


Review

From exploration to exploitation: a shifting mental mode in late life development

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Changes in cognition, affect, and brain function combine to promote a shift in the nature of mentation in older adulthood, favoring exploitation of prior knowledge over exploratory search as the starting point for thought and action. Age-related exploitation biases result from the accumulation of prior knowledge, reduced cognitive control, and a shift toward affective goals. These are accompanied by changes in cortical networks, as well as attention and reward circuits. By incorporating these factors into a unified account, the exploration-to-exploitation shift offers an integrative model of cognitive, affective, and brain aging. Here, we review evidence for this model, identify determinants and consequences, and survey the challenges and opportunities posed by an exploitation-biased mental mode in later life.

Exploration versus exploitation: at the crossroads of human mentation

Every volitional act is the product of a choice to either exploit prior knowledge toward a more predictable outcome, or to explore new sources of information with less certain returns. This tension between exploitation and exploration is pervasive in everyday life. Do we return to the same vacation rental again this summer, or take that overseas vacation? Do we watch our favorite cable news outlet or seek an alternative perspective? Do we rely on stereotypes or actively engage with unknown others? This tension is observed across numerous biological, ecological, and artificial intelligence systems [1]. In humans, the **exploration** (see [Glossary](#)) versus **exploitation** trade-off has been extensively studied in young adults [2–20]. Yet there is growing evidence that the determinants and criteria governing decisions to explore versus exploit are altered over the adult life span, with direct implications for mentation and real-world functioning in later life [21–32].

In this review, we integrate decision science with cognitive and affective aging theories and aging neuroscience research to propose a shifting **mental mode** hypothesis of aging, anchored in the idea that exploration–exploitation trade-offs are increasingly biased toward exploitation over exploration in older adulthood. This hypothesis is grounded in the recognition that the architecture of human cognition undergoes a striking transition over the course of adult development [33]. Fluid control processes, necessary for fast and flexible engagement of cognitive resources, undergo a linear decline with age. Concurrently, prior knowledge of oneself and the world continues to accumulate [34]. We argue that these dual trajectories of cognitive aging favor an exploitative mental mode, one in which the accumulating weight of prior knowledge representations strengthens the prepotency of exploitation over exploration-based choice behaviors. In addition to cognitive factors, affective shifts that occur with age also produce an exploitation bias in older adults ([Box 1](#) and [Table 1](#)). We have deliberately chosen the label ‘mental mode’ here to recognize both the cognitive and affective changes that occur with age, which impact older adult mental functioning. With advancing age, decision-making is increasingly biased toward reliance on more positively valenced information and prior knowledge, resulting in more frequent expression of exploitation-biased behaviors, or a modal shift, from exploration to exploitation-based mentation.

Highlights

Exploration- and exploitation-based search processes underlie goal-directed cognition.

Older adults rely more on exploitation-based search during goal-directed tasks.

Emergence of an exploitation-biased mental mode is coincident with declining cognitive control, knowledge accumulation, altered motivational drives, and brain network changes in older adulthood.

The exploitative mental mode hypothesis may offer a more unitary account of mental functions in late-life development.

The age-related shift in mental mode has both adaptive and maladaptive implications for performance on laboratory-based tasks, as well as real-world functioning in later life.

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Box 1. Integration of cognitive and affective factors increase age-related exploitation biases

In addition to cognitive factors, affective drives and motivations have also been implicated in exploitation-biased mentation in later life [25,29,53]. Socioemotional Selectivity Theory (SST) [52,54] posits that older individuals reweight their goal structures to prioritize emotional satisfaction and meaning. A core prediction of SST is the emergence of exploitation bias in older adulthood. Indeed, the genesis of SST was the observation that the informational value of forming or fostering new relationships (exploration) declines across the life span as experiences accumulate. By contrast, the emotional value of closeness with familiar others (exploitation) increases with age [94]. Thus, SST provides one of earliest theoretical accounts of an age-related exploitation bias, one grounded in affective changes. This raises important questions about the relative contributions of affective and cognitive factors, and how they interact to produce an exploitation bias in older adulthood.

We suggest that these two factors can be readily woven together under our shifting mental mode hypothesis. Behavioral research supporting SST [53,54] converges around the central idea that, with age, emotional goals are increasingly (chronically) activated and require less cognitive control to be maintained in working memory [95], favoring an exploitative mental mode. With repeated activation, emotional goal hierarchies become consolidated into existing prior knowledge structures or schemas [76]. Schemas, or distillations of prior knowledge, comprise association patterns abstracted from individual events. Critically, they integrate both cognitive (e.g., spatial, perceptual, and social associations) and affective elements of past experiences [76]. We suggest that chronically activated schemas (i.e., accumulated prior knowledge), incorporating both affective meaning and cognitive context, bias mentation toward exploitation and away from exploration in older adulthood (see Figure 1 in main text).

There is early evidence for a neural mechanism supporting such affective–cognition interactions. Medial prefrontal cortex (mPFC) has been associated with schema formation [75,76] and is a core node implicated in the affective (motivation) circuit [60] with indirect influences on cognitive (attention) circuits through LC connectivity [36]. Both of these circuits underpin the exploration trade-off in our model (see Figure 1 in main text). Furthermore, the mPFC, becomes increasingly connected to salience network regions, including the anterior insula and anterior cingulate cortex [80,89,90,92], as well as subcortical structures, such as the amygdala [96], all regions implicated in exploitation-based search [36]. We suggest that this connectivity profile positions mPFC as a central processing hub, integrating cognitive and affective information into schema [76,97,98]. These chronically activated schema, in turn, anchor ongoing mentation in prior knowledge, leading to an exploitation bias in older adulthood.

This model (Figure 1) distills the two broad arcs of cognitive aging, declines in fluid processes and gains in prior knowledge, as well as shifts toward affective goals, into a criterion shift, favoring exploitation-based over exploration-driven mentation and action [11,12]. Furthermore, this prepotency for exploitation over exploration in older adulthood is underpinned by specific patterns of age-related brain changes, observable from the level of neurotransmitters to interacting brain networks (Figure 1B). We suggest that a more integrative and holistic perspective on cognitive and affective functioning in aging is urgently needed to better understand this largely uncharted era of late-life human development, one that can extend nearly half a century and continue beyond the tenth decade of life.

The axis of exploration and exploitation

Exploration and exploitation are ‘control states’ [35] and trade-offs between them are thought to shape all volitional, or goal-directed, thought and action [36]. While trade-offs are typically studied in the context of moment-to-moment decisions, here we view exploration and exploitation through a broader lens, one that extends the conceptual model to consider exploration–exploitation trade-offs as a more pervasive decision-making style, subject to genetic, phenotype, and ontological influences. We refer to a bias toward exploration or exploitation as a mental mode and anchor our model in the rich body of research on search and decision-making [1] and changes with age [31]. When preparing to select from an array of response options, individuals can decide to either select from known options or search to identify new, presently unknown, options. This choice has been classically defined as a theory of rational search [37] and encompasses both external (shopping online for that perfect gift) and internal (recalling your favorite film of all time) search decisions [38]. Exploration–exploitation trade-offs have been investigated across species, from field mice to primates; across disciplines from evolutionary biology to computer science and organizational

Glossary

Anterior cingulate cortex: brain region located along the medial wall of the frontal lobes, immediately posterior to medial prefrontal cortex; implicated in salience detection and signaling when action outcomes are misaligned with expectations (i.e., prediction error).

Cognitive control: modulation of thought and action by intended outcomes (i.e., goal states). An umbrella term encompassing specific cognitive processes including working memory, task switching, and inhibition necessary to instantiate, sustain, and update goal hierarchies.

Default network: functionally connected assembly of brain regions, including medial prefrontal cortex, posterior cingulate cortex, as well as lateral and anterior temporal and parietal regions and medial temporal lobe structures; implicated in internally directed mental functions, including memory, future thinking, self-awareness, and social cognition.

Exploitation: a thought or action involving the utilization of existing resources including both material (e.g., food, social contact) and immaterial (e.g., prior knowledge, memories) in which the reward value of choice options is known.

Exploration: a thought or action involving, new learning, a search for new resources, or novel reinforcements in which the reward value of choice options is unknown or cannot be reliably predicted.

