-Khadem et al., 2003; Hurley et al., 2011; see Rosenbaum et al., 2011 for a detailed neuropsychological profile). H.C.'s compromised bilateral hippocampal development appears to have precluded normal development of her episodic memory. Her impairment affects her personal and public event memory more than her personal and general semantic memory (Rosenbaum et al., 2011), which is consistent with other developmental amnesic cases (Gadian et al., 2000). H.C. successfully graduated from a mainstream high school and completed 1 year of technical college. At the time of the first testing session, she was enrolled in a post-secondary culinary program but withdrew after 1 year.

H.C. has formed a normal number of close relationships (Davidson et al., 2012, this issue) and was engaged to be married at the second time of testing.

H.C.'s performance on all measures was compared with that of 18 right-handed, healthy women with no reported history of neurological or psychiatric illness (mean age = 19.4, SD = 1.3; mean education = 13.3, SD = 1.1). All participants gave informed written consent in accordance with the ethics review boards at York University and Baycrest. Participants received monetary compensation for their time.

STIMULI

We employed a novel, naturalistic test of ToM that involved describing others' thoughts and feelings in response to photos of personally familiar others ("pToM" condition) and unfamiliar others ("ToM" condition) engaging in specific events. We also included a condition that involved recollecting past experiences in response to personal photos ("EM" condition; Rabin and Rosenbaum, 2012).

The pToM condition involving personally known others consisted of 15 photos depicting specific events that had been experienced by family members and close friends but not by the participant him/herself. The ToM condition involving unfamiliar others consisted of 15 photos depicting strangers engaged in specific events. The EM condition consisted of 15 personal family photos of events that took place within the past 1–5 years. H.C. and 13 of the 18 control participants appeared in each EM photo to help verify that the participant personally experienced the event. Analyses confirmed that the presence or absence of the control participants in the EM photos did not affect the behavioral results (i.e., average number of internal details did not differ, $t(16) = -0.47$, $p = 0.64$). The pToM and EM photos were collected by a relative or close friend of each participant, whereas the ToM photos were collected by the experimenter. Themes were similar across the three conditions (e.g., birthday party, picnic, vacation) and included both indoor and outdoor scenes. All photos were resized and converted to gray scale.

TASK

H.C. and the control participants were scanned with fMRI while performing the family photos task (fMRI data not reported here). Stimuli were presented in blocks and each block contained five photos from one of the three conditions. There were three blocks for each condition (for a total of nine blocks) and these were presented in pseudorandom order. At the beginning of each block, participants viewed a set of instructions that corresponded to one of the three conditions (i.e., pToM, ToM, or EM). Each photo was presented for 20 s and was followed by three rating scales (see below).

In the pToM and ToM conditions, participants were presented with photos of other people and asked to generate a novel event for each photo while focusing on what one person in the photo might have been thinking and feeling at the time. In order to distinguish imagining from remembering, participants were specifically instructed not to draw on past experiences when generating these events. In the EM condition, participants were presented with their own photos and asked to recollect the event depicted in each photo in as much detail as possible. They were told to focus on what they were thinking and feeling at the time.

Following the presentation of each photo, participants rated the events they imagined/recollected on a number of dimensions. Three ratings scales were presented after each photo. The first rating scale differed for the pToM/ToM and EM events. The pToM and ToM events were rated for likeness to an actual memory (1 = exactly like a memory ... 4 = nothing like a memory), whereas the EM events were rated on the extent to which the events were recollected (1 = don't know event; 2 = familiar with event; 3 = remember event; Gardiner et al., 1998; Tulving, 1985). Participants were instructed to select "remember" if the event was specific to a time and place and they could re-experience it, to select "familiar with event" if the event was familiar to them, but they could not recall any specific contextual or other experiential details associated with the event, and to select "don't know event" if they were unable to recall any aspect of the event. The next two ratings scales were employed for all conditions. One scale assessed the amount of detail generated for each event (1 = not vivid ... 4 = very vivid) and the other scale assessed the spatial coherence of each event (contiguousness of the spatial context: 1 = fragmented scenes ... 4 = continuous scene; Hassabis et al., 2007; not reported in the current study).

Prior to the scan, a short training session was provided to ensure that participants fully understood the task instructions. The photos used in the training session were not used during the scan.

Immediately following the scan, participants took part in an interview in which they viewed the same photos that had been presented in the scanner. Participants were asked to think back to the events they generated in the scanner and to rate each event on the same three scales that were presented in the scanner. The photos with the highest vividness ratings (approximately two-thirds of all photos) were selected for a semi-structured interview in which participants described the events as they had been imagined/recollected in the scanner.[1] High vividness ratings were taken to suggest that participants were indeed imagining or recollecting the events. There was no time limit for participants to describe the events, and participants continued with their descriptions until they came to a natural ending point. The examiner then provided a single, standardized probe to elicit additional details (e.g., "Can you tell me anything else?"). The events were recorded and transcribed for scoring.

Control participants were tested on the family photos paradigm once whereas H.C. was tested on the paradigm on two separate occasions for reliability purposes. However, the EM events that were included during H.C.'s first testing session were excluded because we subsequently learned that she frequently views and rehearses the events depicted in these photos.

SCORING

Narratives were scored using an adapted Autobiographical Interview scoring procedure described by Levine et al. (2002). The

[1]During session 2, H.C. was interviewed on all of the photos presented during the scan as well as eight additional EM events, which were not presented in the scanner, in order to increase power.

pToM, ToM, and EM events were first segmented into distinct details, which were classified as internal (including event-specific, temporal, perceptual, spatial, and thought/emotion details) or external (i.e., semantic facts that were irrelevant to the central event, repetitions, and metacognitive statements). Given the use of visually rich photos as cues, we wanted to ensure that participants' performance was not inflated due to merely describing the details depicted in the photos. Therefore, internal details were further classified as either descriptive (i.e., details that describe the visual content of the photo) or elaborative (i.e., details that go beyond what is visually depicted in the photo; see **Table 1** for scoring criteria).

Scoring of the narratives was conducted by a trained rater who achieved high interrater reliability on the Autobiographical Interview using a standard set of previously scored memories (see Levine et al., 2002). Interrater reliability was also calculated for the elaborative and descriptive details based on criteria developed by JSR. Intraclass correlation analyses indicated high agreement among scorers for pToM (Cronbach's $\alpha = 0.994$), ToM (Cronbach's $\alpha = 0.992$), and EM events (Cronbach's $\alpha = 0.994$).

Data were analyzed using a modified t-test procedure, which compares test scores of a single patient to that of a small control sample (Crawford and Howell, 1998). Two-tailed t-tests were used to compare H.C.'s performance with that of controls on the pToM and ToM conditions, whereas a one-tailed t-test was used for the EM condition given *a priori* hypotheses regarding H.C.'s episodic memory performance.

RESULTS

As mentioned above, H.C. was tested on two separate occasions. For completeness, we report the data separately for the two testing sessions. Each control participant contributed an average of 8.9 pToM events (SD = 0.72), 9.1 ToM events (SD = 0.9), and 9.3 EM events (SD = 0.49) to the analyses. In session 1, H.C. contributed 7 pToM events and 9 ToM events to the analyses. In session 2, H.C. contributed 15 pToM events, 12 ToM events, and 18 EM events to the analyses.

PHENOMENOLOGY OF THE pToM, ToM, AND EM EVENTS

We entered participants' post-scan ratings into the analyses (as opposed to the within-scanner ratings) as these were believed to better correspond with the events participants described during the post-scan interview. **Table 2** presents participants' phenomenological ratings of the pToM, ToM, and EM events. In terms of vividness, H.C. rated the pToM events in session 1 as less vivid than controls, $t(17) = -2.68$, $p = 0.02$; there was no difference for the pToM events in session 2, $t(17) = -0.73$, $p = 0.48$. With respect to the ToM events, vividness did not differ between H.C. and controls for session 1, $t(17) = -0.97$, $p = 0.34$, or session 2, $t(17) = -1.46$, $p = 0.16$. For the EM events, H.C.'s ratings were significantly less vivid than that of controls, $t(17) = -3.89$, $p = 0.0006$. In terms of the ratings assessing likeness to an actual memory, no significant differences emerged between H.C. and controls for the pToM and ToM events in session 1 or session 2 [pToM session 1 and session 2, $t(17) = -1.56$, $p = 0.14$, and $t(17) = -0.38$, $p = 0.70$, respectively, and ToM session 1 and session 2, $t(17) = -0.58$, $p = 0.57$, and $t(17) = -0.58$, $p = 0.57$, respectively]. Finally, as expected, H.C.'s ratings relating to the recollection of EM events were significantly lower than that of controls, $t(17) = -9.73$, $p < 0.00001$.

ADAPTED AUTOBIOGRAPHICAL INTERVIEW

Given the use of visually rich photos as cues, we were most interested in the elaborative details that participants generated. We analyzed the data in two ways. First, we compared the average number of elaborative details H.C. and controls produced in response to each pToM, ToM, and EM event. These absolute numbers, however, are confounded by participants' total verbal output. To overcome this issue, we also calculated the proportion

Table 1 | Classification of descriptive versus elaborative details.

Type of detail	Descriptive details	Elaborative details
Action	Any detail referring to an action that is depicted in the photo (e.g., sitting, walking, standing, posing for the photo)	Any detail describing an action that is not obvious from the photo
Character	Any detail explaining who the people are in the photo (only for the pToM and EM conditions)	Any detail describing who the people are or any detail that refers to the relationship(s) between the people depicted in the photo (only for the ToM condition)
Temporal	N/A	Any detail referring to a specific time period (e.g., year, season, month, date, day of week)
Perceptual	Perceptual details that are depicted in the photo (e.g., big crowd of people, candles everywhere). Describing or naming an object, monument or statue that is depicted in the photo (e.g., Statue of Liberty)	Perceptual details that are not visible in the photo
Emotion/thought	Any detail describing a facial expression (e.g., smiling, frowning)	Any detail describing an emotion or mental state (e.g., happy, sad, tired)
Spatial/Place	Any detail describing a location (e.g., country, city, street, location within a room) that can be inferred from information presented in the photo (e.g., sign)	Any detail describing a location (e.g., country, city, street, location within a room) that is not apparent from information depicted in the photo

Table 2 | Phenomenological qualities of the generated pToM, ToM, and EM events.

	pToM	ToM	EM
Vividness			
H.C. session 1	2.1*	2.7	–
H.C. session 2	2.9	2.5	2.8*
Controls	3.2 (0.4)	3.1 (0.4)	3.6 (0.2)
Remember/know			
H.C. session 1	–	–	
H.C. session 2	–	–	2.6*
Controls	–	–	3.0 (0.04)
Similar to a Memory			
H.C. session 1	2.7	3.3	–
H.C. session 2	3.3	3.3	–
Controls	3.5 (0.5)	3.6 (0.5)	–

*Standard deviations are given in parentheses; pToM, personal theory of mind; ToM, theory of mind; EM, episodic memory; *$p < 0.05$.*

of elaborative-to-total internal details, which provides an index of the weight given to descriptive versus elaborative details.

The mean number of elaborative details produced by participants in response to each pToM, ToM, and EM event is presented in **Figure 1**[2]. In response to the pToM events, H.C. produced significantly fewer elaborative details than controls during session 1, $t(17) = -3.1$, $p = 0.007$, and there was a trend toward impaired performance during session 2, $t(17) = -1.8$, $p = 0.08$. In terms of the ToM events, no significant group difference emerged for session 1, $t(17) = -1.6$, $p = 0.13$, or session 2, $t(17) = -0.98$, $p = 0.34$. With respect to the EM events, as expected, H.C. produced significantly fewer elaborative details than controls, $t(17) = -1.78$, $p = 0.047$[3].

The mean proportion of elaborative-to-total-internal details produced by participants in response to each pToM, ToM, and EM event is presented in **Figure 2**. Analyses revealed that H.C. produced a lower proportion of elaborative details (and therefore a greater number of descriptive details) than controls in response to the pToM events during both session 1, $t(17) = -7.0$, $p < 0.00001$ and session 2, $t(17) = -4.99$, $p = 0.0001$. In contrast, H.C. and controls produced an equivalent proportion of elaborative details in response to the ToM events during both session 1, $t(17) = 0.77$, $p = 0.45$, and session 2, $t(17) = -0.32$, $p = 0.75$. Consistent with our predictions, H.C. generated a lower proportion of elaborative details relative to controls in response to the EM events, $t(17) = -2.57$, $p = 0.01$.

DISCUSSION

H.C., a developmental amnesic person with bilateral hippocampal damage, was impaired at imagining the experiences of personally known others, which resembles her compromised ability to recall past experiences via episodic memory. These impairments stand in contrast to her preserved ability to imagine the experiences of unknown others. This pattern of results held whether we analyzed the average number of elaborative details (i.e., details that go beyond what is visually depicted in the photo) or the proportion of elaborative-to-total-internal details in order to control for verbal output. These results bolster the finding that different neural and cognitive mechanisms support thinking about personally known versus unknown others and that the former may depend on processes mediated by the hippocampus and episodic memory.

The idea that individuals rely on past personal experiences to infer and simulate another's mental state has been suggested by philosophers and cognitive neuroscientists alike (Corcoran, 2000, 2001; Gallagher and Frith, 2003; Buckner and Carroll, 2007; Spreng and Mar, 2012). However, the current findings indicate that reliance on past personal experiences may be pivotal only when imagining the experiences of personally known others. Indeed, knowing an individual for a long period of time and observing that person's behavior in different situations provides a rich source of information from which one can draw when imagining his/her mental states in various situations. Consistent with this interpretation, Krienen et al. (2010) showed that participants reported that they relied on a specific memory or anecdote significantly more often when making judgments relating to friends relative to strangers. In another study, Ciaramelli et al. (submitted) found that participants' level of empathy for a familiar character was modulated by the retrieval of previous episodes involving that character. Furthermore, using the same family photos paradigm employed in the current study, we (Rabin and Rosenbaum, 2012) showed that the pattern of neural activity supporting pToM shares more in common with episodic memory than with ToM. Notably, the greatest degree of neural overlap between pToM and episodic memory was observed within midline regions, including the hippocampus and related MTL structures, regions traditionally associated with the recollection of past events.

Reliance on past personal experiences to infer familiar others' mental states may occur with or without one's intention or awareness. There is accumulating evidence that episodic memory supported by the hippocampus can rapidly and automatically influence performance on non-mnemonic tasks (Westmacott and Moscovitch, 2003; Westmacott et al., 2004; Moscovitch, 2008; Ryan et al., 2008; Greenberg et al., 2009; Sheldon and Moscovitch, 2010). Gobbini and Haxby (2007) suggest that the mere perception of a familiar individual is associated with the spontaneous retrieval of personal knowledge about that individual (i.e., personal traits, attitudes, biographical facts, and episodic memories), which in turn may help to better understand and predict what the familiar other is thinking and/or feeling. These automatic processes may have been at play in the current study given that participants were instructed not to refer to past episodes when generating the pToM and ToM events. It is possible that participants engaged in inhibitory processes to help overcome the prepotent tendency to rely on past memories. Alternatively, other memory regulation processes, such as thought substitution (Benoit and Anderson, 2012) may have been employed.

[2]Due to the small number of elaborative details produced for each event, we were unable to make meaningful comparisons when the details were further divided into the internal detail categories (i.e., event, place, time, perceptual, thought/emotion).
[3]We did not confirm the accuracy of participants' reported memories. However, anecdotal evidence provided by H.C.'s family suggests that she tends to fill in memory gaps. Therefore, H.C.'s EM scores are likely an overestimate of her episodic memory capabilities.

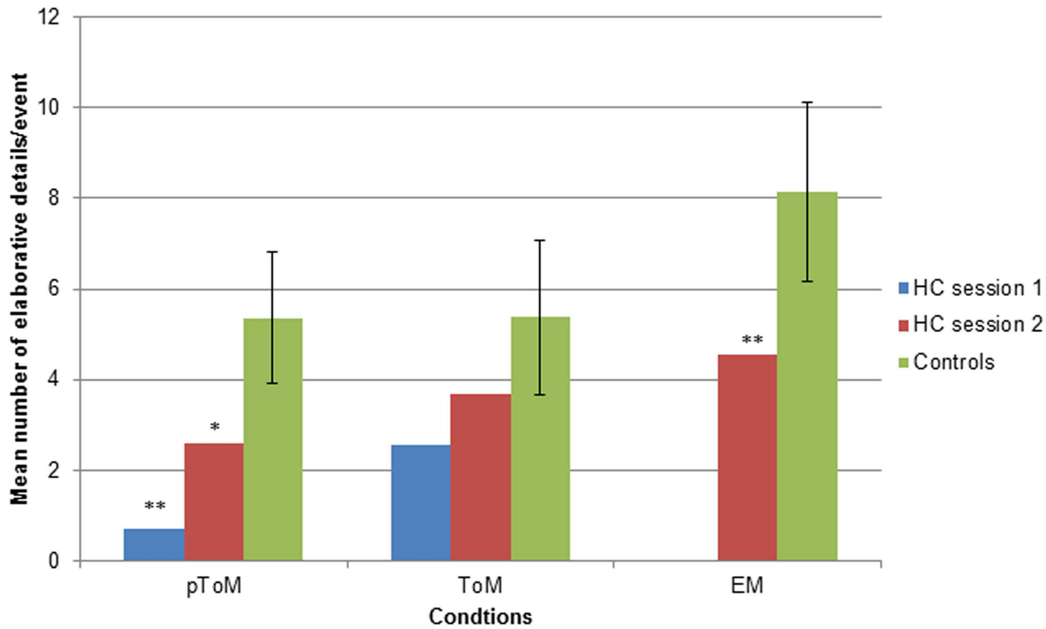

FIGURE 1 | The mean number of elaborative details provided by H.C. and controls in response to each pToM, ToM, and EM event, *$p < 0.08$; **$p < 0.05$. Error bars indicate standard deviations.

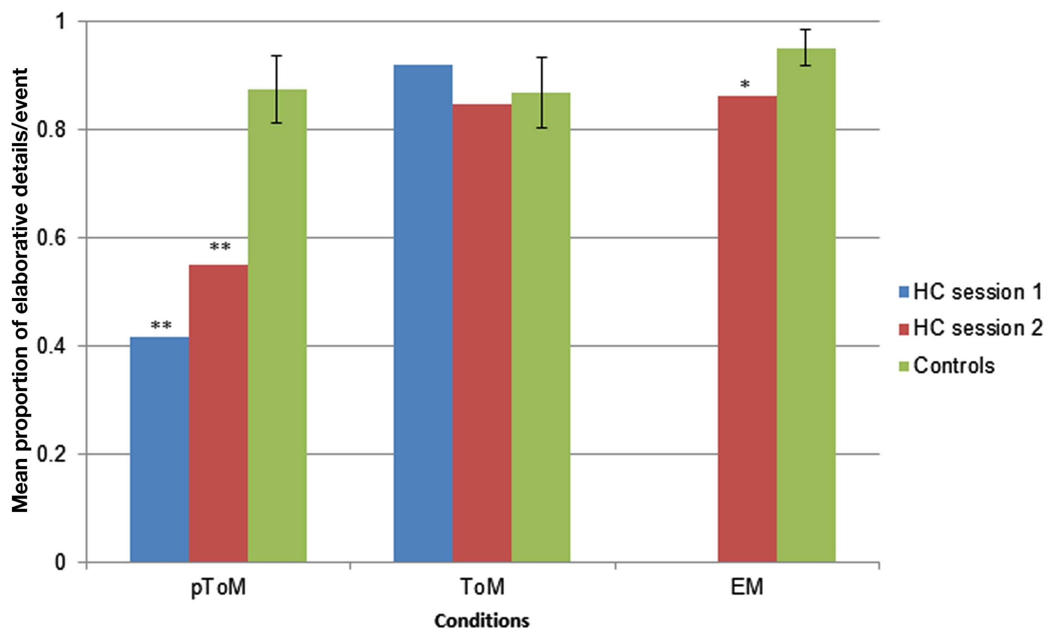

FIGURE 2 | The mean proportion of elaborative-to-total-number of internal details provided by H.C. and controls in response to each pToM, ToM, and EM event, *$p < 0.01$; **$p < 0.0001$. Error bars indicate standard deviations.

