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Decision making in the ageing brain: Changes in affective and motivational circuits

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Abstract

As the global population ages, older decision makers will be required to take greater responsibility for their own physical, psychological and financial well-being. With this in mind, researchers have begun to examine the effects of ageing on decision making and associated neural circuits. A new "affect, integration, motivation" (or AIM) framework may help clarify how affective and motivational circuits support decision making. Recent research has shed light on whether and how ageing influences these circuits, providing an interdisciplinary account of how ageing can alter decision making.

The global population is rapidly ageing. Projections suggest that the proportion of older individuals (those over 65) will double from 2000 to 2050 [1], increasing the relative number of older decision makers in society, particularly in developed countries [2]. Alongside these demographic shifts, governments and businesses have begun to implement policy changes that will increase older individuals' responsibility for maintaining their own health and financial welfare.

Although research has begun to suggest that ageing might alter decision making, little is known about the trajectory or causes of these changes. An emerging interdisciplinary field that combines methods and theories from neuroscience, psychology and economics could bridge these gaps in knowledge, and so inform scientific theory as well as speed the translation of research findings into applications.

Both neurally and psychologically, multiple factors contribute to decision making. By connecting sensory input to motor output, both cognitive and affective capacities play critical roles in decision making, especially when individuals must weigh potential benefits against costs. In terms of cognition, accumulated evidence suggests that although ageing can compromise some cognitive capacities, others are preserved. Specifically, fluid cognitive abilities (such as working memory, attention, and executive control) steadily decline with ageing, whereas crystallized cognitive abilities (such as domain-specific knowledge) remain conserved [3]. Thus older people may fare worse when making decisions that require fluid

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cognitive abilities (that is, choices that require multiple attributes and/or options to be simultaneously considered and compared).

More recent evidence has also revealed different influences of ageing on affect and motivation. Adults report reduced levels of negative affective experience as they age but preserved levels of positive affective experience [4], trends that have been linked to decreased attention to and memory for negative versus positive material [5]. These changes may result either from shifts in motivational goals (which may stem from changing perceptions of remaining time, for example) [5], or from independent physiological changes in neural function, or both. Overall, this evidence implies that older adults might weigh costs and benefits differently than their younger counterparts [6].

Although researchers have made significant progress over the past few decades toward characterizing the impact of healthy ageing on the brain (BOX 1), only recently have they begun to examine how age-related changes in neural structure, chemistry and function influence decision making. Decision making has the potential to recruit almost any brain capacity and thus presents a broad and challenging research target. Different types of decisions may also recruit distinct circuits, either sequentially or in parallel. In this article, we primarily focus on decisions that involve affective and motivational processing [7–12], rather than those that rely upon sensorimotor processing (in which deficits should obviously compromise decisions) or cognitive processing (which has been reviewed elsewhere) [3]. After describing a framework that can link neural activity in circuits implicated in affect and motivation to decision making, we review emerging neuroscientific findings that shed light on age-related changes in value-based decision making[13].

Box 1

Age-related changes in brain structure and function

Neuroimaging studies have documented numerous changes in the structure and function of the ageing brain [41,42,118]. Generally, both cross-sectional and longitudinal studies of brain volume reveal linear and curvilinear changes in grey matter volume, as well as curvilinear changes in white matter volume over the life span. These volumes increase until adulthood and then steadily decrease with senescence [118–120]. More recent studies using diffusion tensor imaging (DTI) have revealed age-related decreases in the connectivity of the major white matter tracts, with the most pronounced declines occurring in anterior and superior cortical regions [121,122]. Studies of neurochemical changes across the life span have focused primarily on changes in the neurons releasing biogenic amine neurotransmitters (such as dopamine and serotonin), which emanate from focal nuclei in the midbrain to project broadly throughout the subcortex and cortex. Positron emission tomography (PET) studies in humans have revealed relatively linear declines across adulthood in serotonin receptors in cortex, in dopamine receptors (both D1-like and D2-like) in prefrontal cortex and striatum, and in dopamine transporters in striatum, but have yielded more mixed evidence for age-related changes in the presynaptic neurotransmitter availability (related to synthesis capacity and vesicular storage) [123,124]. These PET imaging findings were mostly obtained in cross-sectional samples and so are limited by a lack of longitudinal data. Even less research has

examined age-related changes in the availability of basic amino acid neurotransmitters (such as glutamate and GABA) that, although present throughout the brain, support more local and targeted circuit functions [125–127]. Overall, research that links and integrates age-related changes in brain function, structure, and chemistry (such as multimodal neuroimaging studies [128]) could help neuroscientists to pinpoint the circuits most compromised by ageing.