Locus coeruleus (LC): subcortical nucleus located in the brain stem, and the primary source of the neurotransmitter noradrenaline (norepinephrine) in the brain.

Medial prefrontal cortex (mPFC): brain region located along the medial walls of the frontal lobes; comprises three primary divisions: anterior, dorsal, and ventral regions; implicated as a primary site for the integration of affective (emotional), cognitive (mnemonic), and social (self/other) representations.

Mental mode: a bias, or prepotency, toward exploration or exploitation.

Nucleus accumbens (NAc): subcortical nucleus located in the ventral striatum, and a primary source of the neurotransmitter dopamine in the brain.

Prior knowledge: accumulation of learned associations, patterns, generalizations, and abstractions acquired

Table 1. Biasing mechanisms and predictors of an exploitative mental mode in older adulthood

Biasing mechanism	Predictors of exploitation bias in older adulthood	Refs
Declines in cognitive control	Working memory: information compression; integration of fewer decision options Mental flexibility: reduced capacity to shift search strategies based on changing response contingencies Inhibition: inability to overcome a prepotent exploitative mental mode Future planning and prospection: reduced prospective foraging and mental simulations necessary for directed exploration Learning: poor updating based on novel information and feedback; miscalibration of uncertainty	[13,18,26,29,36,47,104–109]
Gains in prior knowledge	Predictable rewards: increased certainty and reward value for known over unknown choice options Processing efficiency (lower control demands): schema, heuristics, gist-based knowledge Greater associative processing: anchoring current mentation to prior knowledge stores (schemas)	[10,25,26,39,43,50,110–113]
Greater motivation towards affective goals (life meaning)	Positivity bias: positively valenced and less detailed (gist-based) recollections promote known over unknown choices Narrowing time horizons: reduced reward value of unknown information; greater reward value of social intimacy; increased risk of novelty-seeking (exploration) Positive reward expectations: reduced uncertainty of choice outcomes; increased propensity to seek known rewards	[21,31,54,60,77,78,79,114,115]

through intentional or incidental learning events and lived experiences.

Salience network: a functionally connected assembly of brain regions, including anterior cingulate cortex, anterior insula with strong connections subcortical brain regions, including LC; implicated in detection of meaningful, personally relevant information and interoceptive perception (i.e., felt experience).

Socioemotional selectivity theory (SST): theory of aging and emotional experience; predicts that, with age and shrinking time horizons, greater priority is afforded to goals related to social and emotional well-being and the avoidance of emotional risk.

behavior; and across contexts from foraging, to reinforcement learning and information search [1,38].

While we draw upon the breadth and depth of this field, it is not our intention to review the expansive body of literature. Many excellent reviews have already been published on this topic [1,8,13,36,39]. Within biological systems broadly, and human mentation more specifically, a mental mode threshold for shifting between exploration and exploitation is determined by environmental, individual, and social factors [39]. Environmental factors include resource availability and predictability, extraction costs, win versus loss probabilities, time horizons, and whether the search is focused internally (mentalization) or externally (perception/action). In addition to these environmental factors, individual differences also influence exploration–exploitation trade-offs. These include demographics, cognitive capacity, physical and psychological abilities, personality attributes, and neurobiology. Finally, social factors also have a role. These include societal levels of competition and cooperation, as well as availability and communal access to knowledge within a social group [39]. With these determinants in mind, in the remainder of this review we describe how many of these factors change with age to promote the emergence of an exploitation-biased mental mode in later life.

A shifting mental mode in older adulthood

We propose that, by incorporating both dimensions of choice in a volitional act (i.e., ‘Should I stay or should I go?’ [36]), exploration–exploitation trade-offs can provide a more integrative, holistic account of aging mentation. The trade-off captures both age-related declines in fluid cognitive ability [34,40], necessary for directed exploration [29], and the accumulation of prior knowledge across the life span [41,42], thereby reducing the informational value of exploration, and

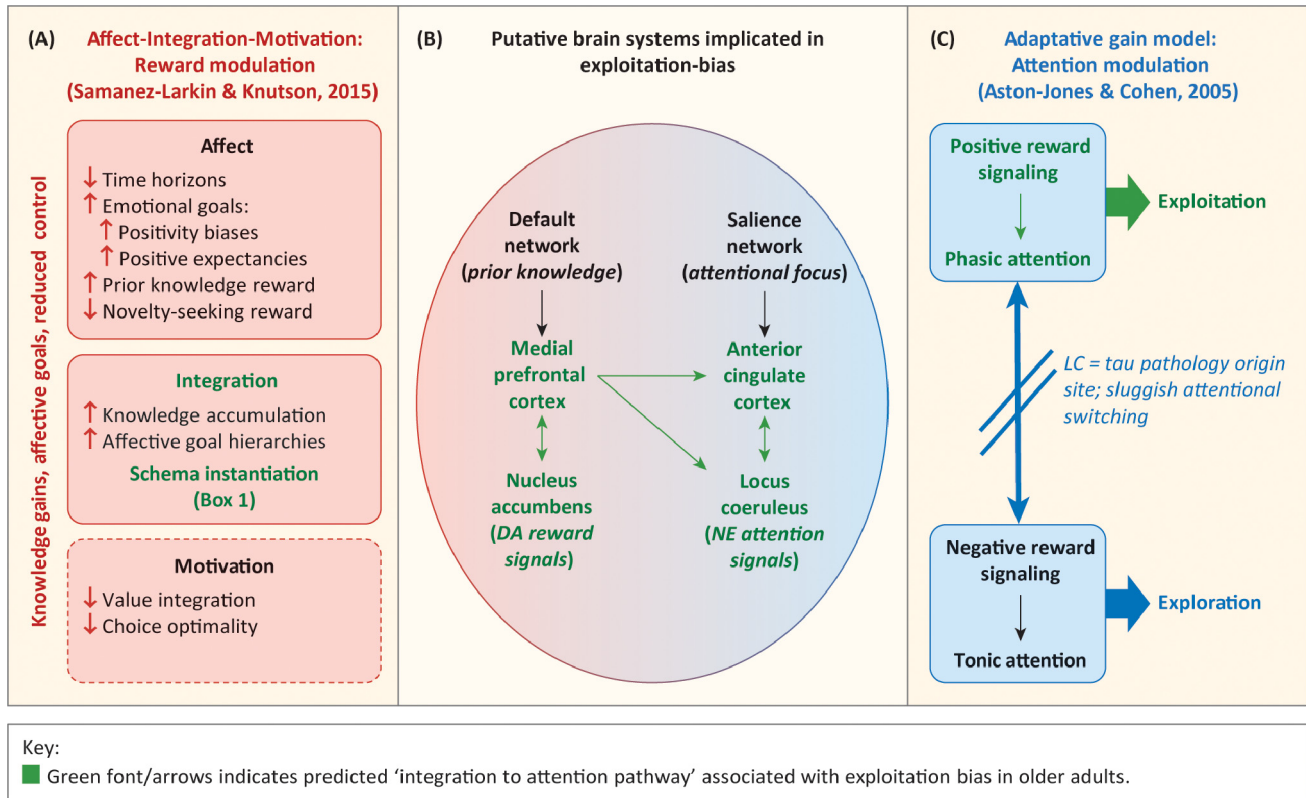


Figure 1. Exploitation biases in late-life development: reward, attention, and associated neural circuits. (A) Reward and motivation circuit. The affective, integrative, and motivation (AIM) framework [58] proposes three processes (affective, integrative, and motivational) that shape exploitation and exploration decisions. Age-related changes to these circuits provide a mechanism for the emergence of an exploitation-biased mental mode. At the affective level, reduced sensitivity to predicted negative choice outcomes in older adulthood [79] increases positive reward expectancies, leading to increased dopamine (DA) signaling to attention modulation circuits (C) (and see below). At the integration level, greater integration of positively valenced affective information [54] and prior knowledge coded in medial prefrontal cortex (mPFC) regions [2] reduces the uncertainty of known choice options, increasing the relative risk of information-seeking (i.e., exploration) behaviors, motivating an exploitation-biased choice. We propose that prior knowledge and affective information are integrated in schema and instantiated in mPFC [76] (see Box 1). The motivation level of the hierarchy is dotted, reflecting our lack of specific predictions regarding age-related changes to this circuit. (B) Putative brain systems. mPFC, a core node of the default network, integrates prior knowledge (via connections to default network regions) and affective value information (via dopaminergic inputs from nucleus accumbens into schema). Positive signaling from mPFC to the attention modulation circuit [anterior cingulate cortex (ACC) and locus coeruleus (LC)] within the salience network biases noradrenergic functioning, promoting phasic attention. (C) Attention modulation circuit. This model describes an integrated neural system for the adaptive regulation of performance [35]. Increased dopaminergic reward signaling from mPFC and associated with positively valenced outcome expectations and value-based enhances noradrenergic signaling from ACC to LC (and DA signaling to ventral tegmental areas, not shown; see [36]). Increased noradrenergic signaling leads to sustained phasic firing in LC. According to Adaptive Gain Theory [35], phasic LC signaling promotes focused attention and a sustained bias toward exploitation-biased choice. Abbreviation: norepinephrine (NE). Adapted from [60] (A) and [35] (C); see original figure captions for full model details.