Another possible explanation for H.C.'s corresponding impairment in both episodic memory and pToM may relate to a deficit in (re)constructing specific episodes. Evidence from neuroimaging studies suggests that imagining specific versus general past and future events elicits greater activity within the hippocampus (Addis et al., 2011; Ford et al., 2011), likely due to the greater relational processing that is required for the former (Addis et al., 2011). Several researchers have argued that individuals are more likely to imagine close others with greater specificity relative to unknown others. In contrast, unknown others are typically represented in more generic and abstract terms (Liviatan et al., 2008; Lieberman, 2012). This may be because we possess idiosyncratic theories about close others' personalities that enable us to richly imagine how well-known others would respond in various scenarios (see Lieberman, 2012). Therefore H.C.'s difficulty in generating specific details may account for her poor performance on the episodic memory and pToM tasks.

It may be the case that for the pToM events H.C. attempted to rely on a strategy that is optimal for people who are able to conjure up contextual and specific details rather than relying on a strategy that would be advantageous for her. Like controls, H.C. may have been engaging in inhibitory processes of past events when generating the pToM and ToM events. However, because her episodic recollection is impaired, she may have generalized this instruction to personal semantic information, which would have likely helped her to generate additional details for the pToM events. It is possible that if she had been probed in a manner that enabled her to draw more effectively on her intact personal or social semantic memory, she may have performed better on the pToM task. Indeed, different methods of cuing can differentially affect task performance. H.C., for instance, was impaired at imagining herself in future episodes when provided with a specific cue word (e.g., "coffee"; Kwan et al., 2010) but showed intact performance when a more general and non-specific cue was provided (e.g., "Imagine something you will be doing this weekend"; Hurley et al., 2011; see also Cooper et al., 2011).

The corresponding deficit that emerged in episodic memory and pToM is unlikely to be due to a deficit in narrative construction, given that H.C. had no difficulty constructing narratives in response to the ToM events. This pattern of results is consistent with those from a recent study showing that the ability to generate a detailed narrative is preserved in adult-onset amnesia (Race et al., 2011; but see Rosenbaum et al., 2009). Although the patients in the study by Race and colleagues produced impoverished descriptions of past and future events, they showed intact performance when asked to tell a story in response to pictures depicting fictional characters in various scenes. It is important to note that while their participants were instructed to generate a story rather than to report what was literally depicted in the picture, to our knowledge, the authors did not examine whether participants adhered to this instruction. In the current study, when examining the extent to which participants relied on the visual content of the photos to generate details, we found that approximately half of the details H.C. produced for the pToM events consisted of descriptive details (vs. 12.5% for controls). The current findings highlight the importance of examining descriptive versus elaborative details when rich visual cues are used.

H.C.'s impairment in episodic memory and pToM contrasts with her preserved ability to imagine the experiences of unknown others during ToM. The latter finding is consistent with her intact performance on a wide range of standard ToM tests that employ strangers or fictional characters as targets (Rabin et al., 2012; see also Rosenbaum et al., 2007). Imagining the experiences of unfamiliar others may be achieved by relying on social semantic memory, which remains relatively intact in H.C. This might include reliance on generic representations about how the average person is expected to think and feel in a given situation (Lieberman, 2012). Generic representations are likely based on routines or schemas that are already bound together and therefore require minimal relational processing. Recent fMRI findings from our laboratory (Rabin and Rosenbaum, 2012), support this interpretation. Using the same family photos paradigm, we recently showed that relative to pToM, ToM involving unfamiliar others elicited greater activity in lateral regions known to be associated with accessing semantic knowledge (Martin and Chao, 2001). Taken together, these data further corroborate the notion that episodic memory may be needed for social cognition, but that its role may be specific to imagining the experiences of personally known, and not unknown, others.

The use of an open-ended ToM task allowed us to gain insight into possible compensatory strategies that H.C. employed when taking the perspective of another person. We found that H.C. generated a significantly greater proportion of descriptive details in response to the pToM photos than did controls, suggesting that she relied more heavily on the visual information depicted in the photos to imagine the experiences of well-known others. This may have included relying on the familiar other's facial expression, body language, and/or the relative spatial relations between people. This strategy may serve her well in social settings when external cues are readily available but may fail when cues are absent or when situations are complex and require the integration of information from the past and present.

H.C.'s performance on the pToM condition was not at floor indicating that her ability to imagine the experiences of personally familiar others is not obliterated. In fact, approximately 50% of the details she generated in response to the pToM events were elaborative details (i.e., details that go beyond what is visually depicted in the photo). However, upon closer examination, even the qualitative nature of the elaborative details she generated differed from that of controls. Specifically, H.C.'s responses tended to reflect more basic emotional states that could be inferred from the visual features of the photo, such as "they're both really excited" or "she looks really happy." In contrast, control participants typically provided more complex mental state inferences such as "they were probably afraid but they are trying to look cool" and "her mother was pleased that her daughter was having so much fun" (see **Figure 3** for narrative samples).

H.C. generated a greater number of elaborative details in response to the pToM and ToM events during session 2 relative to session 1. It is important to note, however, that the overall pattern remained consistent across the two testing sessions in that, in both cases, H.C. produced fewer elaborative details for the pToM versus ToM events. It is possible that the difference across testing sessions reflects a practice effect resulting from experience with narrative generation. Although our two testing sessions took place 3 years apart, H.C. participated in several other studies that required her to generate detailed narratives in the interim (Kwan et al., 2010, 2011; Hurley et al., 2011). In fact, within these other studies, H.C. showed improved performance on tests of future imagining across testing sessions (Kwan et al., 2010; Hurley et al., 2011). A related explanation for H.C.'s inflated scores during session 2 is that she may have learned to use a more effective strategy that enabled her to generate a greater number of details.

pToM involving familiar others

H.C.: That is my cousin and my uncle, so her dad, and I would assume that they went on a big marathon and they had just finished, and that's why my uncle looks really tired and he looks really happy.

Control: Aunty Debra just drove Michelle to school in Kingston, and she's really sad to see Michelle go because Michelle's growing up now, and she said 'You're so grown up'. And Michelle's like, 'Don't worry, I'll be fine' and Aunty Debra says, 'I know, but this is a huge change for me' and all that stuff. And then she says bye and then when Michelle turns around, she's secretly happy that she's leaving her mother.

ToM involving unfamiliar others

H.C.: I imagined they were in Australia because I think that's where koala bears are from and she was trying to convince her mother who was the one taking the photo. And I was imagining she was trying to convince her mother to let her take the koala bear home. It looks like she really wants it.

Control: This dad and his two sons went apple picking and he's like 'Okay follow me guys'. Then they go on a path less traveled. The dad ends up losing his bearings and getting lost a little bit, and his sons realize that they're lost and they're like 'Oh no, we're lost'. The dad finds his way back and the kids keep on asking 'Dad are you lost?' and he's like 'Of course not'. And then the dad finally finds his way back and he's like 'phew'.

EM

H.C.: That's in Florida. That was at my aunt Jill's… my aunt Jill and uncle Bill had a place in Florida so that was in the pool at their like resort condo sort of place, and that was the second pool I went to because that one was warmer because it was a little shallower.

Control: That is my grandparents' wedding anniversary. And I was thinking about the fact that it was also my 18th birthday. And I wasn't particularly pleased to be there, but my aunt turned up. I hadn't realized that she was going to be coming all the way from Germany. So at that point when the photo was taken, she had just come in and I was really relieved. She had turned up, and I was glad that I came. And I also thought about saying a ridiculously long speech about my grandparents that I had to have memorized. And yeah, that was their wedding anniversary.

FIGURE 3 | Representative samples of the pToM, ToM, and EM narratives provided by H.C. and a control participant.

In the current study, we attempted to control for vividness by only including the pToM, ToM, and EM events with the highest vividness ratings in our analyses. Nevertheless, analyses revealed that H.C. rated the pToM events in session 1 and the EM events in session 2 as less vivid than controls. In addition, we cannot rule out that other factors, such as personal significance, differed between H.C. and controls.

In conclusion, using an ecologically valid test of ToM, we formally document that episodic memory supported by the hippocampus may be pivotal for imagining the experiences of personally familiar, but not unfamiliar, others. The current findings complement recent fMRI data and suggest that when imagining other people's experiences individuals are more likely to rely on episodic memory when the target person is personally familiar and on general social semantic memory when the target person is unknown (Rabin and Rosenbaum, 2012). Continued research with H.C. and other amnesic individuals, particularly those that acquire damage later in life, is needed to better understand the role that episodic memory plays in this and other aspects of social cognition.

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Social cognition in a case of amnesia with neurodevelopmental mechanisms

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Episodic–autobiographical memory (EAM) is considered to emerge gradually in concert with the development of other cognitive abilities (such as executive functions, personal semantic knowledge, emotional knowledge, theory of mind (ToM) functions, language, and working memory). On the brain level its emergence is accompanied by structural and functional reorganization of different components of the so-called EAM network. This network includes the hippocampal formation, which is viewed as being vital for the acquisition of memories of personal events for long-term storage. Developmental studies have emphasized socio-cultural-linguistic mechanisms that may be unique to the development of EAM. Furthermore it was hypothesized that one of the main functions of EAM is the social one. In the research field, the link between EAM and social cognition remains however debated. Herein we aim to bring new insights into the relation between EAM and social information processing (including social cognition) by describing a young adult patient with amnesia with neurodevelopmental mechanisms due to perinatal complications accompanied by hypoxia. The patient was investigated medically, psychiatrically, and with neuropsychological and neuroimaging methods. Structural high resolution magnetic resonance imaging revealed significant bilateral hippocampal atrophy as well as indices for degeneration in the amygdalae, basal ganglia, and thalamus, when a less conservative threshold was applied. In addition to extensive memory investigations and testing other (non-social) cognitive functions, we employed a broad range of tests that assessed social information processing (social perception, social cognition, social regulation). Our results point to both preserved (empathy, core ToM functions, visual affect selection, and discrimination, affective prosody discrimination) and impaired domains of social information processing (incongruent affective prosody processing, complex social judgments). They support proposals for a role of the hippocampal formation in processing more complex social information that likely requires multimodal relational handling.

Keywords: episodic–autobiographical memory, social information processing, theory of mind, hippocampus, hypoxia

INTRODUCTION

Memory is divided according to time and content axes, respectively (Markowitsch and Staniloiu, 2012). Along the content axis, five long-term memory systems were described [procedural, priming, perceptual, semantic, and episodic–autobiographical memory (EAM) systems] (Tulving, 2005). These systems are considered to build up on each other ontogenetically and phylogenetically. EAM is considered the last ontogenetic and phylogenetic achievement (Nelson, 2003, 2005; Nelson and Fivush, 2004; Tulving, 2005). It is currently defined as being the conjunction of subjective time, autonoetic consciousness, and the experiencing self (Tulving, 2005). Autonoetic consciousness has been conceptualized in slightly different ways. Wheeler et al. (1997, p. 335) defined it as the "capacity that allows adult humans to mentally represent and to become aware of their protracted existence across subjective time." Lemogne et al. (2006, p. 260) stated that autonoetic consciousness entails a "sense of self in time and the ability to relive subjective experiences from the encoding context by mentally traveling back in time." Markowitsch proposed that autonoetic consciousnes is characterized by a superior ability to reflect upon oneself and distinguish oneself from the social and biological environment (Markowitsch, 2003; Markowitsch and Staniloiu, 2011a). While the latter definition of autonoetic consciousness might suggest a link between EAM and the dialectic of self and others (Suddendorf et al., 2009), the relationship between EAM (Tulving, 2005; Markowitsch and Staniloiu, 2012) and social cognition [theory of mind (ToM), empathy, simulation, social judgment, moral judgment] (Adolphs, 2010a) remains debated, and insufficiently explored experimentally.

Several authors proposed that EAM or autonoetic consciousness modulate an individual's capacity to make inferences about others' mental states and feelings, and distinguish these states from his or her own ones (Batson et al., 1996; Bluck et al., 2005; Saxe et al., 2006; Staniloiu et al., 2010a). Tulving (2005) remarked that Darwin's description of "moral being" had alluded to several features, which may be tied to morality, such as the capability for recollecting the past, the capacity for autonoetic consciousness and the ability to subjectively mentally travel in time, both into past and future. In this vein, difficulties with recollecting emotional events and/or autonoetic consciousness were propounded to exist in offenders with psychopathy, who feature impairments in empathy and affective ToM (Shamay-Tsoory and Aharon-Peretz, 2007; Craig et al., 2009). Croft et al.'s (2010) results suggested that severe EAM impairments due to neurological incidents may affect the updating of moral character judgments and subsequently may influence the way these individuals perceive and behave toward others. The authors compared in their study the performance of patients with bilateral damage to the ventromedial prefrontal cortex to that of patients with bilateral damage to the hippocampal formation (due to hypoxia/anoxia or herpes viral encephalitis) and that of a control brain-damaged group during a task that required the participants to make moral judgments about unfamiliar persons in two conditions (before and after being exposed to various social context scenarios). In contrast to patients with bilateral damage to the ventromedial prefrontal cortex, patients with bilateral hippocampal damage presented with severe impairments in conscious mnemonic processing, interfering with their everyday life. During the moral updating task, they furthermore demonstrated the largest amount of change in moral judgments after social scenario manipulations, compared to patients with bilateral damage to the ventromedial prefrontal cortex, who showed the least amount of change.

Social cognition (ToM) deficits were reported to co-occur with memory impairments in several psychiatric conditions, including dissociative (functional) amnesia (Corcoran and Frith, 2003; Reinhold and Markowitsch, 2007, 2008, 2009; Fujiwara et al., 2008). Kritchevsky et al. (2004, p. 224) described a patient with functional amnesia who after the onset of amnesia became "less aware of the feelings of other individuals." He furthermore did not comprehend jokes anymore and "interpreted them literally" (Kritchevsky et al., 2004, p. 224). Interpersonal difficulties with family members have been reported to occur after the onset of dissociative amnesia and were partly attributed to an impaired ability to properly read the familiar/close others' mental states (Rabin and Rosenbaum, 2012; Staniloiu and Markowitsch, 2012; Markowitsch and Staniloiu, 2013).

Reinhold and Markowitsch (2007) formally assessed emotional processing and social cognition in two female adolescents (age 16 and 18, respectively) suffering from dissociative amnesia. They found that both patients were impaired on the German-language adaptation of the Reading the Mind in the Eyes Test (RMET) (Baron-Cohen et al., 2001; Fleck et al., 2002; Dziobek et al., 2006; Fujiwara et al., 2008) and emotional evaluation of ToM stories (Kalbe et al., 2007). In a case series of five patients with dissociative (functional) amnesia, three out of the four patients in whom the RMET was administered, showed performance deficits on it. Dissociative amnesia is however often accompanied by other psychiatric or medical comorbidities, such as major depressive disorder (Staniloiu and Markowitsch, 2012). One could furthermore argue that, even when the co-occurring symptoms of depression do not reach the threshold for a diagnosis of an affective disorder according to the international nosologies' diagnostic criteria (so-called subclinical symptoms of depression), they can still impact on ToM functions (Cusi et al., 2011). It was speculated that in some psychopathological conditions (Corcoran and Frith, 2003), which are known to have a neurodevelopmental basis, the co-occurrence of EAM and ToM deficits may reflect a developmental arrest of closely in time emerging neurocognitive functions, which are at that stage functionally interdependent (Perner, 2000; Bird et al., 2004; Nelson and Fivush, 2004). Other authors proposed that in certain forms of psychopathologies, an idiosyncratic way of making inferences about the mental states of others might take place, due to a failure of inhibition of own perspective and/or a poverty of models of the inner world of others (Newen and Schlicht, 2009). Functional neuroimaging studies suggested common (but also distinct) neural substrates for EAM and ToM (Spreng et al., 2008; Rabin et al., 2010; Spreng and Grady, 2010; Abu-Akel and Shamay-Tsoory, 2011). A recent investigation of healthy female participants revealed that the degree of neural overlap depends on the target person involved in the ToM task; when participants engaged in making inferences about the mental states of familiar others as opposed to unfamiliar others, they seemed to recruit more EAM-related brain areas, suggesting the use of a different cognitive strategy (despite identical task instructions) (Rabin and Rosenbaum, 2012).

By contrast, there are reports of patients with amnesia secondary to neurological brain insults incurred in adulthood with no detectable deficit on ToM functions (as assessed by using standardized laboratory tasks). Rosenbaum et al. (2007) investigated with a battery of widely employed tests (Stone et al., 1998; Castelli et al., 2000; Baron-Cohen et al., 2001; Dennis et al., 2001; Stuss et al., 2001) two patients with amnesia with onset after severe traumatic brain injury [patient K.C. (Rosenbaum et al., 2005) and patient M. L. (Levine et al., 1998, 2009)] and found that their performance did not significantly differ from that of 14 control participants on all measures. In addition, despite speculations that social cognition and EAM might depend on each other during early development (Perner, 2000; Nelson and Fivush, 2004), a recent study of an adult female patient (HC) with developmental amnesia showed that the patient performed within normal limits on a variety of standardized tests that assessed her capacity for ToM (Rabin et al., 2012). The applied testing battery consisted of: the False belief and the Faux pas tests (Stone et al., 1998), the 36 black and white photographs variant of the RMET (Baron-Cohen et al., 2001), the Sarcasm and Empathy Test (Dennis et al., 2001), the Visual Perspective-Taking and Deception Test (Stuss et al., 2001), and the Animation Test (Castelli et al., 2000).

The term developmental amnesia is a non-DSM-IV-TR (2000) terminology that designates a syndrome that occurs in childhood and is caused by relatively selective damage to hippocampi (usually resulting in more than 30–40% bilateral volume reduction of hippocampi in comparison to controls). Some involvement of the basal ganglia (bilaterally), thalamus (bilaterally), and right retrosplenial cortex, which was demonstrated in voxel-based morphometry studies had been reported as well (Vargha-Khadem et al., 1997, 2003; Isaacs et al., 2003). Consistent with the hypoxia-anoxia pathogenetic model (see below), in a patient with developmental amnesia white matter changes (e.g., thinning of the corpus callosum) were additionally remarked and in another cerebellar atrophy was noted (Vargha-Khadem et al., 1997; Gadian et al., 2000; Connolly et al., 2007).

The most common cause of relatively selective hippocampi damage is single or recurrent episodes of ischemic-hypoxia, which were reported to occur perinatally or in childhood until prepubertal period. Affected children can still acquire knowledge about facts and language skills depending on their intellectual ability that can range from low to normal, but show severe impairments in the episodic–autobiographical domain and everyday memory (Markowitsch and Staniloiu, 2012; Willoughby et al., 2012).

Most recently, studies of young adults with childhood developmental amnesia have focused on investigating the ability to imagine the future and on distinguishing between recollection/recall and familiarity/recognition (Kwan et al., 2010; Maguire et al., 2010). Little has, however, been devoted to a thorough investigation of social information processing in these cases, according to our knowledge.

Herein we provide a review, interpretation and critical discussion of results obtained with various tasks tapping on social cognition as well as other aspects of social information processing in a young adult male patient with amnesia with neurodevelopmental mechanisms. When we speak of social information processing, we use as guiding framework the classification described in **Table 1** of Adolphs (2010a). In this table, Adolphs (2010a) depicted the following three stages of social information processing: *social perception* (perception of pheromones, face and speech perception, and perception of social touch and biological motion), *social cognition* (affective and cognitive ToM, simulation, empathy, social judgment, moral judgment), and *social regulation* (cognitive control, emotion regulation, monitoring/error correction, self-reflection, deception).

CASE REPORT

ML is a 29-year-old man who was 27-year-old at the time of the neuropsychological testing in our clinic. He is the oldest of three children, coming from a middle class family. Both of his siblings achieved higher education. His parents divorced when ML was a teenager. ML was born prematurely, at 33 weeks of gestation. After birth, he required a 2-week hospitalization for lung immaturity in a neonatal intensive care unit, where he received oxygen therapy. In terms of developmental milestones, ML began talking at age 13 months. Some stuttering was noted in childhood, but it ceased later on. From age 3 months until age 1 year, ML received physical therapy for problems with motor tone and muscle coordination. Sitting was delayed (he was older than 1 year when he was able to sit). He began walking at age 18 months and completed toilet training at age 3 years. At age 2 years, ML underwent another course of physical therapy. Both therapies followed the model developed by Vaclav Vojta (Sadowska, 2001) and were successful; however they were perceived by ML's mother as having been psychologically traumatizing. Clumsiness and other (usually transient) problems with motor skills were reported in other patients with developmental amnesia, who sustained hypoxic-ischemic events during the first year of life (Gadian et al., 2000; Vargha-Khadem et al., 2003). However, the reported difficulties were milder than the ones experienced by ML. Although postulated, a connection between the basal ganglia (and thalamic) damage and motor impairment in cases of developmental amnesia remained unclear (Gadian et al., 2000; Vargha-Khadem et al., 2003; de Haan et al., 2006).