Neural circuits that promote choice

Beyond merely arising in reaction to the outcomes of decisions, mounting evidence suggests that affect can also proactively influence decision making [14,15]. Throughout the twentieth century, affect was indirectly inferred from measures of self-reported experience, physiology, or nonverbal behaviour. Consistent with the predictions of pioneering psychologist Wilhelm Wundt [16], psychometric research revealed that emotional experience can be described using two independent dimensions – subjective valence and subjective arousal [17]. Positive arousal might increase the motivation to approach opportunities, whereas negative arousal might increase the motivation to avoid threats [18,19]. If positive and negative arousal reflect ongoing activity of independent mechanisms, additional mechanisms might integrate their influences to promote the next appropriate behavioural response. These elements – affect, integration, and motivation – form core components of the skeletal framework for neural circuits that promote choice proposed below.

Functional, chemical, and structural circuit characteristics

Neuroimaging methods with enhanced spatial, temporal, and depth resolution (such as FMRI) have enabled investigators to track activity in neural circuits that support affect and motivation. Resulting evidence suggested that positive subjective arousal correlates with nucleus accumbens (NAcc) activity, whereas negative subjective arousal correlates with anterior insula (AI; and possibly reduced NAcc) activity [20]. When affect motivates behaviour, these findings imply that during consideration of choices, NAcc activity should promote approach behaviour, whereas AI activity should promote avoidance behaviour [21–23]. Indeed, these predictions hold across diverse choice scenarios [24]. Activity in these circuits also precedes social approach and avoidance: NAcc activity predicts cooperation whereas AI activity predicts defection in dyadic interactions with strangers [25].

Although approach and avoidance responses might suffice to drive simple choices, more complex value assessments require integration of these basic tendencies with other considerations (such as the potential likelihood, length of waiting time, or effort required to obtain something). Researchers found evidence that the medial prefrontal cortex (MPFC) played a prominent role in value integration in situations in which attributes both within and across choice options must be integrated [21,26–29]. Currently, several meta-analyses of functional neuroimaging studies have implicated NAcc, AI, and MPFC activity in affect and choice [24,30–33]. To motivate behaviour, these components must then activate circuits that prepare motor output, including the dorsal striatum and premotor cortical regions [34]. FMRI evidence indicates that activity in all of these circuits can both precede and predict choice.

These combined components therefore represent promising candidates as neural circuits that promote choice (FIG. 1).

Chemically, both dopaminergic and noradrenergic neurons broadly but differentially innervate these regions, and can rapidly shift their firing rates in response to environmental opportunities and challenges. Specifically, the NAcc receives dense dopaminergic projections from the ventral tegmental area (VTA), but not noradrenergic projections from the locus coeruleus (LC). The MPFC and AI receive both dopaminergic projections from the VTA and noradrenergic projections from the LC. Dopamine reuptake mechanisms, however, primarily reside in the striatum (including the NAcc), enhancing both the release and clearance of synaptic dopamine [35].

Structurally, both primate and human studies of these circuits suggest evolutionarily conserved patterns of connectivity. VTA dopaminergic neurons project through the medial forebrain bundle to the NAcc, which then projects via GABAergic neurons indirectly through the globus pallidus to the medial thalamus. From there, glutamatergic neurons project to the MPFC and then back down to the ventral striatum (including the NAcc and adjacent ventral putamen and medial caudate). The glutamatergic projections from the MPFC to the NAcc are notably unidirectional. This indirect “looping” connectivity of striatal to frontal regions and back continues in an upward spiralling pattern that progresses through the medial caudate and the anterior cingulate to the dorsal caudate and premotor cortex, [36] and is thought to facilitate the conversion of motivation to action [34]. Although structural connections between the AI and these regions have not received extensive characterization in primates, the AI does send unidirectional glutamatergic projections to the NAcc [37], and also projects forward to lateral aspects of the prefrontal cortex [37,38], potentially allowing the AI to directly influence NAcc and indirectly influence MPFC activity (FIG. 1).

The Affect-Integration-Motivation (AIM) framework

The findings described above thus converge upon a framework in which affective neural components first anticipate gains (via dopaminergic projections to the NAcc) and losses (via noradrenergic and dopaminergic projections to the AI) that are then integrated with further evaluative considerations (via glutamatergic projections to the MPFC) before feeding into a motivational component that promotes subsequent actions (via glutamatergic projections to the dorsal striatum and supplementary motor area; FIG. 1). When there are multiple attributes or options, additional integration (in the MPFC) or comparison (in the dorsolateral prefrontal cortex (DLPFC)) may be required.