promoting more exploitative choices (affective factors also have an important role; Box 1 and Table 1). We propose that these trends can be consolidated into a unified trajectory, consistent with a shift in preferred, or prepotent, mental mode from exploration to exploitation. On balance, neurocognitive aging research has viewed age-related cognitive changes through the lens of declines in fluid cognitive abilities. However, these accounts often fail to enumerate or consider older adults' expanded repertoire of knowledge and lived experience and, perhaps even more importantly, how this accumulation of knowledge intersects with fluid abilities to guide decision-making behaviors in a variety of contexts (Figure 1). Reconceptualizing these dual cognitive trajectories as a unified overarching shift in mental mode opens the way for a more comprehensive model, one that encompasses, and explicitly integrates, these features of cognitive aging.

Cognitive control processes are critically dependent on **prior knowledge**, and this dependency increases with advancing age [33,43]. Yet it is difficult to operationalize and reliably measure this transition in aging cognition, because these processes are typically considered as separate trajectories and assessed in isolation [44]. While much is known about these independent trajectories, relatively little is known about how they intersect and combine to shape goal-directed thought and action in later life. Measuring their combined influence, as opposed to each capacity independently, requires assessing their relative weighting along a single behavioral dimension. We propose that the exploration–exploitation trade-off provides this dimension. Expressing an exploration- versus exploitation-based choice indexes the summative influence of control processes, prior knowledge (as well as affective influences) in producing a single behavioral outcome: the decision to explore versus exploit. As such, any shift in bias (i.e., mental mode) or, more precisely, the threshold at which an exploration–exploitation trade-off occurs, can provide a marker of how these capacities intersect and combine to shape goal-directed behavior. We propose that the dual trajectories of cognitive aging bias older adults toward exploitation-based choice, indexed by an elevated threshold for an exploitation to exploration shift in later life.

Reduced cognitive control

Older adults choose more known versus unknown options during the one-arm bandit gambling task, a reinforcement learning measure of exploratory versus exploitation-based choice. Unlike older adults, younger adults prefer to investigate uncertain possibilities (i.e., explore) that might produce better returns [21]. Notably, this strategy can be altered by changes to the environment that impose additional cognitive load. When control demands increase, younger adults shift their choice strategy away from exploratory search and adopt a more exploitative mental mode ([45] but see [12]). A similar shift has also been observed during random number generation, in which sequences become increasingly predictable (i.e., exploitation based) and less random in the context of diminished executive control resources in aging and brain disease (reviewed in [46]). These findings are consistent with the cognitive control hypothesis of search-related behavior; variability in cognitive control demands influence the selection of exploitative versus exploratory search strategies, or flexibly shifting between them, during goal-directed tasks [28,47].

The cognitive control hypothesis has been called upon to explain the shift toward more exploitative behaviors in older adulthood, because control processes show significant age-related decline [29,31]. Older adults spend more time exploiting known information versus exploring for new options on classic search and decision-making paradigms [23,27,31,32,46], although greater exploratory search with age, or an absence of age-differences, have also been reported [25,28]. The trend toward greater exploitative behaviors with age has been observed across many species, consistent with the idea that the emergence of a prepotent exploitative mental mode across development has phylogenetic origins [21,38,46]. However, both exploration and exploitation may be goal directed and depend on cognitive control processes. During exploitation, cognitive control is needed to maintain the search cue, sustain attention while searching through available knowledge stores, and suppress irrelevant prior knowledge [12]. Our central premise here is that exploration requires greater cognitive control than does exploitation in most contexts. There is significant evidence for this idea. Under conditions of high cognitive control demand, both younger and older adults shift away from exploration and adopt a more exploitative strategy [27,45]. Furthermore, given that control processes decline with age, it follows that choice behaviors become increasingly biased toward exploitation as a prepotent mental mode (random number generation studies are reviewed in [46]). As noted earlier, older adults showed greater exploratory search on a verbal fluency task that indexes internally directed search processes [28]. However, this was attributed to the failure to maintain the search cue, resulting in

an incidental shift toward exploratory search. This differs from the exploitation biases with age observed during volitional choice behaviors [23,27,32,48].

Increased prior knowledge

One might ask why exploitation would serve as a prepotent or ‘starting’ mode for older adults. If exploration is the preferred mode when initially learning about the value of various options [29], why would older adults not calibrate to this mental mode more frequently? Here, we turn to the second dimension in the shifting cognitive architecture in older adulthood: an expanding store of prior knowledge. Greater experience with options typically leads to increased exploitation, because the value of unknown options is diminished and, thus, the risk of exploration is increased [10]. Furthermore, associative learning is increasingly dependent on prior knowledge in later life, with more ready access to a larger repertoire of crystalized knowledge representations in the context of declining control resources [33,49–51]. Older adults thus avail of this expanded store of prior knowledge, rather than facing the risks and costs of exploring for new information with both adaptive and maladaptive consequences (see Figure 2, and Box 2 for an interesting parallel in scientific discovery over the life span).

Shifting motivation and time horizons

Thus far, we have presented evidence that declining control resources and expanded prior knowledge stores promote exploitation as a prepotent mental mode in later life. However, other factors may also have a role (Table 1). Aging is associated with greater neophobia, a reduced interest in, or fear of, novelty. This has been attributed to the fact that the value of novel information gained from exploration is diminished in later life. For older adults, the time