ML entered kindergarten at age 4 years and was described during those time as being reserved and a daydreamer. Since age five ML has seen several health care providers and has been suspected of having several diagnoses such as Minimal Cerebral Dysfunction (MCD), autistic spectrum disorder, Asperger's syndrome, attention hyperactivity deficit disorder. None of these diagnoses was confirmed. ML's case may therefore reflect other cases of developmental amnesia from the literature, where an accurate diagnosis was far from being "straightforward" from the beginning (Gadian et al., 2000). As Gadian et al. (2000) remarked, it is not uncommon for problems with episodic memory–which typically become evident around age 5 or 6 years (in conformity with data on the ontogenesis of episodic memory; Nelson and Fivush, 2004) – to be initially attributed to attention deficits. Several motor tics and substantial problems with school performance were noted when ML was around the age of 7 years, shortly after he had entered the school. Problems with organization, memory for life events as well as performing several real-world memory tasks (Willoughby et al., 2012) were remarked. In the absence of a comprehensive and rigorous neuropsychological investigation at the time, ML's poor school functioning initially was however conjectured to reflect primary attention and concentration difficulties (Lebrun-Givois et al., 2008). On an interpersonal level, ML reportedly experienced difficulties establishing social contact with other peers during his early school years. He often imitated emotions or behaviors of others, instead of expressing his own feelings. Although not commonly reported, social and emotional difficulties were described in other patients with diagnoses of developmental amnesia by other authors (Picard et al., 2012).

ML later on outgrew his tics. Because of his persisting difficulties in school, ML was supervised by a school psychologist. In the following years, ML continued to experience memory impairments and lack of organization. Despite of otherwise good intellectual functions, he continued to fail school, which prompted his family to seek psychiatric help for him. Therefore, at age 16 years ML was brought by his mother for a comprehensive medical and neuropsychological assessment. Contrary to expectations, the neuropsychological assessment revealed above average attention and concentration abilities; verbal short-term memory was average, digit span was above average, his visual short-term memory was average and word fluency was within normal limits. ML was fully oriented. Verbal and visual memory performance after delays of half an hour were however impaired. ML displayed no evidence of distractibility and showed no heightened level of interference. There was no evidence of perseveration or apraxia, stereotypes, or tics. The neuropsychologist's recommendation was that ML should undergo memory rehabilitation training, although no clear diagnosis was provided.

A routine electroencephalography (EEG), which was performed at the time, yielded no evidence of seizures or epilepsy. Both computer tomography (CT) and magnetic resonance imaging (MRI) scans of the head were performed. The CT showed a discrete enlargement of the lateral ventricles downright. MRI revealed a small gliotic mass in the left thalamus and discrete prominence of

Table 1 | Summary of test results.

Test	Result	Below average (PC $<$ 16)	Low average (PC = 16–24)	Average (PC = 25–75)	High average (PC = 76–84)	Above average (PC $>$ 84)	Remark(s)
LATERALITY							
Laterality-preference-inventary							
Eye	Score = +4 (scores reach from −4 [left] via 0 [ambidexter] to +4 [right])						Clearly right oriented
Ear	Score = −4						Clearly right oriented
Hand	Score = −2						More left oriented
Foot	Score = +4						Clearly right oriented
Questionnaire for measuring motor asymmetry							
Handedness	Score = −16 (+8 to +20: right, −7 to +7: symmetrical, −8 to −20: left)						Left
Footedness	Score = 0 (+4 to +2: right, −1 to +1: symmetrical, −2 to −4: left)						Symmetrical
LANGUAGE							
Boston naming test	57 Out of 60 items			X			Unremarkable
PERCEPTION							
Judgment of line orientation							
Correct	35			X			
False	0			X			
NUMBER CALCULATION AND ARITHMETICS							
ZRT							
Number processing							
Written transcoding	Score = 3			X			Normal
Calculation							
Calculation by heart	Score = 6			X			Normal
Written calculation	Score = 6			X			Normal
INTELLECTUAL FUNCTIONS							
Non-verbal							
LPS-4 (logical thinking)	IQ = 130					X	34 Correct
Mosaic-test (HAWIE-R)	Score = 19					X	Maximal score
Matrices-test	Score = 14					X	25 Out of 26 correct, maximal score reached
Verbal							
Finding of commonalities (HAWIE-R)	Score = 11			X			
MWT-B	IQ = 97			X			26 Correct
SHORT-TERM MEMORY							
Numerical							
Digit span forward (WMS-R)	PC = 97					X	8 Digits
Visual							
Block span forward (WMS-R)	PC = 65			X			7 Blocks
WORKING MEMORY							
Numerical							
Digit span backward (WMS-R)	PC $>$ 98					X	7 Digits
Adaptive digit ordering test	10/12 Points					X	7 Digits
Visual							
Block span backward (WMS-R)	PC = 78				X		6 Blocks
ANTEROGRADE MEMORY							
Verbal							
VLMT							
First trial	PC = 60–75			X			8 Words
Fifth trial	PC $<$ 5	X					9 Words

(Continued)

Table 1 | Continued

Test	Result	Below average (PC < 16)	Low average (PC = 16–24)	Average (PC = 25–75)	High average (PC = 76–84)	Above average (PC > 84)	Remark(s)
Total score	PC = 5	X					42 Words
Interference list	PC = 85					X	9 Words
Direct recall	PC = 0	X					1 Word
Delayed recall (30 min)	PC = 0	X					1 Word
Forgetting rate (trial 5 – direct recall)	PC = 0	X					Loss: 8 words
Forgetting rate (trial 5 – delayed recall)	PC = 0	X					Loss: 8 words
Recognition	PC = 0	X					6 Correct, 9 false positives
Logical memory I (WMS-R)	PC = 18		X				21 Details
Logical memory II (WMS-R)	PC = 0	X					2 Details (after request)
Figural							
Rey-Osterrieth figure							
Delayed recall	PC = 0	X					2 Details
Doors and people test							
Doors test A (recognition)	11 Out of 12		X				
Benton visual retention test							
Free direct recall	8						
Number correct	2		X				Expected number correct: 9
Number of errors	0		X				Expected number errors: 1
Free recall, delayed	8	X					For delayed recall no norms exist
Delayed recall recognition			X				
ANTEROGRADE MEMORY FOR EMOTIONAL INFORMATION							
Emotional pictures							
Correct recognitions	24 Out of 40						See text for comments
False recognitions	9						9 Falsely recognized distractors
Picture story for affect induction (BAd)							
Emotional story							
Free recall (immediate)	4 Details						+1 Incorrect detail
Recognition							
Picture 1	5 Out of 7						
Picture 2	3 Out of 7						
Picture 3	3 Out of 7						
Picture 4	7 Out of 7						
Picture 5	3 Out of 7						
Picture 6	3 Out of 7						
Picture 7	3 Out of 7						
Picture 8	3 Out of 7						
Picture 9	3 Out of 7						
Picture 10	1 Out of 7						
Initial phase (pictures 1–4)	18 Out of 28						64% (Control group [CG]: 83%)
Middle part (pictures 5–7)	9 Out of 21						42.8% (Emotional part; CG: 77%)

(Continued)

Table 1 | Continued

Test	Result	Below average (PC < 16)	Low average (PC = 16–24)	Average (PC = 25–75)	High average (PC = 76–84)	Above average (PC > 84)	Remark(s)
End phase (pictures 8–10)	7 Out of 21						33.3% (CG: 73%; see text)
Non-emotional story							
Free recall (immediate)	4 Details						No difference between the emotional and the non-emotional story
RETROGRADE MEMORY/SEMANTIC OLD MEMORY							
Semantic old memory inventory	80/81 Points						Normal
Famous faces test							
1980–1985 ($n = 10$)	Free recall: 40%, recognition: 10%, together: 50% (age of ML: ≤ 2 years)						
1985–1990 ($n = 10$)	Free recall: 20%, recognition: 0%, together: 20% (age of ML: 2–7 years)						
1990–1995 ($n = 10$)	Free recall: 50%, recognition: 30%, together: 80% (age of ML: 7–12 years)						
1995–2000 ($n = 10$)	Free recall 40%, recognition: 30%, together: 70% (age of ML: 12–17 years)						
2000–2010 ($n = 43$)	Free recall: 57%, recognition: 14%, together: 71% (age of ML: 17–27 years)						
Famous names test ($n = 72$)							Normal
Correct	87.5%						
Incorrect	–						
No response	12.5%						
Famous terms test ($n = 86$)							Unremarkable
Correct	86%						
Incorrect	–						
No response	14%						
Famous events test							
1994 ($n = 5$)	2 Spontaneously recalled, 2 recognized; total: 4 out of 5 = 80% (ML's age: 11 years)						
1995 ($n = 5$)	2 Spontaneously recalled, 2 recognized; total: 4 out of 5 = 80%						
1996 ($n = 5$)	2 Spontaneously recalled, 2 recognized; total: 4 out of 5 = 80%						
1997 ($n = 7$)	2 Spontaneously recalled, 1 recognized; total: 3 out of 7 = 43%						
1998 ($n = 5$)	3 Spontaneously recalled, 2 recognized; total: 5 out of 5 = 100%						
1999 ($n = 5$)	1 Spontaneously recalled, 3 recognized; total: 4 out of 5 = 80%						
2000 ($n = 7$)	2 Spontaneously recalled, 2 recognized; total: 4 out of 7 = 57%						
2001 ($n = 6$)	2 Spontaneously recalled, 2 recognized; total: 4 out of 6 = 67%						
2002–2010 ($n = 17$)	2 Spontaneously recalled, 8 recognized; total: 10 out of 17 = 59% (ML's age: 19–27 years)						
Items altogether ($n = 62$)	Total correct: 42 out of 62 = 67.7%						
RETROGRADE MEMORY/EPISODIC OLD MEMORY							
Autobiographic memory interview (AGI)							
Pre-school time							
1. Autobiographical facts	All existent						
2. Autobiographical recollections	Tells anecdotes his mother had told him, but he himself has no autobiographical remembrances with a context of time, place, or emotion						
Time period in basic school							
1. Autobiographical facts	All existent						
2. Autobiographical recollections	Tells anecdotes, but remembers no autobiographical episodes						
Later time in school/youth							
1. Autobiographical facts	All existent						
2. Autobiographical recollections	One highly emotional episode is remembered (he observed his father jumping out of the window after a fight with his mother)						

(Continued)

Table 1 | Continued

Test	Result	Below average (PC < 16)	Low average (PC = 16–24)	Average (PC = 25–75)	High average (PC = 76–84)	Above average (PC > 84)	Remark(s)
Early adulthood/present life							
1. Autobiographical facts	All available						
2. Autobiographical recollections	Even after repeated asking, no autobiographical remembrances with a context of time, place, or emotion						
PROCEDURAL MEMORY AND PRIMING							
Mirror reading task							
1. Trial	Total reading time for all 10 words/average reading speed for 2 words (=1 card)						
Reading speed for procedural items	25/5 s						
Reading speed for priming items	46/9.2 s						
Reading speed for interference items	16/3.2 s						
2. Trial							
Reading speed for procedural items	15/3 s						
Reading speed for priming items	19/7.2 s						
Reading speed for interference items	36/3.8 s						
Total scores (difference scores)							
Procedural memory	10/2 s						
Priming	27/5.4 s						
Interference	−20/−4 s						
Errors							
1. Trial	0 Errors						
2. Trial	2 Errors (1 priming word, 1 interference word)						
PRIMING							
Gollin incomplete figures	1. Trial – average number of needed pictures: 6.3 out of 10 2. Trial – average number of needed pictures: 4.45 out of 10						
PROSPECTIVE MEMORY							
Rivermead behavioral memory test	Impaired; see text for details						
Grasshopper and Geese prospective memory test	Severely impaired; see text for details						
ATTENTION/COGNITIVE PROCESSING SPEED							
TMT-A	PC = 76				X		
Alertness (TAP[1])							
Without warning signal	PC = 42			X			
With warning signal	PC = 62			X			
Phasic alertness	PC = 76				X		
FWIT/CWIT							
Color naming	$T = 45$			X			
Color word reading	$T = 44 - 45$			X			
ATTENTION/SELECTIVE ATTENTION							
Go-no go (TAP[1])							
Reaction speed	PC = 46			X			
Omissions	PC > 40			X			0 Omissions
Errors	PC > 38			X			0 Errors
ATTENTION/DIVIDED ATTENTION							
Divided attention (TAP[1])							
Reaction speed	PC = 42			X			
Omissions	PC > 66			X			0 Omissions
Errors	PC > 66			X			0 Errors

(Continued)

Table 1 | Continued

Test	Result	Below average (PC < 16)	Low average (PC = 16–24)	Average (PC = 25–75)	High average (PC = 76–84)	Above average (PC > 84)	Remark(s)
ATTENTION/COGNITIVE FLEXIBILITY							
TMT-B	PC = 82–84				X		
Attention switch (TAP[1])							
Reaction speed	PC = 84				X		
Errors	PC < 50			X			3 Errors
FWIT/CWIT							
Interference trial	*T* = 49			X			
VISUO-CONSTRUCTIVE SKILLS							
Rey-Osterrieth figure							
Copy	PC = 58–62			X			Correct and detailed copy
Mosaic test	score = 19					X	No errors
EXECUTIVE FUNCTIONS							
Word fluency							
FAS-test							
Verbal abstraction ability	PC = 12–13	X					
Finding of commonalities (HAWIE-R)	Score = 11			X			
Action planning							
Tower of Hanoi							
3 Disks							
1. Trial	Aborted						Problem definition identified; analytic approach; no tendency towards errors; own errors recognized and thereafter immediate change of strategy
2. Trial	7 Steps			X			
4 Disks							
1. Trial	22 Steps						
2. Trial	15 Steps			X			
Burgau's little verbal planning test							
Time needed and assistance	4/4 Points			X			Autonomous start; action without assistance; time needed: <5 min
Goal reached	4/4 Points			X			All errands correctly classified, 1 error which was corrected spontaneously
Problem solving/concept comprehension							
Mosaic test	Score = 19					X	
WCST[2]				X			No problems, understood the principle of the test even prior to starting with it
Correct responses	36						
Errors	0						
Perseverations	0						
California card sorting test				X			
Number of sortings	8						No problems, normal
Time	4 min, 20 s						

(Continued)

Table 1 | Continued

Test	Result	Below average (PC < 16)	Low average (PC = 16–24)	Average (PC = 25–75)	High average (PC = 76–84)	Above average (PC > 84)	Remark(s)
Cronin-Golomb test							
Abstract concepts	5/8 Correct		**X**				
Concrete concepts	8/9 Correct			**X**			
Altogether	13/17 Correct			**X**			
Cognitive estimation							
TkS[3]	8/16 Points	**X**					
Size	4/4						Impaired
Weight	1/4						
Number	2/4						
Time	1/4						
Risk taking behavior							
Game of dice task							
Risky decisions	5			**X**			No tendency for risky decisions
Safe decisions	13			**X**			
SOCIAL INFORMATION PROCESSING TESTS: PERCEPTION OF EMOTIONAL AND COGNITIVE STATES, INTERPERSONAL SITUATIONS							
Reading the mind in the eyes test	16/24 Points		**X**				Low normal to impaired ($M = 19$, $SD = 2.7$)
Multiple-Choice-ToM-Test (MCTT)	15/16 Points			**X**			Normal; 1 item "too positive"
Movie for the Assessment of Social Cognition (MASC)			**X**				Slightly impaired
Correct	32						
Exaggerated ToM	5						
Reduced ToM	6						
No ToM	2						
Tübingen (Florida) affect battery							
Faces subtests							Comparison scores, healthy Ss[4] ($n = 12$)
Face discrimination	100%			**X**			$M = 98.8$, $SD = 2.7$
Affect discrimination	93.3%			**X**			$M = 91.6$, $SD = 5.6$
Affect naming	86.6%	**X**					$M = 94.8$, $SD = 5.6$
Affect selection	100%			**X**			$M = 96.5$, $SD = 3.7$
Affect matching	86.6%	**X**					$M = 94.3$, $SD = 5.3$
Prosody subtests							
Discrimination of linguistic prosody	100%			**X**			$M = 100$, $SD = 0$
Discrimination of affective prosody	93.3%	**X**					$M = 100$, $SD = 0$
Affective prosody naming	86.6%		**X**				$M = 94.9$, $SD = 7.6$
Incongruent affective prosody							
Congruent	100%			**X**			$M = 98.0$, $SD = 4.7$
Incongruent	84%	**X**					$M = 94.1$, $SD = 6.2$
Intermodal subtests							
Matching of affective prosody to emotional face expression	100%			**X**			$M = 95.5$, $SD = 6.6$
Matching of emotional face expressions to affective prosody	93.3%		**X**				$M = 97.7$, $SD = 3.4$
PSYCHOPATHOLOGICAL AND PSYCHOLOGICAL LOAD SCREENINGTESTS/SCALES							
BDI-II	4 Points						No hint of depressive symptomatology

(Continued)

Table 1 | Continued

Test	Result	Below average (PC < 16)	Low average (PC = 16–24)	Average (PC = 25–75)	High average (PC = 76–84)	Above average (PC > 84)	Remark(s)
SCL-R							
Scales							
Somatization	$T = 35$	X					
Obsessive-compulsiveness	$T = 48$			X			
Interpersonal sensitivity	$T = 36$	X					
Depressive tendencies	$T = 48$			X			
Anxiety	$T = 39$	X					
Anger/hostility	$T = 40$			X			
Phobic anxiety	$T = 45$			X			
Paranoid thinking	$T = 40$			X			
Psychoticism	$T = 42$			X			
Global Indices							
GSI (global severity index)	$T = 35$	X					
PSDI (positive symptom distress index)	$T = 39$	X					
PST (positive symptom total)	$T = 37$	X					
FPI-R							
Scales							
Life satisfaction	Stanine = 1	X					
Social orientation	Stanine = 4			X			
Achievement motivation	Stanine = 3		X				
Inhibition	Stanine = 6			X			
Excitability	Stanine = 4			X			
Aggressiveness	Stanine = 2	X					
Stress	Stanine = 4			X			
Physical complaints	Stanine = 2	X					
Health worries	Stanine = 4			X			
Openness	Stanine = 2	X					
Extraversion	Stanine = 2	X					
Neuroticism	Stanine = 4			X			
Toronto-Alexithymia-Scale							
Scales							
Difficulties in the identification of feelings	PR = 14	X					
Difficulties in the description of feelings	PR = 40			X			
Externally oriented style of thinking	PR = 12	X					
Total score							
Alexithymia	PR = 8	X					
EWL-N (Personal adjectives list)							See text
AUTISM/EMPATHY SCALES							
Autism-spectrum-quotient	AQ = 15			X			$M = 16.4$; no indices for autistic tendencies
Cambridge Behaviour Scale (empathy-quotient)	EQ = 53				X		High average (males: $M = 41.8$, $SD = 11.2$)
Saarbrücken personality questionnaire (**interpersonal reactivity index**)							
Scales							
Empathy	Score = 96			X			$M = 100$, $SD = 10$
Phantasy	Score = 90			X			

(Continued)

Table 1 | Continued

Test	Result	Below average (PC < 16)	Low average (PC = 16–24)	Average (PC = 25–75)	High average (PC = 76–84)	Above average (PC > 84)	Remark(s)
Perspective taking	Score = 104			X			
Personal distress	Score = 85	X					
ADDITIONAL EXPERIMENTAL INVESTIGATIONS OF SOCIAL INFORMATION PROCESSING							
Humor processing (cartoons)							
ToM cartoons (n = 10)							
Average processing time (s)	*M* = 10.8 s, *SD* = 12.37 s, *MD* = 6 s; range: 4–43 s						
Subjective judgment	Humorous/funny: 5, not humorous/not funny: 2, undecided: 3						
Non-ToM cartoons (n = 10)							
Average processing time (s)	*M* = 11.1 s, *SD* = 11.19 s, *MD* = 5 s, range = 4–32 s						
Subjective judgment	Humorous/funny: 3, not humorous/not funny: 1, undecided: 6						
Ultimatum game variant (responder: ML)							
Offers (starting capital 100€)							
10 €	Accepted						
1 €	Accepted						
100 €	Accepted						
Dictator game variant (starting capital 100€)							
Offer made by ML	15€						
Approachability task (42 photographs)							
More positive faces (n = 21) (range: ±2)							
Never to approach	0						
Likely to not approach	0						
May be	0						
Likely to approach	7						
Definitely to approach	14						
Rating of positive faces	1.66 (Bellugi et al., 1999: healthy subjects: *M* = 0.84, *SD* = 1.12; Williams syndrome = 1.32, *SD* = 1.1)						
More negative faces (n = 21)							
Never to approach	0						
Likely to not approach	4						
May be	4						
Likely to approach	6						
Definitely to approach	7						
Mean rating negative faces	0.76 (Bellugi et al., 1999: healthy subjects: *M* = −0.96, *SD* = 0.96; Williams syndrome: *M* = −0.54, *SD* = 1.39)						
Animation of Heider and Simmel (1944)							
Immediate free recall	83 words, reference group[5] (*n* = 40): *M* = 97.5, range = 39–199 words						
Use of animate nouns	No, reference group[5]: use of animate nouns 32.5%, use of geometrical figures: 67.5%						
Description of internal states	No, reference group[5]: description of internal states was used by 22.5% of all reference group[5] subjects						
Use of animate verbs	Yes (fleeing, destroying), reference group[5]: equal use of animate (39 subjects) and non-animate verbs (38 subjects)						
Use of physical verbs	Yes						

(Continued)

Table 1 | Continued

Test	Result	Below average (PC < 16)	Low average (PC = 16–24)	Average (PC = 25–75)	High average (PC = 76–84)	Above average (PC > 84)	Remark(s)
MALINGERINGTENDENCIES[6]/EFFORT							
Rey-memory-test	11 Out of 15			X			Cut-off: 8
Bremen auditory memory test[7]	8 Out of 15	X					Cut-off: 12
Test for assessing memory ability in everyday life[8]	11 Out of 15		X				Cut-off: 12

[1] *TAP, Testbatterie zur Aufmerksamkeitsprüfung (Test Battery for the Assessment of Attention).*

[2] *WCST Wisconsin Card Sorting Test.*

[3] *TkS, Test für kognitives Schätzen (Test of Cognitive Estimation).*

[4] *Ss, subjects (Breitenstein et al., 1996)*

[5] *Replication study: Curci-Marino et al. (2004).*

[6] *Though ML partly showed results in tests of malingering which were indicative of malingering, these cannot be interpreted as malingering as he was usually poor in memory recall in general.*

[7] *Bremer Auditiver Gedächtnistest.*

[8] *Test zur Überprüfung der Gedächtnisfähigkeit im Alltag.*

A T-score is a standard score that sets the mean to fifty and standard deviation to 10.