This proposed “Affect-Integration-Motivation” or AIM framework builds upon previous findings and models that have associated some of these components with valuation [26,32,33] by assigning each component different (but connected) functions that begin with affect and end with motivation. Notably, the AIM framework is sequential and hierarchical. Sequentially, activity occurs first in connections among affective components and propagates over time to motivational components. Hierarchically, affective components can operate with variable input from motivational components, but motivational components cannot operate without some input from affective components. The framework specifies a set of minimal and necessary components that precede and predict choice, but retains flexibility to account

for choice through different combinations of those components, and also remains open to input from additional components. For instance, for the affective components, information about salient options might enter through an amygdalar-orbitofrontal circuit [39], whereas for the integrative component, information about past memories or rule-based knowledge might enter through a medial temporal lobe-DLPFC circuit.

Although the AIM framework applies generally to decision making, it may also help scaffold specific predictions about how healthy ageing influences decision making. Ageing might globally compromise neural structure and function, which should cause general decline in all of the components and their associated functions. However, behavioural research suggests that ageing does not uniformly change cognition and affect. In terms of affect, if ageing decreases anticipation of losses but not gains, components associated with loss anticipation may show functional and structural declines. Similarly, if ageing compromises integration of value, components associated with value integration may show functional and structural declines. These age-related changes could exert specific effects on choice biases or optimality. In terms of cognition, if ageing compromises fluid but not crystallized cognition (BOX 1 and BOX 2) [40–42], it might diminish the function and structure of the prefrontal cortex and medial temporal lobes, which could impair value integration in complex choice tasks that require more attention and memory.

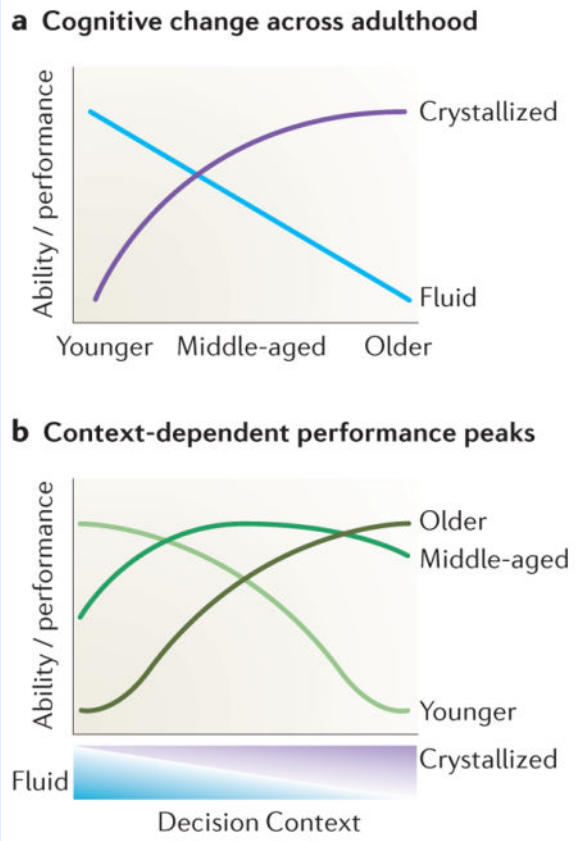
Box 2

Age-related differences in decision performance depend on cognitive demands

Age-dependent differences in performance in decision making tasks depend heavily on the extent to which decisions make cognitive demands or provide opportunities to draw on prior knowledge [129]. Recently, theorists have built upon classic observations of adult age differences in fluid and crystallized cognitive abilities [130] to explain age-related differences in decision performance [97,131,132]. Although fluid cognitive ability decreases linearly across adulthood, crystallized ability increases non-linearly and begins to level off in late middle age [131] (see figure, panel a). These changes imply context-dependent differences in decision performance (see figure, panel b). For example, when a decision requires high fluid ability and low crystallized ability, younger adults should outperform middle-aged and older adults. When a decision instead requires low fluid ability and high crystallized ability, however, older adults should outperform middle-aged and younger adults.

This cognitive account predicts that middle-aged adults may make the most optimal decisions across a broad range of contexts, consistent with a recent suggestion that financial reasoning peaks in middle-age [131]. Even in contexts in which decisions can be made based almost completely on crystallized cognitive abilities, older adults enjoy only a slight advantage over middle-aged adults. Although initial findings reviewed here and elsewhere [97] are consistent with these accounts, and specifically implicate input during value integration from medial temporal lobe and dorsolateral prefrontal cortex, they require further generalization across different decision contexts. When combined with this cognitive account the AIM framework implies that ageing may compromise

performance in scenarios requiring integration of new value information but may enhance or preserve performance in situations that allow greater reliance on previously established value representations.