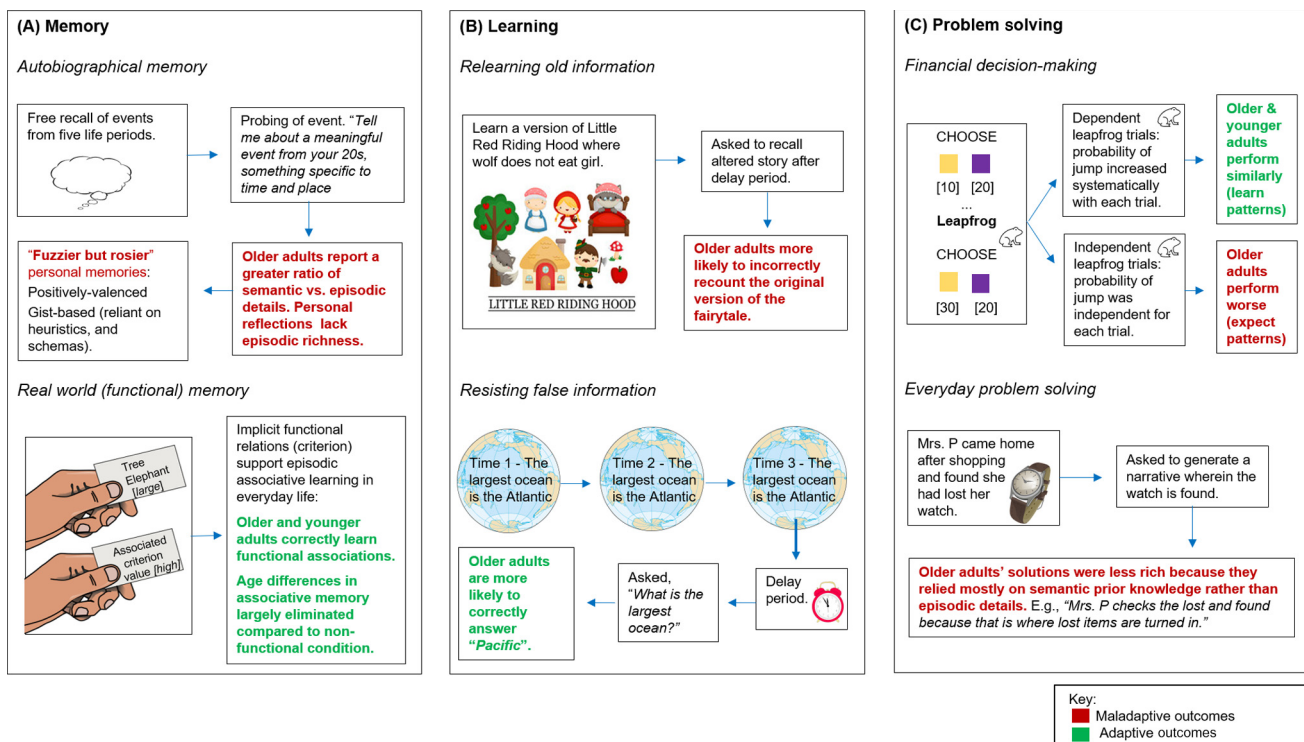


Figure 2. Influence of prior knowledge on cognitive performance in older adulthood. Samples of experimental paradigms in which older adults engage prior knowledge, resulting in either adaptive or maladaptive outcomes in the domains of memory (A), learning (B), and problem-solving (C) [50,110,112,116–118]. For a comprehensive review, see [33].

Box 2. Aging and scientific genius: not all discoveries are created equal

In [Figure 2](#) in main text, we provide a graphic outlining how prior knowledge, and a bias toward an exploitative mental mode, influence performance across different tasks and domains in later life. This shift from exploration to exploitation has a rather striking parallel in the domains of scientific discovery, innovation, and creativity. Einstein once quipped that ‘A person who has not made his great contribution to science before the age of thirty will never do so’. While this idea has gained popular traction, it is not well supported by the data. The most significant scientific discoveries, those later awarded Nobel prizes or scientific medals, occur across the full expanse of middle adulthood with a gradual decline into older age. Indeed, the median age of discovery has continued to increase over the past few decades [99]. Critically, however, the nature of scientific innovation does change with age. When divided by discovery type, conceptual innovations, those depending on deduction, abstraction, and exploration of novel associations occur much earlier than experiential discoveries, which are more inductive and involve exploitation of prior knowledge [99]. By some estimates, this conceptual versus experiential ‘discovery gap’ can be more than 20 years. In considering these data, it is important to highlight that exploration and exploitation can both lead to innovation and discovery. However, it is the basis of discovery (exploring new associations versus exploiting prior knowledge) that appears to change with age.

Similar findings were recently reported in which older adults performed as well as younger adults on a creative (divergent) thinking task [100,101]. Based on these findings, the authors reasoned that older adults were able to exploit a larger store of prior knowledge to fuel creativity in the context of declining cognitive control resources. Of course, the loss of cognitive control and the weight of prior knowledge may eventually stifle creativity into older age, consistent with the steep declines in innovation into older age reviewed earlier. This idea of prior knowledge stifling exploration, while offered tentatively here, was eloquently expressed by Sigmund Freud nearly a century ago in his treatise on *Civilization and its Discontents* (1929): ‘The conceptions I have summarized here I first put forward only tentatively, but in the course of time they have won such a hold over me that I can no longer think in any other way’.

horizon to extract the value of novel information, and to amortize the risks and costs of exploration, is shorter [13,21,52]. Thus, the benefit-to-cost ratio of exploration declines with advancing age. These factors directly interact with shifting affective motivations [23,53] (see [Box 1](#) for a discussion of affective-cognitive interactions). Increased positive affect is associated with a decline in goal-directed search in young adulthood [29]. The **Socioemotional Selective Theory (SST)** of aging posits that older adults show a preference for recollecting more positive experiences, an effect known as the positivity bias [54]. Thus, older adults may be biased toward exploiting familiar, and positively valenced, prior knowledge, resulting in a curtailed search [25], precluding or delaying a switch to exploration (but there is evidence that the influence of a positivity bias may differ across search contexts [55,56]).

Exploitation and exploration shape volitional thought and action across the human life span. As such, exploration–exploitation trade-offs may offer a more integrative measure of the shifting architecture of mentation in later life. We have provided converging evidence that a bias toward exploitation emerges as a mental mode in older adults, attributable to declining control resources, a greater repertoire of prior knowledge, and motivational changes favoring exploitation-based decisions ([Box 1](#) and [Table 1](#)). However, important measurement challenges remain with respect to reliably quantifying and characterizing this putative shift in mental mode across the life span ([Box 3](#); see [Outstanding questions](#)).

An exploitative mental mode in the aging brain

The tension between exploitation and exploration, and the calibration of a mental mode, has been related to subcortical and cortical brain systems [1,8,13,31,36]. Here, we examine specific neurophysiological changes that may predispose older adults toward a prepotent or preferred exploitative mental mode. The adaptive gain model of exploitative versus exploratory behaviors identifies a neural circuit including **medial prefrontal cortex (mPFC)**, **anterior cingulate cortex**, and catecholaminergic subcortical nuclei, including the **locus coeruleus (LC)** and **nucleus accumbens (NAc)** [2,20,35,36]. Additional regions implicated in the exploration–exploitation dilemma also include lateral, orbitofrontal, and rostral prefrontal cortices [1,5,57], intraparietal sulcus [17], and the anterior insula [8], as well as limbic structures, including the

Box 3. Measurement challenges in life span studies of exploration and exploitation

Exploitation and exploration decisions are typically measured in three behavioral domains: information search, foraging, and reinforcement learning (reviewed in [11]). However, a lack of convergent validity was recently reported for behavioral tasks across these search domains, suggesting that specific task characteristics influence exploration–exploitation trade-offs [102].

This represents a significant measurement challenge for life span studies in which cognitive (or affective) changes may interact in domain- and/or task-specific ways with search decisions. A critical research priority will be to conduct cross-sectional, life span convergent validity studies acquiring within-subject measures of exploitation and exploration across domains and search tasks. This would address whether aging is associated with the emergence of a common exploration–exploitation factor, consistent with dedifferentiation theories of cognitive aging [103]. An interesting prediction here would be that the shifting factors highlighted in this review (see Table 1 in main text) would counter the influence of task-specific demands observed in younger adults [102], thereby promoting an exploitative mental mode in later life. Minimizing task-specific factors is a critical measurement challenge for identifying individual and age differences in exploration–exploitation trade-offs and associated neural mechanisms.

Relatedly, detecting exploitation biases in older adulthood also requires disambiguating the impact of the various contributing factors described in Table 1 in main text. Among the most significant measurement challenge in this regard are the cognitive control and learning demands imposed by almost all goal-directed cognitive tasks. This leaves older adult performance susceptible to off-task errors or performance variability that may mimic exploratory responses, and distinguishing these from cognitive control errors (e.g., loss of rule set or poor rule learning) is difficult post hoc. This was observed by Hills and colleagues [28], who reported that older adults made more exploratory-type category switches than younger adults during a semantic fluency task. However, closer inspection revealed that these switches were attributable to the inability of older adults to hold the goal hierarchy in working memory, resulting in more unintended ‘exploratory’ responses. Complex learning demands would pose a similar challenge because age differences in the learning of task rules may manifest as greater exploratory-type responses for older adults [29]. As such, another critical measurement challenge for life span research will be designing task paradigms that involve low levels of cognitive control and impose low learning demands (or sufficient practice). The objective would be to achieve age equivalence in the comprehension and application of task rules, necessary to isolate and quantify life span changes in exploration–exploitation trade-off thresholds.

amygdala [58] and hippocampus [19]. While few direct investigations of large-scale network involvement in exploitation and exploration trade-offs have been reported, the capacity to flexibly shift between exploratory and exploitative behaviors has recently been related to functional connections among distributed brain areas, including regions of the frontoparietal control network and **default network** [59], as well as **salience network** regions [8]. Here, we briefly outline the key circuitry underlying exploratory and exploitation behaviors and how these are altered with age, promoting an exploitation bias in older adulthood (Figure 1).