A percentile (PC) is the value of a variable below which a certain percent of observation fall.

Stanines are standard scores with a maximum of 9. Stanines 1–2 and 8–9 indicate significant deviations from normative data.

Stanines 1–3 on the subscale "Openness" of the FPI-R indicate elevated social desirability limiting the validity of the responses in the entire questionnaire. The gray column in the middle reflects average or normal scores.

the lateral ventricles and of the external cerebrospinal fluid space (increased sulcal cerebrospinal fluid). Hippocampal changes were not described and no comment was made about the significance of the enlargement of the lateral ventricles.

Over the years ML attended several therapies and he graduated from a special needs school. ML completed 10 years of schooling, repeating one school year. His school trajectory might therefore seem different than that of other patients with developmental amnesia described in the literature, who were reported to have attended mainstream schools ("albeit with considerable difficulties in some cases") (Gadian et al., 2000, p. 505) (but, see also Bindschaedler et al., 2011). Incidentally, Picard et al. (2012) recently published two case reports of patients whom they diagnosed with developmental amnesia. One of those patients showed an atypical schooling pathway; she failed normal schooling and similarly to ML, she subsequently attended specialized school.

Since age 20 ML has received external help from a caretaker regarding planning, remembering important appointment dates, and managing finances. He has lived in a supervised setting since finishing school. ML's living situation again points to a difference between ML and other cases of developmental amnesia (Rabin et al., 2012). However it is worth mentioning that other patients with diagnoses of developmental amnesia were described to live in "protective environments" (though not in residential settings) (Picard et al., 2012). In contrast to his everyday memory impairments, ML has shown impressive special knowledge in some fields, which he has no problem to acquire and retrieve. He for example, has a very broad and detailed knowledge of special luxury goods such as watches and car brands. Furthermore, he can learn and remember very well pieces of music. ML joined a dance course 4 years prior to his assessment in our clinic. His substitute decision maker states that ML is a very good dancer and has an incredible ability to learn new forms of dancing. Similarly to other patients with amnesia after adult or early-onset hippocampal damage (Milner et al., 1968; Rabin et al., 2012), ML is aware of his memory impairment; he has learned to partially compensate for it by using strategies such as repetition and reliance on calendars to keep track of scheduled appointments.

On an interpersonal level ML's ability to interact with his peers has significantly improved since his school years. His substitute decision maker however voiced concerns about ML's heightened capacity to trust other people. In spite of being repeatedly told not to give money to other people (and carrying in his portemonnaie a visible note stating that), ML has continued to lend money to people without usually getting it back.

IMAGING FINDINGS

ML underwent several structural MRI at different locations. The most recent imaging was performed when ML was age 29 years, with a 3-Tesla MRI scanner (Siemens Magneto Verio whole-body MRI system equipped with a head volume coil). The procedure was undergone in a neuroradiological center specialized for assessing patients with epilepsy pre- and post-operatively. The imaging data were evaluated by a neurologist with expertise in neuroradiology (Friedrich G. Woermann). Visual inspection revealed grossly reduced (gray matter) density within hippocampi bilaterally (**Figures 1** and **2**). There was no evidence of pathology in the underlying parahippocampal region or other brain regions based on visual inspection. Using voxel-based morphometry (VBM; SPM8, Wellcome Institute, London, UK), a quantitative comparison of 3D T1-weighted images of patient ML with 10 age-matched healthy control participants was performed (for details regarding the method employed here, please refer to Labudda et al., 2012). The hypothesis-driven comparison within a hippocampal volume of interest demonstrated a marked reduction of gray matter volume within both hippocampi of the patient ML [$p < 0.05$, Familywise Error (FWE)], with an anterior and right-sided preponderance. Only when using a whole brain analysis with a less conservative statistical threshold ($p < 0.001$, uncorrected), we evidenced indices of further reductions of gray matter, affecting both amygdalae and basal ganglia (striatum, pallidum) – with a right-sided preponderance as well and pulvinar (bilaterally, but with a right-sided trend).

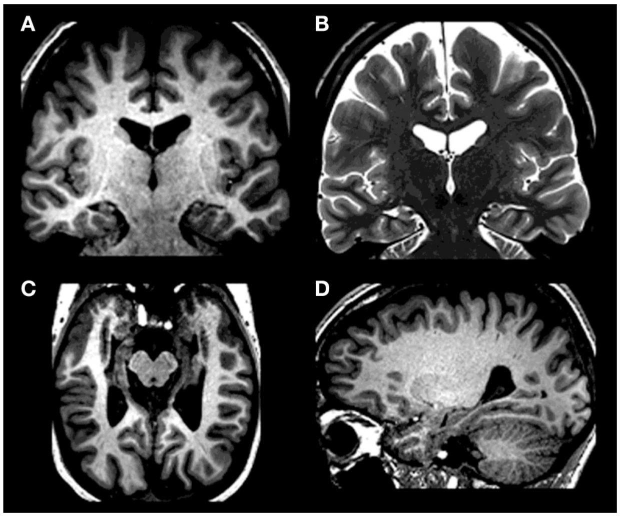

FIGURE 1 | Bilateral hippocampal atrophy in ML with T1-weighted images [(A) coronal; (C) axial; (D) sagittal] demonstrating reduced hippocampal size in all directions – in the absence of marked extrahippocampal atrophy; T2 weighted coronal image (B) demonstrating bilateral loss of internal structure – here: a further marker of bilateral hippocampal atrophy. On clinical MRIs left side of the image is right side of the patient.

TESTS

NEUROPSYCHOLOGICAL ASSESSMENT

The following tests were administered:

- *Standardized tests for handedness and brain lateralization*
  The Lateral Preference Inventory (LPI) for measurement of handedness, footedness, earedness, and eyedness (Ehrenstein and Arnold-Schulz-Gahmen, 1997), and the Questionnaire for measuring motor asymmetry (Reiss and Reiss, 2000). This last test contains 12 queries for assessing handedness and footedness.
- *Standardized tests for the estimation of intelligence and overall cognitive status*
  Abbreviated Wechsler Adult Intelligence Test-Revised (Block test and Picture Completion test) (Dahl, 1972). MWT-B or Mehrfachwahl-Wortschatz-Intelligenztest-B (Lehrl, 2005), a German version of the National Adult Reading Test NART (Nelson, 1982). The reasoning and rule recognition subtest from Leistungsprüfungssystem (LPS-4; Horn, 1983). The Mosaic Test from the revised Hamburg Wechsler Intelligence Test (HAWIE-R; Tewes, 1991), a German-language adaptation of the Wechsler Intelligence Test for Adults-Revised (WAIS-R) (Wechsler, 1981). Matrices Test from Wechsler Intelligence test for Adults (Aster et al., 2006). Commonalities finding test from HAWIE-R (Tewes, 1991).
- *Standardized tests for the evaluation of attention, concentration, and processing speed*
  Trail Making Test A and B (TMT-A + TMT-B; Lezak, 1995; Reitan, 1958); Attention Index of the German version of the Wechsler Memory Scale-Revised (WMS-R; Härting et al., 2000);

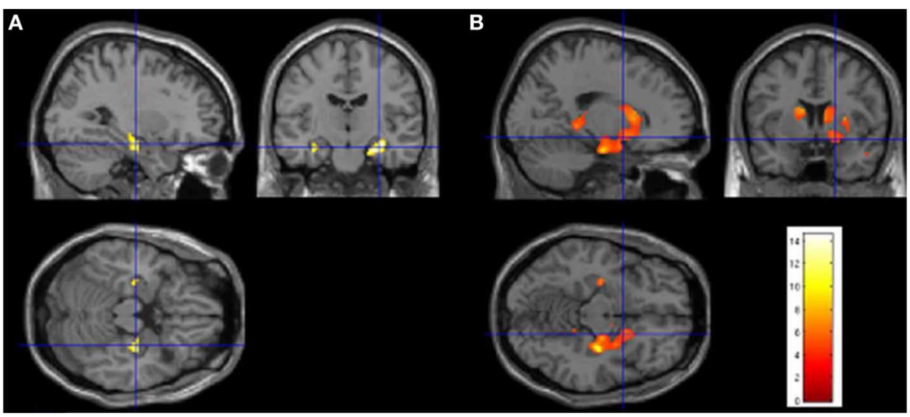

FIGURE 2 | Quantitative comparison of 3D T1-weighted images of patient ML with 10 age-matched control subjects using voxel-based morphometry (VBM; SPM8, Wellcome Institute, London, UK). For details regarding the method used here, please refer to Labudda et al. (2012). **(A)** Hypothesis-driven comparison within a hippocampal volume of interest demonstrates a marked reduction of gray matter volume within both hippocampi of the patient ($p < 0.05$, FWE) which has an anterior and right-sided preponderance (please note that *in SPM* the right side of the picture is the right side of the patient – *see crosshair*). **(B)** Using a whole brain analysis with a less conservative statistical threshold ($p < 0.001$, uncorrected), there are further reductions of gray matter, affecting amygdalae (bilaterally), bilateral dorsal striatum (mainly caudate and putamen, and to a certain extent the globus pallidus), portions of the ventral striatum (bilaterally), and posterior portions of the pulvinaris complex (also bilaterally), again with a right-sided preponderance.

the subtests Alertness, Selective Attention, and Divided Attention of the Test Battery for the Assessment of Attention or Testbatterie zur Aufmerksamkeitsprüfung (TAP) (Fimm and Zimmermann, 2001). The TAP is a computer-based test that assesses attentional performance based on reaction times. The Alertness subtest provides a measure of general slowing. The Selective Attention subtest is a go/no-go task, during which the participant has to selectively react to a group of stimuli, but not to others, and to inhibit a dominant response. The Divided Attention subtest is a "dual task" paradigm that assesses the ability to flexibly switch attention between two ongoing tasks (Fujiwara et al., 2008).

- *Standardized tests for evaluation of short-term memory and working memory*
  Wechsler Memory Scale-Revised; digit span and block span forward and backward; adaptive digit ordering test (Hoppe et al., 2000). In this last test digits which are presented in random order have to be recalled in ascending order (e.g., 4–3–9–3 should be recalled as 3–3–4–9).
- *Standardized tests for the evaluation of constructional functions and planning*
  Copy administration of the Rey-Osterrieth Figure Test (Osterrieth, 1944; Lezak, 1995); Benton Visual Retention Test (Lezak, 1995; Spreen and Strauss, 1998); Burgau Little Verbal Planning Test (*Burgauer Kleiner Verbaler Planungstest*; von Cramon and Zihl, 2012); Test of Cognitive Estimation (TkS; Brand et al., 2002, 2003a,b). The Benton Visual Retention Test taps on many different abilities such as visuo-spatial perception, visual and verbal conceptualizations, and working memory at the border to long-term memory. The Burgau Test requires the planning of a time-based sequence in which several transactions (going shopping) have to be organized within a given time. The TkS is a German-language test for cognitive estimation (Shallice and Evans, 1978), during which participants are requested to estimate numbers, weights, heights/lengths, and time durations.
- *Standardized tests for the evaluation of the verbal and non-verbal explicit anterograde long-term memory*
  Wechsler Memory Scale-Revised (Härting et al., 2000); Verbal Learning Memory Test (VLMT) (Helmstaedter et al., 2001); Rey-Osterrieth Figure; Copy trial followed by delayed recall after 30 min (Lezak, 1995); the Doors Test (visual recognition) of the Doors and People Test (Baddeley et al., 1994; Adlam et al., 2009); Rivermead Behavioral Memory Test (Wilson et al., 1985). The VLMT requires the recall of a list A of 15 presented words for 5 trials, the recall of a second (interference) list B, then again recall of the list A, and recall of it after 30 min delay, and finally the recognition of words of list A from words belonging to lists A and B and to none of the two. The Doors test requires the visual recognition of 12 easily and 12 difficultly to discriminate doors, each from an array of 4 doors. And the RBMT contains a number of subtests assessing retrospective and prospective visual and verbal memory functions.
- *Tests for the evaluation of retrograde memory (standardized or qualitative)*
  Semantic Knowledge Test [Semantic Old Memory Inventory; Schmidtke and Vollmer-Schmolck, 1999 (qualitative description)]; Bielefeld Autobiographical Memory Interview (BAGI; standardized; partly based on the Autobiographical Memory Interview of Kopelman et al., 1990; Fujiwara, 2004; Fujiwara et al., 2008; Fast et al., 2013; Famous Faces Test; standardized; see Jänicke, 2001), Famous Terms, Famous Events and Famous Names Tests [(qualitative descriptions); Leplow and Dierks, 1997; Markowitsch, 2003; Fujiwara et al., 2008]. In the Semantic Knowledge Test general facts are asked ("What is the currency in Switzerland?"), in the BAGI two episodes with time, place, emotional involvement are requested from all periods of the past life, divided into 5- or 10-year epochs.
- *Test for evaluation of prospective memory – qualitative description (Knight et al., 2010; Staniloiu and Markowitsch, 2012).*
  Recalling to perform an intended future action, in particular to ask at the end of the testing for a personal object that the examiner had borrowed from the patient and hid in the examining room, in response to a pre-specified cue, namely the end of the testing. "The Grasshoppers and Geese Prospective Memory Test" (Lanting et al., 2010, 2011), which was developed for ethnically diverse individuals, comprises a task instruction that is embedded semantically. The test requests that the patient reminds the examiner to perform a task when an external (verbal) cue is delivered. If the patient does not respond to the cue, a series of three verbal prompts are provided. Scores range from 0 (no prompts required) to 4 (no recall to perform the action after all three prompts).
- *Tests for the evaluation of priming (standardized) and procedural memory (qualitative description)*
  Mirror Reading Test (von Cramon et al., 1993; Borsutzky et al., 2008, 2010), Gollin Incomplete Pictures Test (Gollin, 1960; Markowitsch et al., 1993; von Cramon et al., 1993).

For the Mirror Reading Test the version that is described in Borsutzky et al. (2008, 2010) was used. This variant allows a differentiation between priming and procedural memory. It comprises a series of 15 cards each consisting of two German words in mirror writing (30 words in total, all words with 8 to 10 letters) which are visually presented to the participants. Participants are asked to read the words as quickly and accurately as possible. Upon correct reading of the two words of one card, the next card is presented. The time by which subjects read both words correctly, constitutes the reading time measure. If they read a word incorrectly, they are told so. However, the correct word is not provided. In addition, all incorrect responses are counted. After a delay of 30 min a surprise second trial is administered. Herein, 10 words (on five cards) are identical with the first trial, 10 words are new and 10 words are also new, but similar in orthography to 10 words of trial 1 (e.g., "Explosion" and "Exkursion"). The sequence of cards is randomized for both trials. Improvement in reading speed from trial 1 to trial 2 of the recurring words serves to measure priming performance ("Priming"). Improvement in reading time of new words is used for an index of skill acquisition, i.e., procedural learning ("Procedural Memory"). Those words of trial 2 that are orthographically similar to words of trial 1 ("Interference") are created to induce interference in reading. We assume that due to these similarities in orthography with the words of trial 1, subjects might be disturbed in automatic reading processes. In trial 2 participants may initially tend to recognize the similarly looking words of trial 1 due to priming effects, but during reading, they would notice most discrepancies and would then have to execute a more effortful analysis. On the one hand, this may lead to longer reading times. On the other hand, if subjects experience deficits in suppressing the activated, but irrelevant memory trace (i.e., the "Interference" words of trial 1), they may produce more mistakes in reading of "Interference" words in trial 2 compared to "Priming" and "Procedural Memory" items.

In the Gollin Incomplete Pictures Test 20 pictures are presented, each picture containing a single familiar item (tree, ship, rabbit, etc.). Each item is given in 10 versions from a barely suggestive drawing (just a few dots or line drawings) to complete figure drawing. The participant has to tell what he or she thinks is to be seen in the drawing. Usually healthy participants recognize the item between versions 5 and 6, when given the first time, but much earlier (version 2 or 3), when it is given the second time.

- *Tests for the assessment of executive functions, problem solving, and cognitive flexibility*
  Trail Making Test-B (Lezak, 1995); Tower of Hanoi (Borys et al., 1982; Spitz et al., 1982; Lezak, 1995); California Card Sorting Test (Delis et al., 1987, 1992); problem solving test of Cronin-Golomb et al. (1987a,b); Wisconsin Card Sorting Test (Nelson, 1976); Game of Dice Task (Brand et al., 2005; Brand and Markowitsch, 2010). (All tests but the problem solving test of Cronin-Golomb are standardized.) In the problem solving test participants are given 17 sheets of paper, one after another; each sheet shows a drawing on the left side of the paper and three drawings on the right side (e.g., a crescent moon on the left side and a penguin, a woodpecker, and an owl on the right side). The participant should tell which of the three drawings on the right side best matches the drawing on the left side; we provide a qualitative description of performance on this test.

The Game of Dice Task is presented via computer. It is a fictitious gambling situation with explicit rules for virtual gains, losses, and winning strategies, which assesses decision-making under risk. A virtual single dice and a shaker are employed. Before throwing the virtual dice for 18 times, participants each time have to choose a single or a combination of 2, 3, or 4 numbers. Each choice is associated with different gains or losses. Participants get visual and acoustic feedback for their former decision.