Changes in decision making with age

A simple but useful theory of optimal decision making states that individuals assess the expected value of options (or the magnitude of each option's value multiplied by its probability of its occurrence) prior to choice [4344]. By separately considering gain and loss, expected value can be deconstructed as an option's magnitude multiplied by the probability of potential gain minus the magnitude multiplied by the probability of potential loss. Expected value can further be modified by other factors (including how long one must wait before receiving an option and the effort required to obtain that option). Expected value can then recommend the best choice among a set of options, and expected value theory can even specify necessary criteria for optimal choice (such as choice consistency within a set of ordered preferences). Expected value theory inspired recent neuroimaging research in which investigators correlated activity in some AIM framework components with different aspects of expected value [45,46]. For instance, NAcc activity was associated with gain magnitude; AI activity with loss as well as gain magnitude; and MFPC activity with value and probability integration (reviewed in [20]).

However, although people often choose options consistent with the predictions of expected value theory, this is not always the case, creating opportunities to experimentally measure and account for suboptimal choices. For example, people often make suboptimal choices (or fail to maximize expected value) when evaluating risks and delays, or when learning about changes in value [47]. An important question is therefore whether older adults make more or less optimal decisions in these scenarios than younger adults and, when differences exist, which underlying neural mechanisms can account for those differences?

Changes in value assessment

As described above, although older adults report similar levels of positive affective experience to younger adults, they report less negative affective experience [4]. Consistent with this age-related asymmetry, experimental research indicates that older adults show reduced attention to and memory for negative material [5]. However, these findings do not specify whether older adults show less negative affect during anticipation of events that have not yet occurred (which could implicate expected value), or in response to events that have already occurred, or both.

In behavioural research in younger adults, anticipation of uncertain monetary gains robustly and reliably elicits positive arousal, whereas anticipation of uncertain monetary losses elicits negative arousal [24]. By contrast, although older adults also report increased positive arousal when anticipating monetary gains, they do not report increased negative arousal when anticipating losses [48,49]. Younger and older adults do, however, report similarly positive affective responses to gain outcomes and negative affective responses to loss outcomes.

With respect to the AIM framework, these findings imply that older adults might show decreased activity in loss anticipation circuits during value assessment (or possibly, increased activity in gain anticipation circuits). FMRI studies in younger adults typically show that anticipation of uncertain monetary gains increases NAcc, AI, and dorsomedial caudate activity, but that anticipation of uncertain monetary losses increases only AI and dorsomedial caudate activity [20,50]. Although older adults show similar increases in NAcc activity during anticipation of monetary gains [49,51] (but see [52]), they do not show the same increases in AI activity during anticipation of monetary losses (FIG. 2a) [49,51]. Interestingly, younger and older adults show similar neural responses in both the MPFC and ventral striatum in response to gain and loss outcomes [49,52–55] (see also [56]). Thus, both affective and neural responses during anticipation of gains are preserved in older adults, whereas affective and neural responses during anticipation of losses are reduced.

The diminished responses of older adults to anticipated losses [5] may impose costs as well as conferring benefits. Specifically, although reduced loss anticipation could enhance well-being, it may also increase susceptibility to threats. For instance, one study found that older adults rated conventionally untrustworthy faces as more trustworthy and responded to these faces with less insula activity than did younger adults [57]. In another study that used a socially incentivized game, older adults responded to unfair offers to divide a financial windfall with less insula activity than did younger adults [58]. Despite this neural difference, however, older adults rejected slightly more unfair offers than younger adults. Although negative arousal correlated with rejection of unfair offers in younger adults, it did not in

older adults, suggesting that other, more cognitive, mechanisms might have driven elders' rejections. These findings broadly suggest that age-related changes in value assessment may sometimes directly influence decisions [57], but need not always alter choice [49,58].

Considered in light of the AIM framework, this evidence suggests that older adults show preserved positive affect and NAcc activity while anticipating gains, but reduced negative affect and insular activity while anticipating losses. Although age-related changes in these responses may influence choice, most of these experiments were designed only to elicit affect and brain activity. In addition, many of these experiments did not require value integration (either across potential gains and losses, or with respect to probability, delay, effort, and other factors). Thus, the impact of age-related affective changes on choice must be assessed rather than assumed, and choices requiring greater cognitive capacity incur the greatest age-related compromise.

Changes in risky decision making

Risky decision making requires, at a minimum, assessing uncertain future gains versus losses. Theorists have historically defined risk in different ways. Financially, expected value can be defined as the mean return of an option and risk as the mean variance of the option [59]. Financial theories further posit that expected value attracts investors, whereas risk repels them. Younger adults generally prefer to avoid financial risk, which can lead to suboptimal decision making [60]. Financial risk preferences show substantial individual differences, however, and also vary as a function of situational factors [61].

Perhaps because older adults generally avoid physical risks, people often assume that they will show even greater financial risk aversion than younger adults. These suspected differences, however, do not consistently emerge in well-controlled behavioural tasks [62]. In fact, a recent meta-analysis showed no evidence of systematic age-related differences in risk taking [63]. Rather, in tasks in which risk taking increased earnings, older adults avoided more risk, but in tasks in which risk taking decreased earnings, older adults sought more risk — suggesting that older adults made more mistakes overall. Furthermore, older adults performed more poorly than younger adults in tasks that required them to learn from recent experience, but not in tasks that did not require learning [63]. Finally, older and younger adults did not differ in their tendency to take risks when choices were framed as gains versus losses. Together, this evidence is consistent with an account in which older adults evince cognitive limitations rather than different risk preferences [64].