Attention and reward circuits implicated in exploration and exploitation

While multiple brain systems have been implicated in the trade-off between exploration and exploitation, we focus on two circuits here, because these offer the greatest promise in understanding the emergence of a prepotent exploitative mental mode in older adulthood (Figure 1). We first describe the adaptive-gain model of LC function and attentional control [35], which has been explicitly identified as a neural mechanism underpinning the exploitation–exploration trade-off [36]. The second is the affective, integrative, and motivation (AIM) model of motivation and reward in decision-making behavior [60]. While this model has not been explicitly associated with exploitation and exploration trade-offs, the importance of reward processing, particularly for exploitative decisions (Box 1 and Figure 1A), and known changes to these circuits with age, strongly implicate the AIM model as a candidate and complementary neural mechanism underpinning changing exploration and exploitation thresholds with age. These accounts encompass two critical dimensions of the exploitation–exploration trade-off, attention modulation and reward expectation, and the role of their respective noradrenergic and dopaminergic circuits in modulating choice behaviors (Figure 1). Critically, both models converge on a pivotal role for the medial prefrontal cortex, and its ventral aspect (vmPFC) more specifically, in the integration and valuation of choice options (see [2] for a recent converging account). As we review herein, the vmPFC is also a core

node of the default network. This network is a functionally connected assembly of brain regions, implicated in the encoding, representation, and instantiation of prior knowledge and schema (Box 1), and is selectively vulnerable to changes in aging and brain disease [61,62]. We consider changes to this network, and the mPFC specifically, to be a central feature in the emergence of an exploitation-biased mental mode in later life.

Adaptive gain model

The adaptive gain model [35] was proposed as a model of attentional control centered on LC, the primary noradrenergic nucleus producing nearly all norepinephrine (NE) in the brain. The LC displays phasic activation during exploitative behaviors, while more tonic activation is associated with exploration [36]. Although specific neurocognitive mechanisms are still being investigated, evidence is converging on goal-directed attentional control as a primary determinant of the shift between exploration and exploitation. Phasic activation of the LC is observed during the occurrence of targets on a goal-directed task, promoting attentional engagement to the current target category, consistent with an exploitative mental mode. By contrast, tonic LC activity expands the window of attentional engagement to include both goal-relevant and -irrelevant stimuli, consistent with a more exploratory mode, which requires shifts in attentional set [7,36]. A critical question is how, and perhaps why, this shift from phasic to tonic signaling (or vice versa) of LC occurs. In part, the answer lies in a parallel catecholaminergic neurotransmitter: dopamine (DA). The DA circuit includes the ventral tegmental area, NAc, and its dense connections to prefrontal brain regions [36]. Consistent with this model, elevated DA-based reward signaling dampens exploratory and motivates exploitative or rewarding behaviors [63–65]. As reward processing in ventromedial and orbitofrontal cortices decreases with ongoing exploitative behaviors, the dorsal anterior cingulate cortex evaluates this altered reward signaling and, in turn, signals a shift from phasic to tonic firing in LC [66]. This perturbation in LC firing shifts goal-directed behaviors from an exploitative to a more exploratory mode.

In the context of this (admittedly simplified) adaptive gain model, we suggest that age-related changes in LC-NE signaling favor exploitation over exploration as a prepotent mental mode of choice (i.e., decision-making) behavior. Age-related changes have been observed in LC, which is considered to be an origin site of tauopathies [67]. Tauopathies occur when the tau protein necessary for sustaining the structural integrity of neurons is altered, leading to neurotoxic changes associated with common brain diseases, including Alzheimer's disease (AD) [68]. Furthermore, changes in LC volume are evident in normal aging, long before the emergence of neurodegenerative disease [69,70]. Age-related structural and functional changes in projection systems from LC to cortical association cortex, including prefrontal and trans-entorhinal cortices, have also been observed [71–73]. Taken together, degraded LC circuitry with advancing age predicts a sluggishness in noradrenergic signaling and less flexible shifting in attentional focus, necessary to alternate between exploration and exploitation based on shifting reward contingencies (Figure 1C). Put simply, environmental and individual difference factors, such as shorter temporal horizons, neophobia, and a greater repertoire of known reward values that favor exploitation-based decisions in later life (Table 1 and Figure 1A), promote phasic LC signaling. In the context of degraded LC-NE circuitry, flexible shifting from exploitation to an exploration-based attentional frame is reduced, increasing the dwell time for older adults in exploitative search.

Affective, integration, and motivation model

Reduced flexibility in LC-NE functioning and increased dwell time in exploitative search does not necessarily predict the prepotency of exploitation in later life or, as we argued earlier, a different 'starting point' for decision-making in older adulthood. To address this prediction, we turn to the affective, integration, and motivation (AIM) model as our lens for considering age-related changes in corticostriatal dopaminergic circuits underpinning reward and motivation [60,74]

(Figure 1A). In the AIM model, dopaminergic signaling from the ventral tegmental area combines with noradrenergic signaling from the LC in anterior insula to potentiate anticipated gains and losses. These affective signals are then integrated with other inputs (e.g., prior knowledge and reward representations) instantiated as schema in vmPFC [2,75,76], which, in turn, motivate the configuration of action circuits to implement selected behaviors [60] (Figure 1). In older adulthood, expanding prior knowledge stores [41] increase the probability of exploiting known versus exploring unknown choice options. Furthermore, shorter time horizons in later life also reduce the value of information-focused exploratory searches [21,23,31,77]. Finally, age-related shifts toward more affective goal pursuits [53,54,78] and positively valenced predicted decision outcomes [60,79] enhance the relative reward value of exploiting known options, biasing older adults toward a prepotent exploitative mental mode. This shift in reward valuation for exploitation over exploration in turn increases dopaminergic signaling from vmPFC, biasing LC–NE circuits toward phasic signaling which, as predicted by the adaptive gain model, biases attention toward exploiting known options [36].

Cortical networks

A growing body of evidence suggests that alterations within and among large-scale, functionally connected cortical brain networks are a core mechanism of age-related cognitive change [80,81]. Here, we review how age-related changes to the frontoparietal control, default, and salience networks converge to promote an exploitation-biased mental mode in late-life development.

First, age-related declines in the integrity of the frontoparietal control network and altered connections to other transmodal networks are associated with reduced executive control [119]. Reduced cognitive control has been postulated as a mechanism underpinning a shift from exploration to exploitation with age [29] (Box 2). While diminished control processes reduce exploration behaviors, we have argued that this is insufficient to instantiate exploitation as a preferred mental mode; here, we propose that the accumulation of prior knowledge and schemas, incorporating both affective and cognitive elements (Box 1), has a crucial role in the shifting exploration–exploitation trade-off [33].

Engagement of prior knowledge has been associated with default network brain regions, including inferior frontal gyrus, lateral temporal cortices, temporal parietal junction, and temporal polar cortices [82]. The default network also includes mPFC, posterior cingulate cortex, as well as the medial temporal lobe memory system [61]. Structural and functional connectivity of the default network declines with normal aging [62,83]. Furthermore, connectivity between the default and other large-scale brain networks is increased, following a pattern of network dedifferentiation widely observed with increasing age [80,81]. Greater crosstalk between default and frontoparietal and salience networks with age has been associated with memory for meaningful associations [43]; semanticized autobiographical recollection [84], feelings of social closeness [85], and greater vulnerability to financial exploitation [86,87]. Each of these real-world behaviors shares a common feature, in that older adults are able to draw upon prior knowledge to guide goal-directed thought and action, with both adaptive and maladaptive outcomes (Figure 2). Thus, greater connectivity of the default network, and particularly mPFC (Box 1), to other brain regions may provide a neural conduit, allowing prior knowledge to infiltrate and influence ongoing thought and action [33,88].

Finally, the salience network includes both dorsal anterior cingulate, and anterior insula regions, associated with value monitoring and reward expectancy [89,90]. These regions are implicated in the adaptive gain and AIM decision-making models and changes to the salience network likely shape the exploration–exploitation trade-off in later life. Age-related changes include reduced within-network connectivity and, critically, increased connectivity to default network regions, including mPFC [91,92]. Closer coupling of the salience and default networks, and the mPFC

specifically, suggest that the affective valuation of prior knowledge, represented in the vmPFC, exerts greater influence over dopaminergic reward and noradrenergic attention modulation systems, biasing these circuits toward an exploitative mental mode.