- *Standardized tests of verbal fluency*
  Controlled Oral Word Association Test [COW fluency tasks (FAS); Golden et al., 2002]; Supermarket task (word production) (Calabrese and Kessler, 2000); Boston Naming Test (Kaplan et al., 1983; Lezak, 1995; Spreen and Strauss, 1998; Golden et al., 2002); the German version of the Stroop Test (Farbe-Wort-Interferenz Test/FWIT; or CWIT for Color Word Interference Test; Stroop, 1935; Bäumler, 1985).
- *Standardized tests for calculation*
  Zahlenverarbeitungs- und Rechentest (ZRT; Kalbe et al., 2002). In this test various simple and more complex calculations have to be done (additions, subtractions, multiplications, divisions).
- *Standardized tests for evaluation of malingering tendencies*
  Tests of memory malingering/effort [*Rey 15-Item-Test* (Lezak, 1995); tests from the *Test Battery for Forensic Neuropsychology* (*TBFN*; *Bremer Auditory Memory Test; Test for Assessing Memory Ability in Everyday Life*) (Heubrock and Petermann, 2000)]. In the TBFN subjects listen to a number of sounds (e.g., cackling of geese, honking) and later have to name them, or they listen to statements and later get for each statement a choice of four alternatives what was said (e.g., whether a meeting was at 10, 12, 2, or 4 o'clock).
- *Tests for evaluation of emotional processing*
  Florida Affect Battery (translated as *Tübingen Affect Battery*; Bowers et al., 1991; Breitenstein et al., 1996; standardized test); Emotional Pictures Test (von Cramon et al., 1993; performance on this test was qualitatively compared with the performance of the healthy control group and patient HI with septal nuclei damage described in von Cramon et al., 1993); Picture Story for Affect Induction (BAd; Temizyürek, 2003; qualitative description); Interpersonal Reactivity Index (Saarbrücker Persönlichkeitsfragebogen/Saarbrücken Personality Questionnaire; standardized; Beven et al., 2004; Paulus, 2012). In the Emotional Pictures Test 40 photographs with scenes of a neutral, positive, or negative content (e.g., shooting at a person, kissing another person) are presented and after half an hour the 40 original pictures had to be recognized out of 80 photographs. Control healthy participants (von Cramon et al., 1993) performed at a level of 95% correct for emotional and 88.3% correct for neutral pictures in the Emotional Pictures Test.

In the BAd two versions of a story about a family (mother, father, child) are shown – in the neutral version a day in their life is shown in pictures without that the child is involved in a car accident; in the emotional version the child is involved in a car accident. While watching the pictures the participant also listens to a male voice providing a narrative for each picture. The two variants of the story are identical for the first and last third of the pictures, but differ for the second third.

- *Standardized tests for mood, personality and psychopathological, and psychological load screening*
  Beck Depression Interview-II (BDI-II; Hautzinger et al., 2006); The Symptom Checklist Revised or SCL-90R (Hessel et al., 2001); Freiburg-Personality-Inventory-Revised (FPI-R; Fahrenberg et al., 2001); The German version of the Toronto-Alexithymia-Scale (Kupfer et al., 2001); Autism-Spectrum-Quotient (Baron-Cohen et al., 2006); Cambridge Behavior Scale (de Haen, 2006); Eigenschaftswörterliste EWL-N (List of personal adjectives) (Janke and Debus, 1978). The SCL-90R assesses psychiatric symptom load and psychological distress. It has nine subscales, such as somatization, obsessive-compulsiveness, interpersonal sensitivity, depression, anxiety, anger-hostility, phobic anxiety, paranoid thinking, and psychoticism. The general psychological distress level is estimated based on a global severity index, which is derived from all subscales. The FPI-R provides an assessment of personality along 12 dimensions: life satisfaction, social orientation, motivation to achieve, inhibition, excitability, aggressiveness, stress, physical complaints, health worries, openness, extraversion, and neuroticism. The EWL-N is a multidimensional self-administered scale, describing the actual well-being. It contains 15 subscales,

assessing activity, concentration, passivity, fatigue, extraversion, introversion, self-confidence, mood elevation, excitability, interpersonal sensitivity, irritability, anxiety, depressive tendency, dreaminess, and numbness. The scale was given to both ML and his mother who were both requested to choose the personal adjectives that matched ML's characteristics best.

- *Standardized test for visual perception*
  Judgment of Line Orientation (Lezak, 1995; Mitrushina et al., 2005).
- *Tests for social information processing*

Tests for social perception (perception of face, speech perception)

"Tübinger Affekt Batterie," a German-language version of the Florida Affect Battery (Bowers et al., 1991; Breitenstein et al., 1996) was administered.

Tests for social cognition (theory of mind, empathy)

"Augen-ToM-Test," a 24 photographs containing German adaptation of the well-known RMET (Baron-Cohen et al., 2001; Fleck et al., 2002; Reinhold and Markowitsch, 2007; Fujiwara et al., 2008) was administered (for a detailed description of the version of this test, see Dziobek et al., 2006). During the task only the eye regions of female (12) and male (12) faces are presented. The participant has to choose one of the four verbal descriptors (words) that she or he thinks it describes the best the mental state of the character. For a comparison group, we referred to age and educational matched data from Reinhold and Markowitsch (2007) and Dziobek et al. (2006). Mean scores and standard deviations are presented in **Table 1**.

The Multiple-Choice-ToM-Test (MCTT; Kalbe et al., 2001; Adenauer et al., 2005) version that we used requires the participants to read 16 short stories. (The test exists in two versions, one with 30 short written stories and another one with 16 stories. We provide a qualitative description of the performance on the abbreviated version of the MCTT). After each story (see example below) the participant has to make inferences about the mental states of a character of the story by resorting to a forced multiple choice format with four possible answers (only one right answer). The multiple choice format enables differentiation of three different types of mistakes: (a) mental states inferences that are "excessive"; (b) mental state inferences that are "too positive"; (c) choice of the distractor answer that reflects a neutral answer (i.e., a non-mental state inference such as physical causation).

Example of a story from MCTT:

Die Bananenschale (The banana skin; translated from German):

Joseph slips on the footpath on a banana skin and falls down. A woman close to him starts to laugh loudly. What does Joseph think?

(1) Such a silly woman. She should keep her mouth shut.
(2) Well, she is in a good mood.
(3) She definitely smashed the banana skin purposefully to this place.
(4) The woman wears a nice skirt.

The movie for the assessment of Social Cognition (MASC) (Dziobek et al., 2006; Fleck, 2008) requires the participants to watch a video about four individuals in their mid-thirties who gather for a dinner party. The movie is 15 min long, but it is paused and the participants have to answer questions concerning the film characters' emotions, thoughts and intentions. Therefore the test session lasts around 45 min. The test has been applied to healthy participants, patients with Asperger syndrome (see Dziobek et al., 2006) and patients with schizophrenia (Fleck, 2008). For comparison groups, we referred to the study of Dziobek et al. (2006). Mean scores and standard deviations are presented in **Table 1**.

The animation of Heider and Simmel (1944); Lück (2006), and Curci-Marino et al. (2004). The animated and silent short movie created by Heider and Simmel shows three geometrical figures (a large triangle, a small triangle and a small circle), which are moving in the neighborhood of a rectangle. In our study, we used a procedure similar to that of Curci-Marino et al. (2004), who applied this test to 40 German-speaking participants (15 women and 25 men) recruited from a technical university with a mean age of 24.3 years, in an attempt to replicate the original results of Heider and Simmel (1944). The movie was shown twice on a computer screen. As Heider and Simmel, we used a general task, such as "describe in writing what you saw in the movie." The text produced by the participant was then analyzed in a manner similar to that of Curci-Marino and colleagues and the results were qualitatively compared to those obtained by Curci-Marino and colleagues. We recorded the number of total words used and analyzed the use of animate nouns versus nouns designing geometrical figures, the description of internal states, the use of physical verbs versus animate verbs.

Understanding humor (Happé et al., 1999; Shammi and Stuss, 1999; Stuss and Levine, 2002; Uekermann et al., 2006; Bodden et al., 2010a) was qualitatively investigated. In the Humor task that we used, the participant is shown 20 cartoons from popular magazines. Similarly to the design of Happe et al. (1999), the cartoons are grouped in two conditions: 10 ToM cartoons and 10 non-mentalistic cartoons (the latter involved a physical anomaly). Cartoons are randomly shown, one at a time, on a computer screen. The participant is told to look at each cartoon and announce when he understood the joke. He then is asked to try to explain to the experimenter why each cartoon is funny. In addition to providing an explanation, the participant is asked to provide a subjective funniness rating for each cartoon. The mean times needed for processing the ToM cartoons and non-ToM cartoons are recorded (Bodden et al., 2010a).

Tests for social cognition (social judgment)

The *Approachability Task* (Adolphs et al., 1998) assesses the ability to make social judgments of other people. For this study we used an adaptation of the original task of Adolphs et al. (1998), which had been employed by Bellugi et al. (1999) to test 26 participants with Williams syndrome (WMS; mean age 23.6) and 26 healthy participants of similar age and gender ratio (mean age 25.5). Similarly to Bellugi et al. (1999) we used 42 black and white photographs of unfamiliar human faces, which were taken out of a pool of 100 original stimuli (Adolphs et al., 1998); 21 of these photographs depicted faces for which normal controls had given more negative ratings and 21 showed faces for which normal controls had given more positive ratings. The photographs were shown to ML one at a time, in random order. Without time constraints, ML had to rate the approachability of the face stimulus on a five point Likert type scale, which ranged from −2 (very unapproachable) to +2 (very approachable), by indicating how much he would approach and strike up a conversation on a street with the person whose face was depicted in the photograph. ML's performance was qualitatively compared to the results of Bellugi et al. (1999).

Tests for social cognition (moral judgment)

We used variations of the *Ultimatum* and *Dictator Games* which deviated from standard tests in several respects (Koenigs and Tranel, 2007). In the *Ultimatum Game,* ML acted as the responder. The starting capital was 100 Euros (Bolton and Ockenfels, 1998; Vieth, 2003; Oosterbeek et al., 2004). However, in contrast to the standard *Ultimatum Game,* participation was at the end of the experiment compensated with a fixed amount regardless of responses on the task (Koenigs and Tranel, 2007). Furthermore, in this variation, the examiner knew the proposers' identity and the offers were predetermined by the experimenter (Koenigs and Tranel, 2007). In the variation of the *Ultimatum Game* we used, the starting capital was 100 Euros; again, a fixed compensation at the end of the experiment regardless of responses on the task was offered. ML acted as dictator, deciding how much of the capital to keep. Again, the examiner knew both the identity of the "dictator" and "recipient."

Tests for social regulation (cognitive control, emotion regulation, monitoring/error correction, deception)

Game of Dice Test (Brand et al., 2005; Brand and Markowitsch, 2010); Interpersonal Reactivity Index *(Saarbrücker Persönlichkeitsfragebogen/Saarbrücken Personality Questionnaire;* Beven et al., 2004; Paulus, 2012); tests for evaluation of malingering tendencies (see above). The Game of Dice Task was described above under tests for executive functions. The personal distress scale of the Saarbrücken Personality Questionnaire contains queries which tap on emotional regulation.

Prior to starting the testing process, Mr. N. was asked a series of general interview questions, to assess for problems with awareness and orientation.

TESTING RESULTS AND INTERPRETATION

GENERAL BEHAVIORAL OBSERVATIONS

ML came to the assessment accompanied by his surrogate decision maker. Informed written consent was obtained for the participation in the study and publication of the report. The study adhered to the declaration of Helsinki.

ML was eager to participate and to show what he is able to do. In the following we will describe results from testing him over a period of about 8 h (with breaks). A summary of ML's testing results is provided in **Table 1**.

LATERALITY

ML in general was lateralized to the right, though he used his left hand for writing and other ways of motor performance *(Laterality Preference Inventory*). In the *Questionnaire for Measuring Motor Asymmetry* he provided evidence for a symmetrical foot use and more frequent use of his left hand.

LANGUAGE AND WORD KNOWLEDGE

ML's knowledge of terms and words was good *(Boston Naming Test*). He just failed to name *asparagus* and did not know the exact terms for *yoke* and *abacus.*

VISUAL PERCEPTION

Visual perception, as tested with the *Line Orientation Test*, was within normal limits.

ATTENTION, CONCENTRATION, AND PROCESSING SPEED

In all test of attention, concentration, and processing speed ML gained at least within normal limits situated scores. In the *Trail Making Test A and B* his performance was above average; testing results for reaction speed and phasic alertness were indicative of above average performance as well. Performance on divided attention and selective attention tasks was within normal limits (*Test Battery for the Assessment of Attention or TAP*). Stroop test performance was within normal limits as well.

NUMBER CALCULATION AND ARITHMETIC

Number processing and arithmetic were perfectly normal.

INTELLIGENCE AND OVERALL COGNITIVE STATUS

Several assessment procedures were used. In a test for estimating his verbal intelligence (MWT) ML was average. Also his performance in finding commonalities was average. On the other hand in non-verbal logical thinking ML was quite superior (IQ = 130). In other non-verbal tests of IQ his performance was superior to normal.

SHORT-TERM AND WORKING MEMORY

Performances on digit span forward and backward were above average in both numerical and visual tests. The surprising exception was an only average performance in visual block span forward (while the performance on visual block span backward was above average). Also ML was not prone to interference.

VISUAL-CONSTRUCTIVE SKILLS

In the Copy administration of the *Rey-Osterrieth Figure* ML reached points that situated his performance within normal limits. In the *Mosaic test* he was flawless.

LONG-TERM MEMORY

A large number of tests were applied to assess ML's long-term memory abilities. They can be divided into tests of anterograde, retrograde, and prospective memory, episodic–autobiographical, semantic, procedural, and priming memory (cf. Markowitsch and Staniloiu, 2012).

Anterograde memory

On all tests of anterograde memory, ML was below the level of normals (the only exception was that in the interference list of the *VLMT* he behaved substantially above average; this result can, however, be interpreted as reflecting his inability to properly acquire the main list of words, which was given prior to the interference list). Especially when it came to delayed recall of information he scored repeatedly at percentile 0 (*VLMT,* Logical Memory Subtest of the *Wechsler Memory Scale-Revised,* and *Rey-Osterrieth*

Figure, delayed recall). Also in the *Benton Visual Retention Test* his performance was below average.

In more easy tasks of visual recognition he encountered much less problems (simple doors of the *Doors and People Test*) (Adlam et al., 2009). Also in recognition memory tests with emotional material he performed sub-average, but not as poorly as in free recall tests involving emotional material. During the Emotional Pictures Test, ML recognized only 60% of the emotional pictures, which places his performance far below that of the control group described in the study of von Cramon et al. (1993). Even more surprising was the high number (9) of falsely recognized distractors, i.e., of pictures he had not previously seen (cf. **Table 1**).

With respect to ML's performance in the picture story for affect induction (BAd), there were no differences in the free recall task of emotional versus non-emotional variant of the story. This suggests that his mnemonic performance did not benefit from the potential emotional enhancement (Markowitsch and Staniloiu, 2011b). With respect to the recognition task of the emotional version of the story, ML recognized 18 out of 28 details (64%) from the first pictures (1–4), 9 out of 21 (42.8%) details from the pictures presented in the middle (5–7), and only 7 out of 21 (33.3%) details from the pictures presented at the end (8–10). The pictures 5–7 are accompanied in the emotional variant of the story by an emotional narrative delivered by a male voice, while the other pictures are accompanied by a neutral narrative, which is identical for both the "emotional" and "neutral" versions of the story. In the study of Temizyürek (2003) that included 30 participants (mean age: 33.8 + 8.9 years; IQ = 108), the percentage of recognized details from the "emotional" variant of the story was 83% for the first pictures (1–4), 77% for the middle pictures (5–7), and 72.7% for the pictures presented at the end (8–10). The lower recognition of details from the last compared to the first part of the story in the case of ML may reflect forgetting in the context of cognitive overload (Corkin, 1984; Markowitsch et al., 1993).

Retrograde semantic memory recognition

In tests of retrograde semantic memory recognition ML, on the other hand, was principally normal (*Semantic Old Memory Inventory, Famous Faces Test, Famous Names, Famous Terms, and Famous Events Tests*).

Retrograde autobiographical memory recall

As it was evident from the *Autobiographical Memory Inventory,* ML was unable to recall any personal events apart from one outstanding event, where his father made a suicide attempt by jumping out of the window. On the other hand, he could list autobiographical semantic facts (date of birth, place of birth, schooling, and the like).

Prospective memory

His prospective memory appeared impaired (*Rivermead Behavioral Memory Test;* "*The Grasshoppers and Geese Prospective Memory Test*"). In the *Rivermead Behavioral Memory Test* ML did not spontaneously recall to ask back for the loaned item. He required several very explicit cues. After each cue he responded "Yes, there was something," without knowing what. When given alternatives, he finally selected the right response.

On the *Grasshoppers and Geese Prospective Memory Test* ML did not perform the required action after all three prompts. (When extending the prompts to six – which is against instructions – he finally recalled the action he needed to perform.)

Procedural memory and priming

His procedural and priming skills appeared to be intact.

MALINGERING

Tests of malingering partly yielded results which – for an individual with normal memory capacity – would be indicative of malingering. As ML was quite deficient in memory recall of new material in general, these test outcomes cannot be interpreted as providing evidence for feigning or malingering (Sollman and Berry, 2011).

EXECUTIVE FUNCTIONS AND PROBLEM SOLVING ABILITIES

ML's problem solving and executive abilities were to a large extent within normal limits. Cognitive estimation measures were impaired (TkS). In the TkS, ML showed similar deficits as patients with Korsakoff's syndrome (Brand et al., 2003a,b). He exhibited deficits in estimating dimensions "weight," "quantity," and "time," whereby time and weight estimations were the most deteriorated. Size estimation was normal. Deficits in the TkS time items had been speculated to depend on timing deficits combined with remote memory impairment (Brand et al., 2003a). [In the time estimation task used here the participant was asked to estimate the duration of specific events (e.g., duration of a morning shower) without experiencing them in the test situation itself (Brand et al., 2003a).]

In the *Concept Comprehension Test* (Cronin-Golomb et al., 1987a,b) ML's performance was sub-average for abstract, but within normal limits for concrete concepts (Martins et al., 2006). Performance on verbal *FAS* was below average as well, resembling other reports on patients with developmental amnesia (Temple and Richardson, 2006).

SOCIAL INFORMATION PROCESSING: PERCEPTION OF EMOTIONAL AND COGNITIVE STATES AND INTERPERSONAL SITUATIONS

In the German adaptation of the *RMET* ML was only slightly impaired. In terms of qualitative findings, he required a relatively long time to respond. He made eight mistakes, but had no difficulties with reading fear. He rated two female eye pairs as belonging to a male.

In the MASC his performance was again only slightly impaired. ML's performance in this task seemed much closer to that of the 20 healthy controls from the study of Dziobek et al. (2006) (34.8 + 2.7) than to that of the 19 patients with Asperger's syndrome (24.4 + 5.9) from the same study (cf. **Table 1**).

In the *Florida (Tübingen) Affect Battery* ML displayed below average performance in the more complex subtests (affect naming, affect matching, affect prosody naming, detecting incongruent affect prosody, and matching face expression to affective prosody. In the visual affect naming subtest ML incorrectly designated the emotion of "fear" as being "anger" on two occasions. In the affect matching subtest, he made two mistakes, pertaining to the emotions "fear" and "happy," respectively. In the naming of affective prosody, he made two errors, pertaining to the emotion of happiness (which he interpreted as "neutral") and "fear." In the subtest requiring matching emotional faces to affective prosody he made one mistake, which involved the emotion of "fear." The most impaired was his performance on incongruent affective prosody, in which the semantic context was incongruent with prosody (Breitenstein et al., 1998; Snitz et al., 2002; Paulmann et al., 2008; Ward et al., 2012). While the degree of impairment detected in ML's performance should be interpreted with caution given the well-known ceiling effects of the *Florida Battery Test,* the qualitative description of these impairments is intriguing, when it is corroborated with findings from other tests, such as the Approachability Task or EWL-N (see below).

OTHER TESTS OF SOCIAL INFORMATION PROCESSING

The results in the *Humor Appreciation Test* (cartoons) were ambivalent. In the variation of *Ultimatum Game* ML accepted all the offers, including the minimal value (1 Euro) and in the *Dictator Game* he offered 15 Euros, which represents 15% of the starting capital. Although this behavior is difficult to be accurately interpreted due to the non-standardized format of testing that we used, there are, in our opinion some hints of abnormal fairness attitudes (Scheele et al., 2012; Baumard et al., 2013). Incidentally abnormal fairness attitudes and socio-economical decisions have recently been related to amygdala dysfunction (Scheele et al., 2012).