With respect to the AIM framework, these findings suggest that although older adults show reduced loss anticipation during value assessment this may not necessarily translate into biased financial risk-taking. Instead, cognitive limitations and associated compromises in value integration might more prominently influence older adults' financial risk taking. FMRI studies of younger adults indicate that anticipation of expected value is associated with NAcc and MPFC activity, whereas anticipation of risk is associated with AI activity [65]. Furthermore, while NAcc activity and MPFC activity predicts financial risk seeking, AI activity predicts financial risk aversion [66].

Currently, only a few FMRI studies have compared financial risk taking in younger and older adults. Older adults showed greater AI activity and more risk averse choices than younger adults during a gambling task [67], in addition to greater prefrontal activity during a slot machine task [68], consistent with research showing increased prefrontal recruitment in older adults during risky decision making [69] and across a range of cognitive tasks [69–71]. The small number of older adults in some of these studies (Ns~10), however, makes it difficult to generalise from these findings. A study with a larger sample examined age-related differences in risky choice during an investing task designed to elicit both high- and low-risk choices from each subject [54]. The investing task also allows investigators to model the choices of an "optimal actor" and thereby quantify each subject's "mistakes," or deviations from optimal choice [72]. While results showed no age-related differences in risk-averse choices, they did reveal that older adults made more risk-seeking mistakes (FIG 2b) [54]. This behavioural pattern was subsequently replicated in two additional samples [54,73]. Furthermore, older adults showed more random variation over time in NAcc activity, which could statistically account for increased risk-seeking mistakes [54,74]. An independent study using a different task without financial incentives also found increased age-related variability in NAcc and midbrain activity [75]. Although most FMRI studies focus on mean activity, variability may provide an important yet overlooked measure that can also clarify how ageing influences choice [76,77].

Together, these findings suggest that the variability of neural activity during expected value assessment may increase with age – particularly when previous value associations must be adjusted or relearned. Consistent with this account, older adults have more difficulty estimating expected value during reward learning [78]. Apparent age-related differences in risk preferences may therefore result from increased neural variability during the estimation of expected value. The source of this variability may not merely reside in NAcc activity, but could also reflect more variable dopaminergic input from the midbrain, or more variable glutamatergic input from the MPFC. Consistent with this latter possibility, a study of older adults found that individuals with lower earnings in a gambling task with a learning component showed reduced MPFC recruitment [79]. Considered in light of the AIM framework, these early findings suggest that greater variability in a value integration signal conveyed by MPFC projections to the NAcc may destabilize expected value estimates, as well as associated risky choices (a theme that will recur in the value learning section).

Changes in temporal decision making

People commonly devalue (or "discount") potential rewards as a function of the time they must wait to obtain them. The rate at which young adults temporally discount gains is often steeper than the rate at which those gains actually decrease in value over time [80]. This nonlinear devaluation of future gains (called "delay discounting") can provoke suboptimal choices [81]. As with risk preferences, individuals reliably differ in their tendency to discount future gains, and situational factors such as incentive type can also exacerbate delay discounting [82]. Accumulating behavioural research suggests that older adults discount future rewards less steeply than younger adults [83] (a phenomenon also demonstrated in some animal models [84,85]), and consequently the choices of older adults better approximate future rewards' market value [86].

Neuroimaging studies have implicated NAcc and MPFC activity in younger adults' tendency to weight immediate over future rewards (both sensory and financial) [87–90]. Although NAcc activity also has a lesser role in the value assessment of future rewards [90], converging evidence suggests that activity in prefrontal cortex (including the DLPFC and possibly MPFC) has a more prominent role in the ability to imagine and extend value to future rewards [87,91–93]. From the standpoint of the AIM framework, these findings suggest at least three possible accounts of older adults' ability to more optimally balance future and present rewards. Specifically, older adults' reduced delay discounting may result either from reduced anticipation of gain from immediate rewards, increased anticipation of gain from future rewards, or increased integration of future rewards into an overall value assessment.

Only two FMRI studies have directly compared neural responses during temporal valuation tasks in younger and older adults [94,95]. In both studies, younger adults showed more ventral striatal activity in response to immediate rewards than future rewards, whereas older adults showed comparable ventral striatal activity in response to both immediate and future rewards (FIG. 3). Additionally, in adults of all ages ventral striatal activity in response to future rewards predicted individual differences in relative preferences for future rewards [93]. Neither study, however, found differences in prefrontal activity of older versus younger adults during consideration of future rewards.