Taken together, we suggest that altered cortical network dynamics intersect with attention and reward circuits to bias action and mentation toward an exploitative mode. Age-related declines in the frontoparietal control network reduce cognitive control capacity necessary for exploration [29,45]. Critically, these changes in cognitive control occur in the context of behavioral and brain changes that elevate the relevance, salience, and, ultimately, influence of prior knowledge on decision-making. Default network brain regions, implicated in prior knowledge representations and affective valuation (instantiated in schema [76]) become more integrated with both the frontoparietal control and salience networks, providing a conduit for knowledge representations to exert greater influence over attention and reward systems that modulate choice behaviors. There is growing evidence for this model. Interactions between vmPFC and nodes of the salience network, including anterior insular cortex, have been shown to promote exploitative behaviors [93]. These regions also become more functionally integrated with age [80]. Furthermore, greater network connectivity between default and lateral PFC (as proposed in the default-to-executive coupling of aging [33]) may sustain exploitative search strategies by instantiating and sustaining value expectancies for prior knowledge in working memory [12], although there is evidence that goal-directed emotional regulation may depend more on relatively preserved mPFC in older adulthood [91]. Finally, changes to the frontoparietal control network, and associated reductions in cognitive control, may preclude the flexible network reorganization necessary to shift from exploitation to exploratory search [8,59].

Concluding remarks

Here, we have surveyed emerging evidence that the shifting architecture of cognition, affect, and brain function leads to the emergence of an exploitation-biased mental mode in later life; one that favors the exploitation of prior knowledge over exploratory search for novel information, solutions, associations, and experiences. This shift in the exploration and exploitation trade-off reflects reduced cognitive control in the context of growing stores (and influence) of prior knowledge, as well as a shift toward affective goals, and parallels age-related changes to cortical brain networks, attention, and reward circuits. We argue that, by encapsulating the dual trajectories of aging cognition (reduced control and increased prior knowledge), as well as shifts in affectively driven motivations, age-related changes in the exploitation–exploration trade-off provide a more integrative marker, capturing multiple dimensions of aging mentation in a single behavioral outcome.

More importantly, reframing these changes in cognitive, affective, and brain architectures as resulting in a fundamentally altered mode of mentation, highlights the possibility, perhaps even the probability, that older adults approach all volitional mentation and action from a different starting position than younger adults; one that carries both the weight and the wisdom from decades of lived experience with evidence of both positive and negative outcomes (see Figure 2). While the implications have yet to be fully elucidated (see Outstanding questions), we argue that the transition toward an exploitation-biased mental mode represents a fundamental reshaping of human mentation across the rapidly expanding decades of older adulthood. As such, mapping the determinants, correlates, and implications of this largely uncharted epoch of adult development poses a critical challenge for the future of cognitive and affective aging neuroscience.

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Outstanding questions

What is the optimal (reliable, sensitive) behavioral measure(s) to estimate individual and age-group differences in exploration-exploitation thresholds (cf. [39])?

Does the exploration–exploitation trade-off represent a domain-general, common factor that can be reliably associated with specific features of cognitive, affective, and brain aging (cf. [102])?

What are the relative and/or sequential contributions of cognitive control, prior knowledge, and reward motivation to determining exploration–exploitation thresholds in older adulthood? Do these differ by search domain (e.g., foraging, reinforcement learning, or information search)?

How do environmental, social, and other individual difference factors interact with age to influence exploration/exploitation thresholds?

Does an age-related shift toward a prepotent, exploitation-biased mental mode manifest as an automatic response, occurring outside of conscious awareness, or as an intentional choice, involving volitional control processes?

Can differences in exploration–exploitation trade-off thresholds, and associated brain changes, provide reliable behavioral markers of inflection points in late life development, signaling transitions from normative to accelerated and pathological aging?

Declaration of interests

None declared by authors.

References

1. Hills, T.T. *et al.* (2015) Exploration versus exploitation in space, mind, and society. *Trends Cogn. Sci.* 19, 46–54
2. Domenech, P. *et al.* (2020) Neural mechanisms resolving exploitation-exploration dilemmas in the medial prefrontal cortex. *Science* 369, eabb0184
3. Rich, A.S. and Gureckis, T.M. (2018) The limits of learning: exploration, generalization, and the development of learning traps. *J. Exp. Psychol. Gen.* 147, 1553–1570
4. Pezzulo, G. *et al.* (2016) Active inference, epistemic value, and vicarious trial and error. *Learn. Mem.* 23, 322–338
5. Zajkowski, W.K. *et al.* (2017) A causal role for right frontopolar cortex in directed, but not random, exploration. *eLife* 6, e27430
6. Tomov, M.S. *et al.* (2020) Dissociable neural correlates of uncertainty underlie different exploration strategies. *Nat. Commun.* 11, 2371
7. Pajkossy, P. *et al.* (2017) Tonic noradrenergic activity modulates explorative behavior and attentional set shifting: evidence from pupillometry and gaze pattern analysis. *Psychophysiology* 54, 1839–1854
8. Blanchard, T.C. and Gershman, S.J. (2018) Pure correlates of exploration and exploitation in the human brain. *Cogn. Affect. Behav. Neurosci.* 18, 117–126
9. Algermissen, J. *et al.* (2019) Explore or reset? Pupil diameter transiently increases in self-chosen switches between cognitive labor and leisure in either direction. *Cogn. Affect. Behav. Neurosci.* 19, 1113–1128
10. Walker, A.R. *et al.* (2019) The role of uncertainty in attentional and choice exploration. *Psychon. Bull. Rev.* 26, 1911–1916
11. Sang, K. *et al.* (2020) Simple threshold rules solve explore/exploit trade-offs in a resource accumulation search task. *Cogn. Sci.* 44, e12817
12. Cogliati Dezza, I. *et al.* (2019) Should we control? The interplay between cognitive control and information integration in the resolution of the exploration-exploitation dilemma. *J. Exp. Psychol. Gen.* 148, 977–993
13. Wilson, R.C. *et al.* (2021) Balancing exploration and exploitation with information and randomization. *Curr. Opin. Behav. Sci.* 38, 49–56
14. Sadeghiyeh, H. *et al.* (2020) Temporal discounting correlates with directed exploration but not with random exploration. *Sci. Rep.* 10, 4020
15. Schulz, E. and Gershman, S.J. (2019) The algorithmic architecture of exploration in the human brain. *Curr. Opin. Neurobiol.* 55, 7–14
16. Schulz, E. *et al.* (2019) Structured, uncertainty-driven exploration in real-world consumer choice. *Proc. Natl. Acad. Sci. U. S. A.* 116, 13903–13908
17. Laureiro-Martinez, D. *et al.* (2013) Frontopolar cortex and decision-making efficiency: comparing brain activity of experts with different professional background during an exploration-exploitation task. *Front. Hum. Neurosci.* 7, 927
18. Hallquist, M.N. and Dombrovski, A.Y. (2019) Selective maintenance of value information helps resolve the exploration/exploitation dilemma. *Cognition* 183, 226–243
19. Dombrovski, A.Y. *et al.* (2020) Differential reinforcement encoding along the hippocampal long axis helps resolve the explore-exploit dilemma. *Nat. Commun.* 11, 5407
20. Dubois, M. *et al.* (2021) Human complex exploration strategies are enriched by noradrenergic-modulated heuristics. *eLife* 10, e59907
21. Sherratt, T.N. and Morand-Ferron, J. (2018) The adaptive significance of age-dependent changes in the tendency of individuals to explore. *Anim. Behav.* 138, 59–67
22. Lee, M.H. and Ranganathan, R. (2019) Age-related deficits in motor learning are associated with altered motor exploration strategies. *Neuroscience* 412, 40–47
23. Wiegand, I. *et al.* (2019) Hybrid foraging search in younger and older age. *Psychol. Aging* 34, 805–820
24. Qiu, M. and Johns, B.T. (2020) Semantic diversity in paired-associate learning: further evidence for the information accumulation perspective of cognitive aging. *Psychon. Bull. Rev.* 27, 114–121
25. Queen, T.L. *et al.* (2012) Information search and decision making: effects of age and complexity on strategy use. *Psychol. Aging* 27, 817–824
26. Frey, R. *et al.* (2015) The role of cognitive abilities in decisions from experience: Age differences emerge as a function of choice set size. *Cognition* 142, 60–80
27. Chin, J. *et al.* (2015) Information foraging across the life span: search and switch in unknown patches. *Top. Cogn. Sci.* 7, 428–450
28. Hills, T.T. *et al.* (2013) Mechanisms of age-related decline in memory search across the adult life span. *Dev. Psychol.* 49, 2396–2404
29. Mata, R. and von Helversen, B. (2015) Search and the aging mind: the promise and limits of the cognitive control hypothesis of age differences in search. *Top. Cogn. Sci.* 7, 416–427
30. Mata, R. and Nunes, L. (2010) When less is enough: cognitive aging, information search, and decision quality in consumer choice. *Psychol. Aging* 25, 289–298
31. Mata, R. *et al.* (2013) Foraging across the life span: is there a reduction in exploration with aging? *Front. Neurosci.* 7, 53
32. Mata, R. *et al.* (2009) Cognitive aging and adaptive foraging behavior. *J. Gerontol. B Psychol. Sci. Soc. Sci.* 64, 474–481
33. Spreng, R.N. and Turner, G.R. (2019) The shifting architecture of cognition and brain function in older adulthood. *Perspect. Psychol. Sci.* 14, 523–542
34. Park, D.C. *et al.* (2001) Cerebral aging: integration of brain and behavioral models of cognitive function. *Dialogues Clin. Neurosci.* 3, 151–165
35. Aston-Jones, G. and Cohen, J.D. (2005) An integrative theory of locus coeruleus-norepinephrine function: adaptive gain and optimal performance. *Annu. Rev. Neurosci.* 28, 403–450
36. Cohen, J.D. *et al.* (2007) Should I stay or should I go? How the human brain manages the trade-off between exploitation and exploration. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 362, 933–942
37. March, J.G. (1991) Exploration and exploitation in organizational learning. *Organ. Sci.* 2, 71–87
38. Todd, P.M. and Hills, T.T. (2020) Foraging in mind. *Curr. Dir. Psychol. Sci.* 29, 309–315
39. Mehlhorn, K. *et al.* (2015) Unpacking the exploration-exploitation tradeoff: a synthesis of human and animal literatures. *Decision* 2, 191–215
40. Verhaeghen, P. and Cerella, J. (2002) Aging, executive control, and attention: a review of meta-analyses. *Neurosci. Biobehav. Rev.* 26, 849–857
41. Hoffman, P. (2018) Divergent effects of healthy ageing on semantic knowledge and control: Evidence from novel comparisons with semantically impaired patients. *J. Neuropsychol.* 13, 462–484
42. Verhaeghen, P. (2003) Aging and vocabulary scores: a meta-analysis. *Psychol. Aging* 18, 332–339
43. Amer, T. *et al.* (2018) Age differences in memory for meaningful and arbitrary associations: A memory retrieval account. *Psychol. Aging* 33, 74–81
44. Cabeza, R. *et al.* (2018) Maintenance, reserve and compensation: the cognitive neuroscience of healthy ageing. *Nat. Rev. Neurosci.* 19, 701–710
45. Baror, S. and Bar, M. (2016) Associative activation and its relation to exploration and exploitation in the brain. *Psychol. Sci.* 27, 776–789
46. Hills, T.T. (2019) Neurocognitive free will. *Proc. Biol. Sci.* 286, 20190510
47. Hills, T.T. *et al.* (2010) The central executive as a search process: priming exploration and exploitation across domains. *J. Exp. Psychol. Gen.* 139, 590–609
48. Louapre, P. *et al.* (2010) Humans and insects decide in similar ways. *PLoS One* 5, e14251