Results of the *Approachability Task* are indicative of either heightened capacity for trust, or hypersociability (see Bellugi et al., 1999; Martens et al., 2009), or alternatively, decreased aversiveness (such as in patients with amygdala damage; Adolphs et al., 1998, 1999). In the task of Heider and Simmel, ML used a total of 83 words in his description, within the range of healthy participants (Curci-Marino et al., 2004). However, he did not use any animate noun and gave no description of internal states. This finding is interesting in the light of data from Curci-Marino et al. (2004). This study (which was conducted in a technical university and without any explicit indication that it was a psychological study) failed to replicate several findings of Heider and Simmel (1944). The latter had reported a high use of animate nouns in their sample (97.1%). In the sample of Curci-Marino et al. (2004), 27 (59.3% men) out of 40 participants (67.5%, $p < 0.05$) did not use any animate nouns; only 13 participants out of 40 did use animate nouns (32.5%). The description of internal states was done by nine participants (22.5%, $p < 0.01$). Out of these participants six were men. Physical verbs were used by 39 participants and 38 participants described the moves of the figures with animated verbs among others. In contrast to Curci-Marino et al. (2004), the administration of the animation task of Heider and Simmel was done in our study as part of the psychological testing, which in theory could have offered ML a performance advantage.

PSYCHIATRIC RATINGS, EMOTIONS, AND PERSONALITY

The screening instrument *Beck Depression Inventory* did not yield scores suggestive of an affective disorder. ML did not show autistic tendencies (*Autism-Spectrum-Quotient*). In the *Symptom Check List (SCL-90R)* ML reported little tendency to somatize his problems, denied uncertainty in social situations or experiencing feelings of anxiety or inadequacy. In the *FPI-R,* ML answered that he had reduced life satisfaction, few physical complaints, very little aggressiveness, and perceived himself as being reserved and introverted. He experienced himself as being passive and with decreased motivation for achievement. On the openness subscale of *FPI-R,* ML scored significantly lower than his age group, seeming therefore to be very concerned with social conventions and social desirability. The subscale "openness" (willingness to admit minor weaknesses and violations of everyday conventions versus orientation toward making a socially desirable impression/social norms) of the *FPI-R* acts as a validity scale. Low results on this sub-scale point to socially desirable response tendencies. If a low result (stanines one to three) is reached in this subscale, interpretation of all other responses is limited (Fahrenberg et al., 2001; Fujiwara et al., 2008). According to findings from the self administration of *Toronto Alexithymia Scale (TAS-26)* ML did not experience any kind of difficulties with perceiving his own feelings and their accompanying bodily sensations. He scored low on the subscale for external orienting thinking style and perceived himself as being very interested in finding solutions in problematic situations. According to his self assessment, his ability to describe his own feelings was within normal limits. Given the deficient performance of ML on some tasks that objectively assessed emotional processing, one might argue that the results from self-evaluation scales or inventories should be interpreted cautiously. This is one of the reasons why we chose to ask both ML and his mother to complete the personal adjectives self-questionnaire (EWL-N). Both the mother and the patient confirmed that ML experienced no fear and no aggression. Out of 161 adjectives, 33 were judged differently by the two. ML's mother perceived ML as having no symptoms of depression and ML denied feeling depressed. While ML's mother perceived ML as being unconcentrated, undecided, and contemplative, ML viewed himself as being well concentrated, capable of decision making, and rejected all adjectives describing a contemplative or daydreaming nature. We speculate that ML's mother's perception of ML as being non-concentrated and a daydreamer might represent a misinterpretation of his memory difficulties (Gadian et al., 2000).

ML's capacity for empathy appeared even above average as assessed by one scale (*Cambridge Behavior Scale*). In the *Saarbrücken Personality Questionnaire* the only deviant scale score was that for personal distress. With a score of 85 on the latter scale ML supposedly experiences a lower (below average) level of personal distress (self oriented unpleasant feelings) when he is confronted with the distress of others. This scale's queries tap on aspects of emotional regulation. The low level of personal distress when confronted with the distress of others may also be corroborated with ML's view of himself as being interested in finding solutions in problematic situations. This pro-active attitude may be fueled by a decreased level of aversiveness or of conscious fear when confronted with various extreme situations, including the distress of others, which may be related to an amygdala dysfunction. Personal distress elicited by the distress of others is a self oriented motivated response directed toward self regulation of overarousal, which may be associated with fearfulness and emotional vulnerability (Cheetham et al., 2009). Too much personal distress might hinder the capacity for empathic concern; the amygdala and its connections seem to modulate the balance between the two (Feinstein et al., 2011; Roth-Hanania et al., 2011). The decreased level of aversiveness (probably due to an amygdalar dysfunction) may also account for the results on the approachability task, which were discussed above and for the behavior during administered variations of the economic games.

ML's scores on the fantasy scale, perspective-taking scale, and empathic concern scale fell within the average range (90–110), with the highest score (104) being achieved on the perspective-taking scale. Findings of average scores on the fantasy scale support its relationship with measures of verbal intelligence (Shamay-Tsoory et al., 2009). The perspective-taking scale was repeatedly related to interpersonal functioning, increased self esteem and social competence (Shamay-Tsoory et al., 2009).

The conduction of a psychiatric interview in conformity with DSM-IV-TR (2000) did not provide evidence of meeting full diagnostic criteria for a concomitant major depressive disorder, dysthymic disorder, or bipolar disorder (or other psychiatric disorder, with the exception of adjustment disorder). No substance use disorder was diagnosed. ML did not meet diagnostic criteria for a pervasive developmental disorder. [However, in line with the results of a new small study showing that some individuals with autism spectrum disorder may lose their diagnosis, one could argue that ML might have outgrown a range of symptoms later on (Fein et al., 2013).]

DISCUSSION

According to our knowledge, this is one of the first reports about a comprehensive evaluation of social information processing in a patient with amnesia with neurodevelopmental mechanisms (probable developmental amnesia). ML has a long standing history of difficulties with acquiring EAMs for long-term storage and with everyday memory performance (Vargha-Khadem et al., 1997, 2003; Willoughby et al., 2012). These impairments occurred in the context of postnatal hypoxia and reduced hippocampal formation volumes bilaterally. The reduction in hippocampal volumes likely happened due to the hypoxic incident; as mentioned above, a bilateral enlargement of the lateral ventricles (which suggests hippocampal volume reductions; Calabrese and Penner, 2007) had been noted more than 10 years prior to ML's most recent MRI imaging. Our voxel-based morphometry data confirmed markedly reduced gray-matter density within the hippocampus bilaterally, with an anterior and right-sided preponderance. Only when we used a whole brain analysis with a less conservative statistical threshold ($p < 0.001$, uncorrected), we identified further regions showing reductions of gray matter, such as both amygdalae and bilateral striatum and pallidum, bilateral thalamus (pulvinar) – again with a right-sided preponderance. Our findings partly overlap with the voxel-based morphometry results of Vargha-Khadem et al. (2003). One potentially intriguing result in our study is the reduction in the amygdala gray matter, when using a less conservative statistical threshold. The lack of reports of amygdala gray matter reductions in previous studies might be accounted for by the statistical threshold applied and/or the fact that apart from hippocampal formation, other medio-temporal lobe regions did not undergo rigorous volumetric quantifications (Vargha-Khadem et al., 2003; Rosenbaum et al., 2011). In line with other studies showing damage to thalamic areas after episodes of (perinatal) hypoxia (Jacob and Pyrkosch, 1951; Voit et al., 1987; Markowitsch et al., 1997; Cowan et al., 2003; Macey et al., 2005; de Haan et al., 2006), we identified indices of reductions in gray matter density in thalamus, namely in the pulvinar, when we applied a less conservative statistical threshold ($p < 0.001$, uncorrected).

The right-sided preponderance of the identified structural brain changes is relevant, given data suggesting a right hemispheric bias for emotional processing (Schore, 2002), EAM (Fink et al., 1996; Markowitsch et al., 2000) and "high-order consciousness" (Keenan et al., 2005) (however, for different results, see Nyberg et al., 2010; Viard et al., 2012).

On the behavioral level, ML shared several similarities with patients with developmental amnesia, but also displayed some distinct features (such as atypical school trajectory, different level of functional independence). He showed evidence of at least average intelligence; in some measures of intelligence his performance even was substantially above the normal level. His attention and concentration abilities were at least average and for some tests, above average. The same held true for executive functions and problem solving abilities, which were to a large degree within normal range. In the *Concept Comprehension Test* (Cronin-Golomb et al., 1987a,b) ML showed intact performance for concrete concepts, but sub-average for abstract concepts (Martins et al., 2006; Quian Quiroga, 2012). This result is congruent with data suggesting a role of hippocampal formation in facilitation of more complex problem solving, via comparison computations (Olsen et al., 2012). In the TkS, ML showed impairments comparable to those of patients with Korsakoff's syndrome (Brand et al., 2003a). These results may have to do with the test's specification. As mentioned above, deficits in the TkS time items had been conjectured to depend on timing deficits combined with remote memory impairment (Brand et al., 2003a).

ML's major and in fact very severe problems were identified in the domains of long-term memory. This was evident in anterograde memory tests where he almost did not recall anything after half an hour delay. It was – if this comparison is possible – even more evident when it came to EAM recall. ML was completely unable to provide authentic memories for personal events, aside from one, where his father jumped out of the window in a suicide attempt. The recall of this extraordinary event can be compared with the islands of knowledge that had been found in patient H.M. of Scoville and Milner (1957) and Corkin (2002). (After surgical removal of his medial temporal lobe regions bilaterally, H.M. was completely anterogradely amnesic. Exceptions were that he could recall the death of his parents, the killing of President Kennedy, and a particular song. All these were, however, semanticized memories; cf. Markowitsch, 1985.)

ML showed impairments in both semantic and episodic–autobiographical anterograde memory. He for example had no recollection of a previous meeting with one of his examiners (AS), although he admitted to a feeling of familiarity. He was able to recall factual aspects of his meetings with examiner SB, but these memories did not have an episodic quality. In particular they lacked contextual details and the subjective feeling of reliving. In contrast to his performance on various anterograde explicit memory tests, his old semantic knowledge was good, which suggests a use of compensatory strategies (Rosenbaum et al., 2011). His performance on free recall was worse than that on recognition which is consistent with findings from patients with developmental amnesia (Adlam et al., 2009). Adlam et al. (2009) reported a dissociation between recall and recognition; this was however incomplete, in the sense that their patients with developmental amnesia displayed (similarly to ML) a subtle, but significant visual recognition impairment in the Doors test. ML's poor performance on prospective memory tests mirrors data suggesting a role for hippocampal formation in prospection (however, see Markowitsch and Staniloiu, 2012 for controversial results). Prospective memory impairments have been linked not only to deficits in executive functions, but also to deficits in semantic memory and episodic-autobiographical memory (Hainselin et al., 2011). Apart from the hippocampal formation, the amygdala was also suggested to be involved in the simulation of future emotional events. In particular, a strong connectivity between rostral anterior cingulate cortex (ACC) and amygdala was observed during the imagination of positive future events (Sharot et al., 2007) and was postulated to underlie traits like optimism bias.

ML's performance on tasks that tap on social information processing abilities revealed both domains of preserved performance and impairment. In the *Florida (Tübingen) Affect Battery* ML performed well on simple tasks, but he displayed below average performance in the more complex subtests. Difficulties with emotional processing were also apparent on tests that assessed recognition and free recall of emotional stimuli. In the picture story for affect induction (BAd), his performance showed only a marginal benefit from the enhancing effect of emotional connotation. From a neurobiological perspective, ML's difficulties with emotional processing may be related to his gray matter reductions in hippocampal formation (with an anterior preponderance; Fanselow and Dong, 2010; Viard et al., 2012), and/or possible amygdala, basal ganglia (caudate), and pulvinar dysfunctions (Adolphs, 2010b; Markowitsch and Staniloiu, 2011b; Geschwind et al., 2012; Kemp et al., 2012; Nguyen et al., 2013; Saalmann and Kastner, 2013). Performance on affect-related memory tasks had been found to be impaired in patients with bilateral amygdala calcifications due to a genetic disorder (Urbach-Wiethe disease), compared to normal participants (Sarter and Markowitsch, 1985a,b; Cahill et al., 1995; Siebert et al., 2003). Similarly to the amygdala (Markowitsch and Staniloiu, 2011b), the pulvinar has been postulated to play a role in detecting salience (van Buren and Borke, 1972; Pessoa, 2011) and, due to its extensive connections with cortical areas, in the processing of emotional material (Pessoa, 2008, 2011; Pessoa and Adolphs, 2010). The hippocampal formation has been attributed a role not only in cognition, but also in emotional processing. In particular, the anterior hippocampus (which was significantly affected in our patient) has been assigned a function in emotional processing, reward, goal proximity, and arousal (Fanselow and Dong, 2010; Viard et al., 2012); the nature of functional specialization within the hippocampal formation in particular (and medio-temporal lobe, in general) is yet not a solved issue, however (Chua et al., 2007; Markowitsch and Staniloiu, 2012). Furthermore, it has been proposed that the function of the hippocampus extends beyond the mnemonic domain, to support other cognitive areas (such as perception, problem solving) via relational binding and comparison (Abu-Akel and Shamay-Tsoory, 2011; Olsen et al., 2012).

Some authors hypothesized that the hippocampal formation may play a role in the experience of emotions about others' mental states (Immordino-Yang and Singh, 2013). Negative correlations were found in a study between vocally expressed nervousness and regional cerebral blood flow in the right hippocampus (Laukka et al., 2011). Right temporal cortices (including right anterior temporal structures), the right thalamus, and also the amygdala and orbitofrontal cortices have been involved in affective-prosodic comprehension by some studies (Ross and Monnot, 2011). Additionally, basal ganglia have at times been implicated in emotional prosody decoding (Paulmann et al., 2008; Frühholz et al., 2012). While some authors had linked affective prosody decoding with the right hemisphere, several others have challenged this view (for a review, see Snitz et al., 2002; Frühholz et al., 2012). It is perhaps worth mentioning that the performance of ML on affective prosody tasks resembled in several respects that of the seven patients with Korsakoff syndrome, who were examined by Snitz et al. (2002). Those patients showed in comparison to control participants impairments in naming affective prosody when semantic content was incongruent, while both linguistic and affective prosody discriminations were intact. The authors did not provide a neurobiological explanation for their findings, though they made speculations about the involvement of the basolateral circuit.

On several standard laboratory tests for ToM, ML showed normal performance or only mild impairment. These results are consistent with largely preserved core ToM functions: however, our findings are slightly different from those of Rabin et al. (2012) who reported normal performance on standardized tests for ToM in an adult woman with developmental amnesia. There are several factors that may account for the observed differences, such as the use of different test adaptations (e.g., the German adaptation of the RMET) and the presence of neural correlates' and sex differences (Schulte-Rüther et al., 2008; Frank, 2012; Kemp et al., 2012; Nguyen et al., 2013; Saalmann and Kastner, 2013). In particular, the imaging study of Frank (2012) found that young men recruit during a false belief task more brain regions known to be implicated in episodic memory than young women.

In the Heider and Simmel animation paradigm ML partly deviated in his responses from those of comparison groups. Contrary to controls he did not use animated nouns and gave no description of internal states (Ross and Olson, 2010). On the other hand, self questionnaires yielded no indications of difficulties with empathy or perspective-taking apart from the Saarbrücken Personality Questionnaire (personal distress scale). As commented above, low personal distress elicited by the distress of others may reflect decreased conscious fearfulness (Cheetham et al., 2009), perhaps in the context of an anterior hippocampus and/or amyg-dalar dysfunction (Maren and Holt, 2004; Fanselow and Dong, 2010; Feinstein et al., 2011). Incidentally, on the EWL-N [List of personal adjectives] (Janke and Debus, 1978), both ML's mother and ML consistently rejected adjectives synonyms to "fearful" as applying to ML.

ML's results on the approachability task could be interpreted as evidence of increased sociability and/or decreased aversiveness. He tended to overrate (both negative and positive) faces as being approachable. These findings corresponded to observations from

ML's everyday life behavior. From a neurobiological perspective, an interaction between insula (which has bidirectional connections to amygdala) and hippocampus was found to be important for processing of untrustworthy faces (Tsukiura et al., 2012). Furthermore, decreased aversiveness and/or hypersociability have been related to various amygdala dysfunctions (Bellugi et al., 1999; Martens et al., 2009). It is possible that the hypersociability may stem in ML's case from decreased fearfulness/aversion, which may be underlain by an anterior hippocampus and/or amygdalar dysfunction (Maren and Holt, 2004; Fanselow and Dong, 2010; Feinstein et al., 2011).

No tendency for risky behavior was identified in ML by his performance in the Game of Dice Task. This finding is in some contradiction with his increased trustworthiness leading him to engage in potentially risky or dangerous behaviors.

Tests of malingering partly yielded results which – for an individual with normal conscious mnemonic processing abilities – would be indicative of feigning. As ML was quite deficient in memory recall of new material in general, these test outcomes cannot be interpreted as indicative of feigning. Based on our objective multidimensional assessment and the collateral information we obtained, we concluded that it was extremely unlikely that ML was trying to feign his impairments (either for an external incentive, such as in malingering or for deliberately trying to assume the sick role).

CONCLUSION

Episodic–autobiographical memory contains a wealth of information about people and social interactions; this led several authors to hypothesize that the exchange of EAM might facilitate social cognition, such as understanding of others' inner world and perspective (Nelson and Fivush, 2004; Spreng et al., 2008) and subsequently might connect and "draw the world together" (Casey, 2000, p. 313). In a review article, Abu-Akel and Shamay-Tsoory (2011) argued that, while primarily perception-based, the representation of mental states of others might also be computed by resorting to internally stored information such as from episodic-autobiographical memories. Data coming from a study of healthy participants suggested that laboratory ToM tasks engage more cognitively economical ways than accessing own EAMs (Rabin et al., 2010), relying on semantic knowledge and/or implicit processing (Adolphs, 2010a; Staniloiu et al., 2010b). Yet another study, which investigated the role of hippocampus in emotional mentalizing, proposed that mentalizing is modulated by memories of past events (Perry et al., 2011). Interesting data came from a recent study of Rabin and Rosenbaum (2012), which showed that in healthy female participants the functional relation between autobiographical memory and ToM is modulated by the familiarity of the target person in a ToM task, which in turn affected the employment of cognitive strategies.

Herein we used a broad variety of tests and found objective evidence of intact areas as well as impaired domains of social information processing in a young adult male patient with amnesia with neurodevelopmental mechanisms, which preponderantly afflicted episodic–autobiographical mnemonic processing. Consistent with data from other authors (Rabin et al., 2012), we identified in ML's case largely preserved ability to perform on a number of tasks testing core ToM functions; this is in line with suggestions that neither intact EAM nor an intact hippocampal formation are essential for core social cognitive processes (Rosenbaum et al., 2007; Rabin et al., 2012). Impairments were however detected in ML's case on certain tasks taping on complex social perception or complex social judgments. These results could be interpreted in different ways. The hippocampal formation has been attributed roles in relational binding (flexible association of disparate items) and comparison computations (Olsen et al., 2012). The hippocampus-related relational binding was proposed to underlie constructive processes linked to EAM, mental scene construction, and self-projection (Spreng et al., 2008; Addis et al., 2009; Rosenbaum et al., 2009; Spreng and Grady, 2010) (but, see McKinlay et al., 2009; Squire et al., 2010 for different opinions). Furthermore, hippocampus-mediated constructive processes were suggested in a recent study to be implicated in both EAM and ToM tasks targeting familiar individuals (Rabin and Rosenbaum, 2012). An interesting idea was however put forth by Olsen et al. (2012). The authors stated: "Thus, while binding and comparison computations may be mediated by multiple neural regions, the hippocampus is critical for these computations when relational information must be maintained over longer delays and/or when information has a high degree of conceptual/perceptual overlap, regardless of whether the information must be maintained over a delay or merely discriminated in the present moment" (Olsen et al., 2012, p. 10). Along this vein we could argue that our findings support ideas that an intact hippocampal formation might be necessary for adequate performance on tasks that require demanding, complex (perceptual) information processing, involving complex relational information and/or a need for longer online holding of complex relational information (Olsen et al., 2012).