These neuroimaging results are consistent with behavioural findings indicating that although younger adults value immediate rewards more than future rewards, older adults value the two more similarly. With respect to the AIM framework, these findings either support the notion that immediate rewards evoke less gain anticipation, or future rewards elicit more gain anticipation in older adults, but do not implicate compromised value integration. Reduced responsiveness to immediate rewards might imply that ageing could compromise midbrain dopaminergic input to the ventral striatum [94], but pharmacological data call this account into question [96]. Enhanced responsiveness to future rewards instead might imply that ageing preserves midbrain dopaminergic input or MPFC glutamatergic input to the ventral striatum during contemplation of future gains, thereby optimizing temporal choice [9597]. Future research using causal affective manipulations could compare the plausibility of these accounts, and might also test whether older adults' more optimal temporal choices result from physiological changes, experience, or both [98].

Changes in value learning

Traditional theories of valuation often do not consider the source of those values. Although some values may have innate origins, most are learned, and may require continual adjustment to accommodate changing environmental circumstances. Value learning can be dynamic and complex, potentially recruiting and recalibrating any of the valuation mechanisms described above. Even in the case of simple probabilistic learning, although people can eventually learn that one option is more likely to yield gains than another, they often show suboptimal patterns of choice in the process. As with other types of valuation, individuals reliably differ in learning performance, and situational influences may speed or slow learning.

Possibly due to variable task demands, behavioural comparisons of value learning in older and younger adults have produced mixed results. For instance, although some studies suggest decreased responsiveness to gains during learning in older versus younger adults [99,100], others suggest decreased responsiveness to losses [101–103]. When studies find decreased sensitivity to gains in older adults, it tends to appear in the very old [103,104], which may reflect a slight decrease in positive affect at the end of life [4]. Across studies, however, researchers have generally noted slower learning about both gains and losses in older adults [10], consistent with general age-related decrements in value learning.

With respect to the AIM framework, these findings suggest that ageing may compromise either gain anticipation or value integration during probabilistic learning. In FMRI studies of younger adults, gain learning tasks typically elicit correlated activity in the NAcc and MPFC, whereas loss learning tasks more often elicit correlated activity in the AI [22,23]. Consistent with decreased learning performance, FMRI studies have shown reduced NAcc activity during learning in older adults [105]. Moreover, electroencephalographic studies have also shown decreased frontal potentials during learning in older adults [101,106]. Recent research has explored whether these neural differences reflect diminished updating of reward prediction, as modelled by reward prediction errors[55,102,107]. Two FMRI studies of incentive learning specifically showed reduced neural activity associated with reward prediction errors in the MPFC and NAcc of older adults relative to younger adults [55,102]. Furthermore, in a combined FMRI and pharmacological study, administration of a drug that increased dopamine availability improved learning and restored NAcc activity associated with reward prediction errors in underperforming older adults [107].

Age-related decreases in NAcc recruitment during reward learning might seem inconsistent with preserved NAcc activity during value assessment (described above). To directly compare value assessment and learning, an FMRI study examined older adults' neural responses to gains in tasks with and without probabilistic learning demands. As in previous learning studies, older adults showed reduced MPFC and NAcc activity associated with reward prediction errors in the context of probabilistic learning, but preserved NAcc responses to monetary gains in a value assessment task [55,107]. Thus, age-related decreases in NAcc activity during value learning seem not to stem from a lack of physiological responsiveness to reward, but rather from a slowness to alter existing reward predictions based on feedback. From the standpoint of the AIM framework, older adults may not suffer from reduced gain anticipation associated with NAcc activity, but rather from a lack of responsiveness to new information that corrects gain predictions, possibly conveyed by MPFC glutamatergic projections to the NAcc.

To specifically test whether frontostriatal connections could account for age-related decrements in reward learning, a diffusion tensor imaging (DTI) study assessed the structural coherence of mesolimbic white matter pathways in a community adult life-span sample. Measures of tract coherence were tested for associations with performance on a probabilistic learning task. Not only did ageing diminish the coherence of frontostriatal pathways (specifically, tracts that connect the thalamus to the MPFC, and the MPFC to the NAcc), but decreased coherence of these pathways could fully account for ageing's influence on learning [108]. With respect to the AIM framework, these findings highlight the

importance of considering connections between components, and specifically imply that age-related decreases in frontostriatal signalling might account for decreased reward learning. Thus, an age-related compromise of value integration might account for deficits in reward learning – and may extend to any tasks that require reward learning (including dynamic risk taking). Age-related changes in implicit reward learning, however, must be distinguished from age-related changes in explicit memory, with respect to both relevant neural circuits and psychological processes [73].