49. Naveh-Benjamin, M. *et al.* (2005) Divided attention in younger and older adults: effects of strategy and relatedness on memory performance and secondary task costs. *J. Exp. Psychol. Learn. Mem. Cogn.* 31, 520–537
50. Brashier, N.M. *et al.* (2017) Competing cues: older adults rely on knowledge in the face of fluency. *Psychol. Aging* 32, 331–337
51. Umanath, S. and Marsh, E.J. (2014) Understanding how prior knowledge influences memory in older adults. *Perspect. Psychol. Sci.* 9, 408–426
52. Carstensen, L.L. (2006) The influence of a sense of time on human development. *Science* 312, 1913–1915
53. Samanez-Larkin, G.R. and Carstensen, L.L. (2011) Socioemotional functioning and the aging brain. In *The Handbook of Social Neuroscience* (Decety, J. and Cacioppo, J.T., eds), pp. 507–524, Oxford University Press
54. Charles, S.T. and Carstensen, L.L. (2010) Social and emotional aging. *Annu. Rev. Psychol.* 61, 383–409
55. Weller, J.A. *et al.* (2019) Information use in risky decision making: do age differences depend on affective context? *Psychol. Aging* 34, 1005–1020
56. Levin, F. *et al.* (2021) Positivity effect and decision making in ageing. *Cognit. Emot.* 35, 790–804
57. Costa, V.D. and Averbeck, B.B. (2020) Primate orbitofrontal cortex codes information relevant for managing explore-exploit tradeoffs. *J. Neurosci.* 40, 2553–2561
58. Costa, V.D. *et al.* (2019) Subcortical substrates of explore-exploit decisions in primates. *Neuron* 103, 533–545
59. Allegra, M. *et al.* (2020) Brain network dynamics during spontaneous strategy shifts and incremental task optimization. *NeuroImage* 217, 116854
60. Samanez-Larkin, G.R. and Knutson, B. (2015) Decision making in the ageing brain: changes in affective and motivational circuits. *Nat. Rev. Neurosci.* 16, 278–289
61. Andrews-Hanna, J.R. *et al.* (2014) The default network and self-generated thought: component processes, dynamic control, and clinical relevance. *Ann. N. Y. Acad. Sci.* 1316, 29–52
62. Damoiseaux, J.S. (2017) Effects of aging on functional and structural brain connectivity. *NeuroImage* 160, 32–40
63. Cinnotti, F. *et al.* (2019) Dopamine blockade impairs the exploration-exploitation trade-off in rats. *Sci. Rep.* 9, 6770
64. Castrellon, J.J. *et al.* (2019) Mesolimbic dopamine D2 receptors and neural representations of subjective value. *Sci. Rep.* 9, 20229
65. Chakroun, K. *et al.* (2020) Dopaminergic modulation of the exploration/exploitation trade-off in human decision-making. *eLife* 9, e51260
66. Tervo, D.G.R. *et al.* (2021) The anterior cingulate cortex directs exploration of alternative strategies. *Neuron* 109, 1876–1887
67. Mather, M. and Harley, C.W. (2016) The locus coeruleus: essential for maintaining cognitive function and the aging brain. *Trends Cogn. Sci.* 20, 214–226
68. Avila, J. *et al.* (2004) Role of tau protein in both physiological and pathological conditions. *Physiol. Rev.* 84, 361–384
69. Betts, M.J. *et al.* (2019) Locus coeruleus imaging as a biomarker for noradrenergic dysfunction in neurodegenerative diseases. *Brain* 142, 2558–2571
70. Weinschenker, D. (2018) Long road to ruin: noradrenergic dysfunction in neurodegenerative disease. *Trends Neurosci.* 41, 211–223
71. Lee, T.H. *et al.* (2020) The decline in intrinsic connectivity between the salience network and locus coeruleus in older adults: implications for distractibility. *Front. Aging Neurosci.* 12, 2
72. Theofilas, P. *et al.* (2017) Locus coeruleus volume and cell population changes during Alzheimer's disease progression: a stereological study in human postmortem brains with potential implication for early-stage biomarker discovery. *Alzheimers Dement.* 13, 236–246
73. Ehrenberg, A.J. *et al.* (2017) Quantifying the accretion of hyperphosphorylated tau in the locus coeruleus and dorsal raphe nucleus: the pathological building blocks of early Alzheimer's disease. *Neuropathol. Appl. Neurobiol.* 43, 393–408
74. Karrer, T.M. *et al.* (2017) Reduced dopamine receptors and transporters but not synthesis capacity in normal aging adults: a meta-analysis. *Neurobiol. Aging* 57, 36–46
75. Gilboa, A. and Marlatte, H. (2017) Neurobiology of schemas and schema-mediated memory. *Trends Cogn. Sci.* 21, 618–631
76. Lieberman, M.D. *et al.* (2019) Social, self, (situational), and affective processes in medial prefrontal cortex (MPFC): causal, multivariate, and reverse inference evidence. *Neurosci. Biobehav. Rev.* 99, 311–328
77. Mather, M. and Carstensen, L.L. (2005) Aging and motivated cognition: the positivity effect in attention and memory. *Trends Cogn. Sci.* 9, 496–502
78. von Helversen, B. *et al.* (2011) Performance benefits of depression: sequential decision making in a healthy sample and a clinically depressed sample. *J. Abnorm. Psychol.* 120, 962–968
79. Samanez-Larkin, G.R. *et al.* (2007) Anticipation of monetary gain but not loss in healthy older adults. *Nat. Neurosci.* 10, 787–791
80. Setton, R. *et al.* (2021) Functional architecture of the aging brain. *BioRxiv* Published online April 23, 2021. <https://doi.org/10.1101/2021.03.31.437922>
81. Wig, G.S. (2017) Segregated systems of human brain networks. *Trends Cogn. Sci.* 21, 981–996
82. Hoffman, P. and Morcom, A.M. (2018) Age-related changes in the neural networks supporting semantic cognition: a meta-analysis of 47 functional neuroimaging studies. *Neurosci. Biobehav. Rev.* 84, 134–150
83. Spreng, R.N. and Turner, G.R. (2013) Structural covariance of the default network in healthy and pathological aging. *J. Neurosci.* 33, 15226–15234
84. Spreng, R.N. *et al.* (2018) Semanticized autobiographical memory and the default - executive coupling hypothesis of aging. *Neuropsychologia* 110, 37–43
85. Laurita, A.C. *et al.* (2020) Default network interactivity during mentalizing about known others is modulated by age and social closeness. *Soc. Cogn. Affect. Neurosci.* 15, 537–549
86. Weissberger, G.H. *et al.* (2020) Functional connectivity correlates of perceived financial exploitation in older adults. *Front. Aging Neurosci.* 12, 583433
87. Spreng, R.N. *et al.* (2017) Financial exploitation is associated with structural and functional brain differences in healthy older adults. *J. Gerontol. A Biol. Sci. Med. Sci.* 72, 1365–1368
88. Turner, G.R. and Spreng, R.N. (2015) Prefrontal engagement and reduced default network suppression co-occur and are dynamically coupled in older adults: the default-executive coupling hypothesis of aging. *J. Cogn. Neurosci.* 27, 2462–2476
89. Uddin, L.Q. (2015) Salience processing and insular cortical function and dysfunction. *Nat. Rev. Neurosci.* 16, 55–61
90. Seeley, W.W. (2019) The salience network: a neural system for perceiving and responding to homeostatic demands. *J. Neurosci.* 39, 9878–9882
91. Mather, M. (2016) The affective neuroscience of aging. *Annu. Rev. Psychol.* 67, 213–238
92. Kupis, L. *et al.* (2021) Brain dynamics underlying cognitive flexibility across the life span. *Cereb. Cortex* Published online June 18, 2021. <https://doi.org/10.1093/cercor/bhab156>
93. Mehta, P.S. *et al.* (2019) Ventromedial prefrontal cortex tracks multiple environmental variables during search. *J. Neurosci.* 39, 5336–5350
94. Carstensen, L.L. (1992) Social and emotional patterns in adulthood: support for socioemotional selectivity theory. *Psychol. Aging* 7, 331–338
95. Scheibe, S. and Blanchard-Fields, F. (2009) Effects of regulating emotions on cognitive performance: what is costly for young adults is not so costly for older adults. *Psychol. Aging* 24, 217–223
96. Tomasi, D. and Volkow, N.D. (2012) Aging and functional brain networks. *Mol. Psychiatry* 17, 471, 549–558
97. MacCormack, J.K. *et al.* (2020) Affect in the aging brain: a neuroimaging meta-analysis of older vs. younger adult affective experience and perception. *Affect. Sci.* 1, 128–154
98. Roy, M. *et al.* (2012) Ventromedial prefrontal-subcortical systems and the generation of affective meaning. *Trends Cogn. Sci.* 16, 147–156
99. Jones, B.J. *et al.* (2014) Age and scientific genius. In *Handbook of Genius* (Simonton, D., ed.), pp. 422–450, John Wiley & Sons
100. Adnan, A. *et al.* (2019) Intrinsic default-executive coupling of the creative aging brain. *Soc. Cogn. Affect. Neurosci.* 14, 291–303