Alternative explanations for our results may be linked to our voxel-based morphometry data, which pointed to indices of reduced gray matter in amygdala, basal ganglia, and pulvinar, when a less conservative threshold was used. All these structures were described to make contribution to social cognition and social information processing (Jacobson, 1986; Adolphs et al., 1998, 1999, 2005; Shaw et al., 2004; Pessoa, 2008, 2011; Adolphs, 2010a,b; Bodden et al., 2010a,b; Pessoa and Adolphs, 2010; Kemp et al., 2012; Nguyen et al., 2013; Saalmann and Kastner, 2013). Furthermore, several of these structures were reported to be affected in various memory disorders (Zingerle, 1912; Schuster, 1936; Smyth and Stern, 1938; Stern, 1939; Guard et al., 1986; Kuljis, 1994; Mori et al., 1999; Siebert et al., 2003; Allen et al., 2006). While white matter changes were not detected on visual inspection in the case of ML, subtle white matter changes due to hypoxia cannot be ruled out and would require more refined imaging techniques in order to be captured (Paus, 2010). Their detection may however be relevant for a number of reasons: there are numerous reports on amnesia arising after white matter lesions (Horel, 1978; Zola-Morgan et al., 1982; Markowitsch et al., 1990; Calabrese et al., 1995; Markowitsch and Staniloiu, 2012); furthermore, there are some reports of ToM impairments occurring after white matter tract damage (Bach et al., 1998; Happé et al., 2001).

Due to their non-uniformity, our findings draw attention to the need of employing several tests for assessing social information processing. Furthermore, they call for testing social cognition in real life settings or conditions that approximate real life settings, in order to fully assess the extent of disability and appreciate any contribution that EAM may play to understanding the inner world of others and "drawing the world together" (Casey, 2000, p. 313).

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Growing up with Asperger's syndrome: developmental trajectory of autobiographical memory

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Autobiographical memory (AM) and social cognition share common properties and both are affected in autism spectrum disorders (ASD). So far, most of the scant research in ASD has concerned adults, systematically reporting impairment of the episodic component. The only study to be conducted with children concluded that they have poorer personal semantic knowledge than typical developing children. The present study explores the development of both components of AM in an 8-year-old boy diagnosed with Asperger's syndrome, based on three examinations in 2007, 2008, and 2010. On each occasion, he underwent a general neuropsychological assessment including theory of mind (ToM) tasks, and a specially designed AM task allowing us to test both the semantic and the episodic components for three lifetime periods (current year, previous year, and earlier years). We observed difficulties in strategic retrieval and ToM, with a significant improvement between the second and third examinations. Regarding AM, different patterns of performance were noted in all three examinations: (1) relative preservation of current year personal knowledge, but impairment for the previous and earlier years, and (2) impairment of episodic memory for the current and previous year, but performances similar to those of controls for the earlier years. The first pattern can be explained by abnormal forgetting and by the semanticization mechanism, which needs verbal communication and social interaction to be efficient. The second pattern suggests that the development of episodic memory only reached the stage of "event memory." This term refers to memory for personal events lacking in details or spatiotemporal specificity, and is usually observed in children younger than five. We conclude that the abnormal functioning of social cognition in ASD, encompassing social, and personal points of view, has an impact on both components of AM.

Keywords: autobiographical memory, autism, child, theory of mind, episodic memory, semantic memory

INTRODUCTION

A growing body of research has demonstrated that autobiographical memory (AM) and social cognition share several common properties (Spreng and Mar, 2012). Given this functional overlap, we would expect AM to be affected in Autism Spectrum Disorders (ASD), as social cognition is impaired in this pathology. ASD includes a range of neurodevelopmental disorders including autism, Asperger's syndrome, and pervasive developmental disorders that are characterized by abnormalities in three core areas: verbal and non-verbal communication, social interaction, and restricted interests, and stereotyped behaviors. Within this spectrum, Asperger's syndrome differs from autism in that there is no clinically significant cognitive or language delay.

Autobiographical memory refers to personal knowledge and events relating to our own lives, and contributes to the development of social cognition, from both a social and a personal point of view. First, our memories of the past or of social interactions may help us to infer the mental states of others and allow us to adapt our own behavior accordingly. Hence, these memories help to increase our interpersonal knowledge. Second, we shape our own selves by extracting meaning from some of our autobiographical memories, described as self-defining memories, to update our self-concept and create a dynamic self-memory system (Singer, 2004). Crane et al. (2010) recently showed that ASD patients are unable to elicit meaning from their memories, which may render the self-memory relationship static, unlike that of typical adults.

Social cognition encompasses to the cognitive processes used to decode and encode the social world. It encompasses the perception of others, the self, and interpersonal knowledge (Beer and Ochsner, 2006). Theory of mind (ToM) is the social cognitive ability to impute mental states (intentions, beliefs, emotions, desires, etc.)

to oneself and to others, and to use these attributions to understand, predict, and explain the behavior of oneself and others. A ToM impairment is clearly established in ASD and Baron-Cohen et al. (1985) were the first to formulate the hypothesis of a link between ToM deficit and the abnormalities in communication and social interaction displayed by individuals with ASD. Difficulties with mentalizing or ToM clearly influence episodic memory in different ways. Episodic memory relies on a dynamic sense of self as differentiated from others or the ability to consider that the self is continuous over time, from past to future, as this allows children to organize and integrate personally experienced events within their self-concepts (Povinelli et al., 1996). Because these abilities mature late in typical development, true episodic memory does not emerge until around the age of 4 or 5 years (Perner and Ruffman, 1995; Wheeler et al., 1997; Newcombe et al., 2007) and continues to develop until adolescence (Piolino et al., 2007; Willoughby et al., 2012). Converging behavioral and neuroimaging data indicate that it is the psychological or interpersonal component of the self, or higher-order psychological self-awareness that is affected in ASD (Lind, 2010; Williams, 2010; Uddin, 2011). In ASD, the restricted ToM, or more specifically "theory of own mind," as suggested by Williams (2010), has an impact on the internal state language associated with memory narratives (Crane et al., 2010, 2011). This unstructured psychological self cannot act as an effective memory organizational system, and thus precludes individuals from recollecting specific autobiographical memories. Furthermore, the poor social skills associated with ASD limit individuals' social interactions. These social interactions, especially parent-child interactions, play a central role in the development of AM, by allowing children to construct narratives about their personal events (Nelson and Fivush, 2004). Limited linguistic interactions may adversely affect the development of AM in ASD, and also prevent the external rehearsal of narratives which, in typical individuals, enhances memory.

The personal narratives provided in response to autobiographical questionnaires allow us to distinguish between personal semantic memory or personal knowledge, and specific or episodic memory for autobiographical events (Cermak, 1984). All of the scant research conducted in adults with ASD has reported significant difficulties, mainly concerning the episodic component (Goddard et al., 2007; Crane and Goddard, 2008; Lind and Bowler, 2010; Tanweer et al., 2010; Crane et al., 2012a). When invited to evoke memories, ASD patients provide a list of facts, rather than truly specific personal experiences (Goldman, 2008), lacking in details and with few insight terms in their narratives (Crane et al., 2010). These memories are very similar to the event memories produced by young children before the emergence of the episodic memory system, as previously suggested by Maister and Plaisted-Grant (2011). Access to AM is also impaired in ASD, according to Crane et al. (2010, 2012a). It seems to take individuals with ASD longer to retrieve specific memories than it does typical adults, and unlike the latter, self-relevance cues do not facilitate their retrieval of specific details. However, the methodologies adopted by researchers may influence performance levels. Thus, greater impairment of the episodic component has been observed when participants with ASD are given a fluency task rather than an interview task (Crane and Goddard, 2008), and they perform just as well as controls on yes-no personal life event questions that do not require them to remember any specific details (Bruck et al., 2007), or when they are asked to write down their memories-a task that limits social interaction (Crane et al., 2012b).

Episodic AM impairment can be observed in children with ASD from the age of 8 (Losh and Capps, 2003) and as early as 5 years (Bruck et al., 2007). To date, the most recent study conducted in children with ASD in this domain was published by Brown et al. (2012), and interestingly focused on the quality of event reports. When the authors analyzed memory narratives provided by a group of children with ASD aged 6–14 years, they noticed that these children included fewer emotional, cognitive (thoughts and beliefs), and perceptual terms than typical controls. Contrary to their predictions, the children with ASD produced just as many social terms as controls. However, they listed general events lacking in details and social interactions. These results are consistent with previous data published by Lee and Hobson (1998). They were interested in the social attributes of the self, as seen mainly through social interactions, and reported that children and adolescents with ASD produced fewer social self-statements than typical controls. This observation, like the smaller number of emotional and cognitive terms found in personal narratives, can be explained by the affective and cognitive ToM impairment. Given the difficulty they have understanding their own beliefs and emotions, coupled with their inability to adopt other people's perspectives, children with ASD cannot spontaneously produce as many details as typical controls when they recall an event.

Unlike the episodic component, the semantic component seems intact in ASD adults, with no effect of lifetime period (Crane and Goddard, 2008). However, as demonstrated by Bruck et al. (2007), it does appear to be affected in children, which Lind (2010) believes reflects delayed development of the self-concept. Despite this hypothesis, there has been surprisingly little research on the development of AM in ASD, and no follow-up studies have been conducted so far, even though this approach is very useful for investigating the development of AM. First, it allows researchers to control for the interindividual variability that characterizes typical development (two individuals matched on chronological age may well be at different stages of cognitive development). This variability is even greater in ASD than in typical development, and some impairments reported in published case studies would not emerge in a group analysis. Second, longitudinal studies are a unique means of investigating how memories change over time and of testing the hypothesis of the delayed development of certain cognitive skills in ASD.

We conducted a longitudinal study of a young boy with ASD focusing on general cognitive functions and both components of AM. The purpose of this investigation was to extend our understanding of the development of personal semantic knowledge and episodic autobiographical memories by administering three examinations over the space of 4 years. Assuming that the self-memory relationship in ASD is static, rather than dynamic, owing to both limited linguistic interaction and impaired episodic AM, we predicted that Simon's personal semantic knowledge would be strongly related to the present, or here and now, and liable to be forgotten. Concerning the episodic component, memories would presumably take the form of "event memories," rather than truly episodic memories (Maister and Plaisted-Grant, 2011). If our assumption was correct, we would find that Simon's earliest memories, elaborated before the age at which episodic memory normally develops, were similar to those of typical children. His more recent ones, however, encoded after the age of 6 years, would contain fewer details than those of typical children. This gap in performances between typical children and our child with ASD would increase with age, despite the therapeutic interventions.

MATERIALS AND METHODS

CASE REPORT

We describe the neuropsychological follow-up of Simon, a young boy who was diagnosed with Asperger's syndrome on the basis of the ICD-10 criteria and the Autism Diagnostic Interview-Revised (ADI-R; Lord et al., 1994), an experimenter-administered parent interview that yields ratings for social, communicative, and repetitive behavior symptoms based primarily on behavior reported for the 4–5 year age period. This clinical instrument was used with Simon's mother at the age of 8 years. Three neuropsychological examinations were administered in August 2007, October 2008, and March 2010. Initial neuropsychological examination was conducted just after the diagnosis at 8 years of age, and the two others during the therapeutic follow-up.

Simon is the first-born of his family. During the first psychiatric consultation and the ADI-R interview, the mother reported that delivery, pregnancy, and motor development were all normal. Simon had no language delay: he said his first words at about 21 months and his first sentences at about 2 years. His mother started to worry when Simon, by then aged 4 years, appeared reluctant to interact socially with his peers. While he was at primary school, Simon was seen by a child psychiatrist and a speech therapist, who suggested to his parents that he might be a gifted child.

At the time of the first assessment, Simon was attending regular classes and did not receive special educational assistance. He had poor eye contact. His verbal communication initially seemed quite advanced, but he was pedantic in his choice of words. His voice was often too loud and his intonation theatrical. He often seemed to become lost in his own thoughts, and this had a considerable impact on his ability to hold conversations. Simon continually repeated sentences he had heard in cartoons. At school, he was a poor mixer, standing alone, and reading a book in the playground. Simon was unable to give his parents a chronological account of what he had done at school that day. For example, he might be able to tell his parents in incredible detail how he had fallen down in the schoolyard, but nothing else either before or after. He had no knowledge of social rules. He frequently committed faux pas in everyday life, such as asking people in the street if their dogs had fleas. It was very difficult to gain access to his own representations, feelings, emotions, and beliefs.

Simon had compulsive behavior, such as counting the steps as he went up or downstairs, or putting his things in his schoolbag in a particular manner. Simon was resistant to minor changes, such as switching between short-sleeved and long-sleeved clothes. He also displayed considerable restlessness, having difficulty sitting still in class.

Simon had a sensory/perceptual hypersensitivity. He was worried by sounds such as applause, a baby crying, a vacuum cleaner, or a hairdryer. He often put his hands over his ears, even when his parents could not hear anything. This auditory hypersensitivity was associated with acute attention to visuospatial details. By 4 years, he could already complete quite complex jigsaws. Simon was exceptionally good at construction toys. Whenever his father bought a piece of flat pack furniture, Simon was always the first to understand how to put it together.

Therapeutic interventions during these 3 years included psychiatric consultations, individual psychotherapy sessions, educational interventions, psychomotor therapy, and cognitive remediation. Cognitive remediation is a specific and individualized training program designed to reduce symptoms and improve cognitive functions and psychosocial functioning. It consists of exercises and practice of increasing difficulty, using a range of materials. This program of cognitive remediation took place twice a week over an 18 month period, and focused on a range of abilities thought to underlie social interaction, including emotion perception, ToM, and pragmatic conversational abilities. The program targeted the comprehension of complex social emotions, the attribution of mental states (intentions, beliefs, feelings), the learning, and comprehension of social rules, the estimation of the consequences of one's own behavior, and the comprehension of humor, irony, metaphoric utterances, and indirect requests. Simon also joined a social skills training group for a year. Social skills training seeks to improve social functioning. It is a structured method designed to teach the social interaction skills needed to build and foster interpersonal relationships, and promote the maintenance and generalization of these skills in everyday life. Group-based training in social skills means that the group dynamics can be used to facilitate therapeutic interactions in the "here and now." The program consisted of 20 sessions over 7 months and targeted the following social skills: recognizing non-verbal communication, identifying, and expressing emotions, introducing oneself, and listening to others, starting, maintaining, and ending a conversation, making demands, making, and receiving compliments and criticism, reacting to teasing, giving, and receiving presents. All the sessions followed the same sequence of activities: (1) joke of the day, (2) review of the previous week's homework assignments, (3) introduction of a new skill, (4) practice (direct instruction, modeling, role play, etc.), (5) presentation of the new homework assignments, and (6) social play time.

NEUROPSYCHOLOGICAL EXAMINATIONS

A general cognitive assessment was conducted three times. It covered intellectual ability (Wechsler Intelligence Scale for Children, WISC-IV; Wechsler, 2005), attention, executive functions (Tower of London, Visual attention, Auditory attention, Response set, and Verbal fluency subtests of the Developmental Neuropsychological Assessment, NEPSY; Korkman, 2003; Stroop-Drawing; Pennequin et al., 2004), working memory (WISC-IV, Corsi blocks; Pagulayan et al., 2006), and episodic memory (Rivermead Behavioral Memory Test; Wilson et al., 2000).

Theory of mind abilities were assessed using a false-belief task (Desgranges et al., 2012). This task was based on false-belief cartoon tasks such as "Sally and Ann" (Wimmer and Perner, 1983). We used eight short comic strips illustrating first-order false-belief scenarios that had been developed within our laboratory. Each comic strip comprised three pictures with a short written description (for examples, see Bon et al., 2009; Desgranges et al., 2012). The aim was to understand the story by reading the scenario, then answer a question with two possible responses. There were two conditions. In the ToM condition, the question was about the belief of one of the characters in the story. In the control condition, the question probed Simon's understanding of the reality of the cartoon scenario. The pictures and written descriptions remained visible throughout.

Autobiographical memory was assessed using an adaptation of the *Test Episodique de Mémoire du Passé autobiographique* (TEMPau task), a semi-structured autobiographical questionnaire validated in school-age children (Piolino et al., 2007; Picard et al., 2009). Briefly, this task explored personal information and specific events pertaining to three different lifetime periods (current school year, previous school year, and earlier school years).

For each period, personal information had to be recalled on four different topics: the names of acquaintances, personally relevant famous names (heroes, stars, etc.), information about school life, and personal addresses and regular activities. Specific instructions were given for each period (e.g., "Can you give me the names of three people from among your acquaintances during this period, such as the name of a friend, a neighbor, or a teacher?"). Simon was asked to supply this information as accurately as possible. In particular, he was asked to avoid giving information that was applicable to several periods and to provide information specific to the period under examination.

Concerning personal events, Simon was asked to recall specific, personally experienced events associated with specific dates for the current year period and prompted by three general topics (i.e., a school event, a trip, or vacation, and a family event) for the other two periods. For the current school year, six questions were used to conduct a chronological study of the previous months (last summer, last Christmas, last week, 2 days ago, yesterday, and today). Simon was asked to remember specifically experienced events that had lasted less than a day and which he could relive with details and situate in time and space (e.g., "Describe out loud and with as many details as possible, what happened, as if you were reliving it: what you did and felt, the circumstances, with whom, where, and how it happened"). Specific instructions were given for each theme, such as "Give details of a particular event that took place in your family life." Simon was always asked to give as many details as he could. Where necessary, if he had difficulty carrying out the task, two types of help could be provided. If he failed to produce any recollections, he was prompted with cues (e.g., "A day with a teacher or a school friend"). If he produced a general memory, he was encouraged to be more specific about the spatiotemporal context and to describe the circumstances of a particular incident ("Does this remind you of a particular day?", "Did this only happen once?"). The autobiographical questionnaire was provided to Simon's parents before the test to collect specific information about his life and all the recollections he produced were checked with his parents after the test.

Scores were calculated separately for personal information and events, and for each period. For personal events, each event was scored on a four-point episodic scale, which took into account the specificity of the content (single or repeated event), the spatiotemporal context (place, date, and time), and the presence of specific details (perceptions, thoughts, images, emotions, etc.). An overall personal event score was obtained by adding up the points recorded per period, taking all types of recall into account, both specific and generic. For each period, the maximum score was 12 (four points *per* topic and three topics *per* period). Each accurately recalled item of personal information was scored half a point, in order to have a maximum score of 12 *per* period, to compare with personal event score.

Performances were compared with those of controls published in Piolino et al. (2007). Controls were typically developing volunteer children, recruited from elementary and junior high schools. None of them had any neurological or psychiatric medical history and repeated a year. For this study, Simon's performances collected in 2007 and 2008 were compared with those of 14 controls aged from 7 to 8 ($M = 8.14$ years, $SD = 0.77$ years), and for the last examination conducted in 2010, performances were compared to those of 14 controls aged from 9 to 10 years old ($M = 10.02$ years, $SD = 0.56$ years). Two independent experts rated each child's production: the tester who was different for the control group and Simon and a rater blind to the age of children who was the same for all children. In cases of disagreement, the data were re-examined until a consensus was reached.

RESULTS

The three general cognitive assessments yielded normal results for most of the tests (**Table 1**). Results on the WISC-IV indicated that Simon consistently performed within the average range, albeit with a significant decline in verbal comprehension, and superior perceptual abilities indicated by the Perceptual Reasoning Index. The neuropsychological examinations did not reveal any attention or executive disorders, and although we noted a significant impairment in the ability to generate words from a phonemic cue (NEPSY Verbal Fluency), Simon performed normally in the third examination. Verbal and visuospatial working memory was normal. Episodic memory, as measured with the Rivermead Behavioral Memory Test, was also normal. The second assessment of ToM with a first-order false-belief task (Desgranges et al., 2012) yielded pathological results, but Simon's performance was normal in the third examination. For example, in the famous story "Maxi and his chocolate," a young boy called Maxi puts some chocolates in a green cupboard. After Maxi has left the room, his mother moves the chocolate to a blue cupboard. Maxi returns and wants his chocolate (Wimmer and Perner, 1983). Simon was asked where Maxi would look for the chocolate. The first time, Simon answered that Maxi would look for his chocolate in the blue cupboard because "his mother put it here." In the second examination, however, Simon concluded that Maxi would look for his chocolate in its original location, because "he doesn't know his mother moved it," adding "Nobody is telepathic!" Another story features a young boy who, because of his small stature, has to stand on a box to speak to

Table 1 | General cognitive assessment.