Conclusions and implications

Growing interdisciplinary research has begun to link age-related changes in decision making to shifts in affective and motivational brain circuits. Specifically, emerging evidence suggests that, in older adults, gain anticipation and correlated NAcc activity are preserved but loss anticipation and correlated AI activity are relatively reduced. Older adults show more variable risky choices, which are related to more variable NAcc activity as they contemplate risky options. Older adults may place greater value on future rewards, which may be associated with relatively increased NAcc activity in response to future prospects. Finally, older adults show reduced reward learning, which may be related to diminished NAcc responsiveness to violated reward expectations, as well as degraded structural connectivity from the MPFC to the NAcc.

These findings suggest that ageing does not uniformly degrade decision performance, and under some circumstances may improve it. Optimal criteria for decision making are difficult to define, but according to expected value theory, people should prefer options that return greater value, and should consistently choose in a way that matches their preferences. Consistent with optimal choice, older adults seem to anticipate gains (but not losses) to the same extent as younger adults. Older adults also tend to show more optimal choices in temporal valuation. Inconsistent with optimal choice, however, when value assessment dynamically varies or requires integration across many attributes or options, as in the case of risky choice or probabilistic learning, older adults appear to choose less optimally than younger adults.

The findings also paint a varied picture of how ageing influences neural activity preceding choice, which does not neatly fit a profile of global age-related neural decline. As an alternative, we introduce the AIM framework, which delineates different critical neural components and connections that can together promote optimal decision making. This hierarchical and componential framework might provide a richer and more accurate view of the diverse effects of ageing on decision performance. For instance, if gain anticipation circuits including the NAcc are relatively preserved with ageing, but value integration associated with the MFPC and its connections to the NAcc degrade, gain anticipation might be preserved, but dynamic updating in the context of risky choice and probabilistic learning might be compromised [55,109].

The AIM framework thus fills a theoretical gap and complements existing neural accounts of age-related changes in attention, memory, and cognitive control [71,110–114]. Many of these cognitive contributions to decision making may enter the AIM framework at the value

integration phase, deranging this component's contribution to decision making while leaving other types of input intact [64,93,115,116]. For instance, a recent study using a purchasing task found that older adults made similarly optimal choices to younger adults with respect to simple choices, but not complex choices requiring working memory. Older adults who showed increased MPFC activity during complex choices, however, were able to match younger adults' performance [117]. An exciting future research agenda involves connecting the AIM framework to existing cognitive models of the influence of ageing on decision making.

Beyond organizing previous findings and generating future research questions, knowledge of neural components could inspire more specific ideas for applications. Complex decision tasks probably engage more components of the AIM framework, making performance failures more challenging to diagnose. Although different components may produce similar choices, understanding the underlying mechanisms could help investigators identify targeted interventions with the best chance of optimizing function. Thus, an important goal of neurally deconstructing decision making is to use this knowledge to inform the design of interventions that can enhance performance across the life span (BOX 3). However, before innovating interventions, it will be critical to verify that laboratory behaviour connects to decision making in the real world (BOX 4).

Box 3

Innovating targeted decision aids

When older adults' decision performance trails behind that of younger adults, research might identify opportunities for intervention. Building from the finding that age-related changes in risky choice may result from impairments in updating expected value, recent work demonstrated that providing graphical representations of expected value information could improve financial risk taking [73]. With these targeted decision aids, older adults chose as optimally as younger adults without decision aids (see also [133]).

Although promising, this early research is still several steps away from real-world implementation. The complexity and changing nature of many significant financial choices often resists easy graphical or numerical depiction. Furthermore, providing helpful information does not necessarily guarantee implementation. Adopting new strategies requires motivation as well as information. For instance, a recent study that trained individuals to use an expected value based decision strategy was less effective in older than younger adults [134], since older adults drifted from the suggested strategy within minutes. Research has yet to clarify whether elders' shift occurred due to memory decay or active doubts about the usefulness of recommended strategies. Novel decision-making strategies may prove difficult to substitute after a lifetime of using other effective or familiar strategies.

Precise value calculations, however, may not be necessary for solving most decision problems outside the laboratory. In fact, some theorists suggest that rapidly grasping the gist rather than exact verbatim details of most decision problems provides critical leverage for success in the real world [135,136]. In many situations, older individuals might play to their strengths without sacrificing decision quality by choosing simpler strategies [137,138].

In contrast to a general degradation account of neurobiological function, a componential approach like the AIM framework naturally implies targeted interventions for specific age-related changes in decision making [139,140]. Through the lens of the AIM framework, the studies reviewed imply that decision aids for older adults should strive to focus on gains rather than losses, leverage emphasis on long-term gains, build on rather than changing existing value associations, and present simple and limited sets of options. Combined with an appreciation of cognitive limitations, decision neuroscience may eventually yield more effective decision aids for people of all ages.