101. Adnan, A. *et al.* (2019) Creative aging: functional brain networks associated with divergent thinking in older and younger adults. *Neurobiol. Aging* 75, 150–158
102. von Helversen, B. *et al.* (2018) Foraging, exploration, or search? On the (lack of) convergent validity between three behavioral paradigms. *Evol. Behav. Sci.* 12, 152–162
103. Baltes, P.B. and Lindenberger, U. (1997) Emergence of a powerful connection between sensory and cognitive functions across the adult life span: a new window to the study of cognitive aging? *Psychol. Aging* 12, 12–21
104. Cogliati Dezza, I. *et al.* (2017) Learning the value of information and reward over time when solving exploration-exploitation problems. *Sci. Rep.* 7, 16919
105. Badre, D. *et al.* (2012) Rostrolateral prefrontal cortex and individual differences in uncertainty-driven exploration. *Neuron* 73, 595–607
106. Frank, M.J. *et al.* (2009) Prefrontal and striatal dopaminergic genes predict individual differences in exploration and exploitation. *Nat. Neurosci.* 12, 1062–1068
107. Daw, N.D. *et al.* (2006) Cortical substrates for exploratory decisions in humans. *Nature* 441, 876–879
108. Mata, R. *et al.* (2010) Learning to choose: cognitive aging and strategy selection learning in decision making. *Psychol. Aging* 25, 299–309
109. Worthy, D.A. and Maddox, W.T. (2012) Age-based differences in strategy use in choice tasks. *Front. Neurosci.* 5, 145
110. Musielak, C. *et al.* (2014) To what extent does the existence of functional relations in a learning setting change the pattern of differences between younger and older adults' performances? *Exp. Aging Res.* 40, 455–476
111. Castel, A.D. (2005) Memory for grocery prices in younger and older adults: the role of schematic support. *Psychol. Aging* 20, 718–721
112. Blanco, N.J. *et al.* (2016) Exploratory decision-making as a function of lifelong experience, not cognitive decline. *J. Exp. Psychol. Gen.* 145, 284–297
113. Chin, J. *et al.* (2009) Adaptive information search? Age-dependent interactions between cognitive profiles and strategies. In *Proceedings of the 27th International Conference on Human Factors in Computing Systems* (Olsen, D.R. *et al.*, eds), pp. 1683–1692, ACM Press
114. Brainerd, C.J. and Reyna, V.F. (2015) Fuzzy-trace theory and life span cognitive development. *Dev. Rev.* 38, 89–121
115. Samanez-LarkinKnutsen, A. (2014) Reward processing and risky decision making in the aging brain. In *The Neuroscience of Risky Decision Making* (Reyna, V. and Zayas, V., eds), pp. 123–142, American Psychological Association
116. Levine, B. *et al.* (2002) Aging and autobiographical memory: dissociating episodic from semantic retrieval. *Psychol. Aging* 17, 677–689
117. Dalla Barba, G. *et al.* (2010) Confabulation in healthy aging is related to interference of overlearned, semantically similar information on episodic memory recall. *J. Clin. Exp. Neuropsychol.* 32, 655–660
118. Sheldon, S. *et al.* (2011) Episodic memory processes mediated by the medial temporal lobes contribute to open-ended problem solving. *Neuropsychologia* 49, 2439–2447
119. Plaschke, PN *et al.* (2020) Age differences in predicting working memory performance from network-based functional connectivity. *Cortex* 132, 441–459