	Tasks	Simon's scores		
		2007	**2008**	**2010**
WISC-IV	Verbal comprehension index	110	90	82
	Perceptual reasoning index	135	114	124
	Working memory index	109	103	112
	Processing speed index	88	83	86
Stroop-drawing	Control condition 1	47	68	73
	Control condition 2	55	64	64
	Interference condition	30	40	44
Verbal fluency (NEPSY)	Semantic criterion	8	23	26
	Phonemic criterion	3*	4*	14
Visual attention (NEPSY)	Precision (/40)	39	37	38
Auditory attention and response set (NEPSY)	Score (/132)	105	105	102
Tower of London (NEPSY)	Score (/20)	13	13	14
Knock and tap (NEPSY)	Score (/30)	26	26	29
Digit span	Forward	6	6	5
	Backward	3	4	5
	Corsi blocks	5	5	7
Rivermead behavioral memory test	Score (/22)	20	18	21
First-order false-belief	Score (/8)	/	3*	8

The WISC-IV indices are shown in standard score format (M = 100 ± 15), whereas the other measures are shown as raw scores.
**Indicates pathological scores.*

his new neighbor over a high garden wall. Later on, his neighbor is in the street and thinks she recognizes the boy. The final picture in this comic strip shows two boys looking very similar, apart from their different sizes (a tall one and a short one). Simon was asked to say which one the neighbor would think she had chatted to. In 2008, Simon responded that it was the small boy, because "he is small and has to stand on a box." In 2010, however, Simon gave the correct response (the tallest boy), adding that "She thinks he is tall because of the box."

Concerning AM, Simon exhibited a deficit in both components – personal information and personal events (**Figure 1**). For personal information, Simon performed just as well as controls for the current school year (except for the second assessment). However, for the previous year and earlier years, Simon performed below average in all three examinations.

Conversely, for personal events, at all three examinations, Simon exhibited pathological performances for the current year, below those of controls (though not significantly so) for the previous school year, and as good as those of controls for the earlier school years.

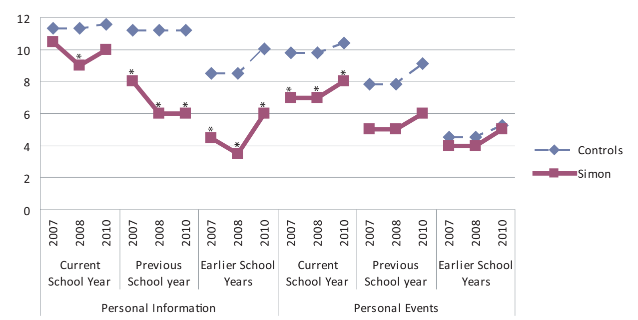

FIGURE 1 | Production of personal information and events across the three lifetime periods. *$p < 0.05$. Legend: Simon's scores were compared with those of controls matched on chronological age and published in Piolino et al. (2007). Simon obtained pathological scores ($Z < 1.777$; $p < 0.05$; df = 13) for personal information for the previous school year and earlier school years, as well as for the current school year, though only in 2008. Personal event scores were only pathological for the current school year period, although they were slightly low for the previous school year period ($1.35 < z < 1.77$; $0.10 < p < 0.05$).

DISCUSSION

By distinguishing between events and personal information, and by looking at how these memories change in the course of development, our investigation of Simon's AM revealed the relative preservation of personal knowledge for the current year, but impairment for the two previous periods. In terms of episodic AM development, Simon produced normal childhood memories, but his more recent ones were impaired.

SEMANTIC AUTOBIOGRAPHICAL MEMORY

Bruck et al. (2007) also reported impairment of the semantic component of AM, but without the preservation of the most recent period. However, in their study, the authors assessed the current year using 23 questions that were far more specific than those administered in the present study (e.g., the names of the child's doctor, teacher, principal; the age and occupation of his or her parents). This more detailed exploration may have been more sensitive to mild impairment than our task. Nonetheless, the pathological results regarding the two earlier periods suggest that Simon forgot a significant proportion of his personal or self-related information. In the 2010 examination, for example, concerning information about his current school, Simon knew the name of his teacher and could provide some details about his classroom, such as the location of his desk. For the previous school year, however, Simon was only able to give his teacher's name, and for the earlier period, Simon was not able to produce any details associated with his school. The longitudinal approach we adopted proved highly informative. In 2007, Simon listed the names of three ferries he used to travel on when he lived in another country. By 2008, he had forgotten two of them and only produced the third one when the examiner prompted him with the first two names. In 2010, he was not able to cite a single name. Some personal information may be recalled with cues, but some may be completely forgotten, as attested by some false productions (e.g., in 2008, the name of the teacher he had had 2 years earlier). These results suggest that personal information fades, with retrieval difficulties first, followed by genuine, accelerated, long-term forgetting. There are two possible explanations, not necessarily mutually exclusive. First, this semantic pattern may be explained by an abnormal mechanism of consolidation *per se* that needs verbal communication and social interaction to be efficient. Limited linguistic interactions and personal thoughts in ASD prevent rehearsal which, in a typical context, strengthens semantic memories (Kopelman and Bright, 2012). Second, there may be a deficit in semanticization, or the episodic-to-semantic shift, which also relies on verbal communication and social interaction to turn episodic memories into semantic ones via a mechanism of repetition and updating (Cermak, 1984). The limited verbal interaction associated with the episodic memory deficit may also hinder the addition of new semantic information, not least encyclopedic knowledge, as demonstrated by the decrease in verbal comprehension assessed with the WISC-IV.

EPISODIC AUTOBIOGRAPHICAL MEMORY

As regards the episodic component of AM and in accordance with our predictions, results suggested a deficit in the production of personal events associated with objective (i.e., spatiotemporal context) and subjective phenomenological details, including thoughts and emotions. These results mirror previous findings of impaired episodic AM in high-functioning individuals. The representations of events held by individuals with ASD are more general and temporally non-specific (Crane and Goddard, 2008). They resemble the event memories produced by younger typically developing children before episodic memory has fully developed (Maister and Plaisted-Grant, 2011). If Simon's performances were similar to those of controls for the earliest lifetime period (earlier school years), it is because personal event memory for this period is not yet truly episodic. Children with ASD are able to produce fragmented memories based mainly on perceptual images, sometimes with disconcertingly specific details, but these are not integrated into a temporal continuum (Newcombe et al., 2007). This developmental limitation explains why the ability to produce episodic autobiographical memories associated with distant lifetime periods does not improve when children grow up (Picard et al., 2009). Hence, the development of episodic memory may be limited to a primary level containing some specific details but without recollective abilities or the subjective experience of mental time travel. For example, in 2008, Simon recalled his birthday party, which had taken place 5 months earlier. He was able to list the people who had been at the party, where it was with some specific places, what he had eaten and some of the presents he had received, but all these details were produced as though he were describing a picture. When he was asked if he remembered that event and something he did there, he answered "no." He had no subjective experience allowing him to recollect this personal event.

There are important interdependencies between episodic and semantic AM. First, the semantic impairment may contribute to the encoding and retrieval deficits in episodic memory. The acquisition of complex episodic memories relies on semantic information, while personal knowledge allows us to access specific sensory/perceptual episodic memories. Episodic AM and semantic AM are highly interconnected, especially during the early stages of retrieval when personal semantic knowledge can aid memory search and retrieval operations (Conway and Pleydell-Pearce, 2000; Svoboda et al., 2006). Moreover, semantic AM develops earlier and provides a foundation for the later and more gradual development of episodic AM in typically functioning children (Picard et al., 2009).

SOCIAL COGNITION AND AM

The follow-up showed an improvement in performances on the first-order false-belief task. This may have contributed to the improvement in Simon's episodic AM by increasing his ability to understand that that which is brought to mind during the act of remembering refers to the mental state of a past experience (Perner, 2000; Naito, 2003; Perner et al., 2007). In young adults with Asperger's syndrome or high-functioning autism, correlations have been found between performances on a test which assesses the affective ToM (the Reading the Mind in the Eyes Test) and performances on an AM task (Adler et al., 2010). Therapeutic interventions may have contributed to this relative improvement in episodic AM. These interventions encourage verbalization and narrative abilities, and may thus have affected Simon's ability to recount personal experiences. However, this improvement may not be enough for children with ASD to reach a normal level of AM function. Furthermore, false-belief task performance may not always be a reliable indicator of representational ToM among these children, who may draw on other cognitive abilities to perform this task (Lind and Bowler, 2009a,b). Thus, on the basis of Simon's results, we cannot entirely rule out the possibility of impaired ToM. Further investigations are needed to conclude on this point.

CONCLUSION

This longitudinal approach yielded further explanations for the atypical functioning of AM in ASD. First, when we assessed personal information associated with specific and limited lifetime periods (e.g., previous year), we were able to confirm the impairment of the semantic component of AM that has previously been reported in children with ASD. This impairment may also be present in adulthood, but up to now, researchers have chosen to use questionnaires assessing longer lifetime periods than in the present study, covering more than 1 year (5 years for Crane and Goddard, 2008). Second, we also demonstrated an impairment of current and recent personal event memories, with the preservation of remote ones referring to event that occurred before the age of 7 years. These results suggest that patients with ASD may have a basic form of episodic memory resembling the event memory observed in children under six. Third, we observed an encouraging qualitative improvement in AM that may have resulted from a combination of different factors, including development, family support, and therapeutic interventions.

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Autobiographical memory and mentalizing impairment in personality disorders and schizophrenia: clinical and research implications

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Clinicians in the fields of mental health, neuroscientists, and social psychologists have been increasingly interested in how persons with psychiatric conditions experience a range of difficulties related to how they think about themselves and others. These difficulties include problems forming and retrieving the specific autobiographical memories (AM) that ground a sense of personal identity (McAdams, 2001). They have also involved diminishments in the capacity to engage in acts of mentalization or metacognition which allow for the understanding of mental states. Both of these forms of dysfunction are of increasing relevance given that each has been commonly observed across different psychiatric conditions, appears relatively independently from symptoms, and is uniquely linked to functional impairment (Dimaggio and Lysaker, 2010; Liu et al., in press).

To date deficits in AM and metacognition have mostly been analyzed separately. Psychopathology research has tended to explore either one or the other, thus neglecting the larger issue of how metacognition and AM are produced by systems which are likely closely related and likely feed and support one another (Markowitsch and Staniloiu, 2011). In development, AM and Theory of Mind (ToM) tend be influenced by common factors (Nelson and Fivush, 2004). Persons who present with overgeneralized AM also experience mentalizing problems including reduced affect awareness and poorer ToM (Palmieri et al., 2012).

Psychotherapy research and general neuroscience have begun to examine how these functions support one another and how disruptions in either AM or metacognition might lead to decrements in the other. To explore this issue we review psychopathology research concerned separately with problems in AM and metacognition in two forms of mental illness: schizophrenia and personality disorders (PD). We then discuss the advances from psychotherapy research and neuroscience for understanding how these two phenomena are related and comment on opportunities offered by these insights for scientific and clinical work.

AUTOBIOGRAPHICAL MEMORIES IN PERSONS DIAGNOSED WITH PSYCHIATRIC DISORDERS

AM are understood to be a core aspect of healthy function across the human life span (Conway, 2005; Singer et al., in press). Being able to retrieve personal memories allows persons to form representations of themselves as unique beings who exist with meaningful continuity over time. They also provide a context for making sense of what is happening interpersonally in the moment.

Such processes often seem disrupted in persons suffering with significant forms of psychopathology. Instead of resorting to key past events as a prototype for meaning-making and action predictions, patients might resort to overgeneralized memories or intellectualizations, in order to make sense of their choices, dilemmas and conflicts. For instance, patients with Narcissistic PD might respond to an interpersonal conflict not by recalling specific memories about their live in which the conflict was solved, but rather with a generalization about others as inept or ungrateful. Patients diagnosed with psychosis might respond to the same dilemma without any clear recollection from the past, or if the past was recalled it might be disjointed and not clearly related to the problem in the moment.

To date, qualitative and quantitative work has suggested at least six different though related ways (Dimaggio and Semerari, 2001; Lysaker et al., 2001) in which AM are disturbed in psychosis and PD. First, AM in persons with these conditions often lack clear space and time boundaries. It is difficult to detect where and when an event has taken place. Second, when memories are retrieved they are often made sense of through the use of intellectualization and moral rules, without a nuanced sense of what actually happened between the specific people involved in the memory; for instance it might be recalled that certain people were ungrateful or demanding without there being sufficient detail to determine what might have led up to that event. Third, descriptions of others present in the narrative episode are often sketchy and the sequences of the actions and reactions are difficult to follow and bereft of detail.

Fourth, within the narrative episode the dialogue that takes place among the characters is often repetitive and stereotyped. Exchanges between people may be recalled but they tend to follow more of a formula than to reflect recollections of a unique conversation. Fifth, the narrative theme of the memory may be redundant, often reflective of the most basic or gross set of motives, and the story itself tends to be formulaic; memories may center around threat and fight/flight responses and end without any resolution or an irreversible resolution (e.g., a severing of connection to another person). A sixth problem is that AM recollected lack a pictorial quality which might enable a listener to imagine what happened. Memories may lack details related to visual, auditory, olfactory, or gustatory cues, elements which would lend an opportunity to understand the memory as a unique experience.

Turning to explorations of specific disorders, research has suggested that many patients with avoidant, dependent and obsessive-compulsive PD featured reduced AM specificity (Spinhoven et al., 2009). Similarly, narratives of patients with borderline PD have frequently been found to be overly general (Maurex et al., 2010), less often concerned with prototypical life events and moreover less coherent (Jørgensen et al., 2012). Autobiographical narratives produced by patients with borderline PD portray life events as either imbued with dysregulated affect and lacking any sense of agency (Adler et al., 2012).

Regarding schizophrenia, fundamental disruptions have been observed (Lysaker and Lysaker, 2008). Many with schizophrenia are less able to spontaneously recall memories which involved discrete events that occurred in a specific time and place (Corcoran and Frith, 2003; Riutort et al., 2003; D'Argembeau et al., 2008). There may be lesser recall of specific or well-defined memories, and a tendency to recall more public than private events (Cuervo-Lombard et al., 2007; Raffard et al., 2010). Further, the specific AM of patients with schizophrenia are less consistent with the overall self-image they endorse and the self lacks agency; this suggests a deficit not just in retrieving memories but also in integrating different aspects of identity into a coherent whole (Bennouna-Greene et al., 2012).

METACOGNITIVE/MENTALIZING DYSFUNCTIONS IN PERSONALITY DISORDERS AND SCHIZOPHRENIA

Literature also suggests that patients with PD and schizophrenia suffer from a wide array of dysfunctions in thinking about themselves and others. Referred to as dysfunction in metacognition or mentalizing, this includes difficulties recognizing mental states, correctly naming them and using them in a flexible way and as a reliable source of information.

Research has specifically suggested that many with PD experience difficulties describing their own emotions, seeing links between emotion and thoughts (Semerari et al., 2007; Nicolò et al., 2011), and seeing their own thought processes in a detached and reflective way (Bateman and Fonagy, 2004; Semerari et al., 2005; Dimaggio et al., 2009a,b). Difficulties appraising the mental states of others has also been noted (Fonagy et al., 2002) though relatively less impairment has been observed in more basic laboratory ToM tasks (Domes et al., 2009; Ghiassi et al., 2010). The combination of poor mentalizing and PD have also predicted poorer vocational outcome (Bly et al., 2012); poorer mentalizing skills in patients with avoidant and borderline PD is a negative predictor of psychotherapy outcome (Gullestad et al., in press). In general, persons with PD appear to have limited abilities to use mentalization in order to respond to psychological problems (Carcione et al., 2011). The ability to reading the mind of the others within tasks that call for empathy have been found to be problematic for persons with narcissistic PD, and a deficit of which they are unaware of (Ritter et al., 2011).

More pronounced metacognitive deficits have been found in schizophrenia. Compared with persons without psychosis, deficits have been noted in a broad array of assessments of both cognitive and affective ToM tasks (Brüne, 2005; Penn et al., 2008), and these problems are associated with negative symptoms and poor social functioning (Brüne et al., 2011). The narratives of persons with schizophrenia feature severe inabilities to identify mental states, to see the world from multiple perspectives, and to use that knowledge to respond to psychological challenges (Lysaker et al., 2007; Mitchell et al., 2012) both as a trait marker (Lysaker et al., 2011b) and as a result of trauma (Lysaker et al., 2011c). Empathy has been found a problem for many with schizophrenia (Derntl et al., 2009).

NEUROSCIENCE AND THE LINK OF AUTOBIOGRAPHICAL MEMORY WITH METACOGNITION

In parallel with these developments, neuroscientists have also offered evidence of a close relationship between AM and metacognition. For instance imaging studies have suggested that AM is supported with brain areas which partially overlap with ones devoted to attributions to mental states (Rabin et al., 2010; Spreng and Grady, 2010; Mar, 2011; Rabin and Rosenbaum, 2012). Spreng and Mar (2012) have noted that even non-overlapping cortical areas linked with AM and mentalistic attributions, share a network of connections. Whitehead et al. (2009) have suggested that the ability to engage in pretend play is coupled with activations in cortical areas implicated in both ToM and narrative processes.

THE INTERPLAY OF IMPAIRMENTS IN AM AND METACOGNITION IN PSYCHOTHERAPY

While much psychopathology research has considered impairment in AM and metacognition separately, recent work in psychotherapy has begun to urge that successful treatment requires a consideration of the relationship of the two. Among those are mentalization-based treatment (Bateman and Fonagy, 2004), metacognitive interpersonal therapy for PD (Dimaggio et al., 2007, 2012), and metacognition-oriented psychotherapy for psychosis (Lysaker et al., 2007, 2011a; Buck and Lysaker, 2009; Salvatore et al., 2009, 2012). These approaches share the idea that a key aspect of therapy is to help patients to narrate specific AM—instead of resorting to overgeneralized memories or intellectualizations—as specific AM are the most fertile soil to think about for mental states (Dimaggio et al., 2010, 2012; Lysaker et al., 2011a). In other words, the enrichment of AM may promote improvements in metacognitive capacity. To address this possibility these procedures train therapists to seek specific memories. For instance, overgeneralized recalls have been suggested as a cue to explore for the specifics of narrative episodes (Dimaggio et al., 2012).

The rationale for seeking and thinking about specific episodes is based on the assumption that metacognitive reflection is at its heart a consideration of real life events, and as such impoverished AM offer little fertile ground for metacognitive activity. Accordingly, for many patients the appearance of more nuanced AM precedes the development of the ability to think in more complex ways about oneself and others; narrative episodes may provide opportunities for patients to recognize actual chains of thoughts, affects and behaviors in interpersonal interactions (Dimaggio et al., 2012). Other patients though may need to reach some basic level of access to mental states, in particular awareness of affects and their links with thoughts and behaviors, before their AM emerge. Formal analysis of case studies has shown that successful therapy involves the progressive growth of narrative capacity and aspects of metacognition, with the ability to narrate one's own story improving first, then followed by awareness of one's own states and awareness of the mental states of the others (Lysaker et al., 2005, 2007).

IMPLICATIONS FOR TREATMENT AND RESEARCH IN PSYCHOPATHOLOGY

While difficulties in AM and metacognition have been treated separately as factors which are present and influence outcome in significant forms of mental illness, psychotherapy, and neuroscience research suggests the need for these phenomena to be studied together. More efforts would seem to have the potential to answer several questions, including whether one form of deficit emerges before the other. Do metacognitive dysfunctions result in impoverished AM or diminished AM leave persons less able to think about mental states (Dimaggio et al., 2008, 2009a,b)? Are AM and metacognition best thought of as two networks operating together or a reflection of a single core psychological process? Are they decoupled in a similar way in nonclinical subjects and in different forms of psychopathology?

There is reason to believe that narrative enrichment (Gonçalves et al., 2012) and promoting mentalization (Bateman and Fonagy, 2009) are features of successful therapies; research addressing their interplay may guide the development of these interventions.

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