Box 4

Generalizing from the laboratory to the real world

The field of decision neuroscience is both interdisciplinary and young, and researchers have yet to link most laboratory measures of decision performance to significant real-world outcomes. Nevertheless, some links have begun to emerge. Individuals who make more optimal choices (or fewer "mistakes") in a laboratory financial investment task also report having accumulated more real-world assets [54]. In probabilistic value learning tasks, individuals who learn to acquire gains more rapidly also report having accumulated more real-world assets, whereas individuals who learn to avoid losses more rapidly report having less financial debt [141]. Some of these measures have been validated not only with self-report but also with independent financial records (for instance, credit reports) [132,141].

The possibility of associating a laboratory measure with real-world behaviour is limited by the reliability of both the measure and the behaviour, which could present significant challenges for some traditional measures of economic choice. Fortunately, interdisciplinary collaboration can encourage innovation of measures with improved reliability when traditional measures do not suffice. Furthermore, the extent to which laboratory findings can be generalized to the real world may be limited by varying choice conditions. For instance, older individuals may not have the opportunity to avoid choices in the laboratory that they might in everyday life [62].

Beyond providing evidence for the validity of laboratory-based tasks, improving the predictive power of laboratory assessments could also help researchers to identify vulnerable individuals who are prone to making suboptimal choices in the real world [142]. The elderly may be disproportionately targeted by fraudulent financial appeals, although evidence does not strongly suggest that they are more susceptible [143]. Researchers are currently studying older individuals at heightened risk for making financial mistakes (based on prior victimization, for example) to understand how potential vulnerability to financial fraud relates to physiological, psychological, and behavioural variables across the adult life span. Future research should attempt to link laboratory measures to real-world decisions [131,144] so as to ensure that findings are consequential and have the best chance of improving the wealth and health of individuals, as well as the broader society they inhabit.

The application of neuroscience methods to address age-related changes in decision making has just begun, and raises more questions than it answers. For instance, in which decision scenarios is diminished loss anticipation helpful versus harmful? To what extent are age-related changes in decision performance due to physiological changes versus psychological strategies for coping with those changes? Although some evidence suggests age-related diminutions in dopamine activity [107], other evidence points towards broader age-related neurochemical changes (in noradrenergic and glutamatergic activity) [108], all of which could influence decision performance. Furthermore, to what extent do structural changes influence communication between critical components, which connections are central to decision making, and can they be targeted and modified with interventions? Finally, how can neuroscience improve the design and assessment of decision aids (BOX 3)?

As scientific research on ageing and decision making grows, so will societal interest in using this research to inform policy. Findings may inform the development of more targeted behavioural and neural interventions that leverage strengths and minimize weaknesses of the ageing brain. As increasing numbers of elders strive to make more optimal decisions, this new information may offer the best hope for improving their aim.

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Glossary Terms

Fluid cognitive ability
The ability to flexibly generate, transform, and manipulate new information.

Crystallized cognitive ability

The ability to invoke previously stored information drawn from experience or accumulated knowledge.

Cross-sectional studies
Studies that compare individuals (e.g., of different ages) at one simultaneous time point.

Longitudinal studies
Studies that compare the same individuals (e.g., of different ages) repeatedly over multiple time points to assess change.

Diffusion tensor imaging
A neuroimaging technique that uses the restricted diffusion of water around neural membranes and myelinated fibres to map anatomical connectivity between brain areas.

Positron emission tomography (PET)
A nuclear imaging technique that produces three-dimensional images of brain activity by detecting photons that are emitted by a positron-emitting radionuclide tracer.

Affect
A combination of subjective valence and arousal that is sometimes depicted in two-dimensional space.

Valence
The subjectively positive or negative feeling evoked by an experience.

Arousal
The subjective level of alertness, activation, or energy elicited by an experience.

Functional magnetic resonance imaging (FMRI)
A functional imaging technique that uses a magnetic field and radio waves to measure the blood-oxygenation-level-dependent signal, which indexes regional brain activity.

Probabilistic learning
Learning in which individuals use recent feedback to guide future choices among options of uncertain value.

Reward prediction error
A quantity denoting the difference between the received versus expected reward.

Reward prediction
A quantity denoting the expected reward.

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Online Summary

- Research has begun to explore how age-related changes in brain systems implicated in affect and motivation influence decision making.
- Older and younger adults show similar affective and neural sensitivity to anticipated financial gains during value assessment, as well as to gain and loss outcomes. Older adults, however, show reduced affective and neural sensitivity to anticipated financial losses.
- Older adults make more suboptimal choices during financial risk taking, which appear to be related not to shifts in risk preference, but rather to increased variability in NAcc activity.
- Older adults make more optimal choices during delay discounting by assigning higher value to future gains, which appears to be related to increased NAcc activity during consideration of future rewards.
- Older adults make more suboptimal choices when engaging in probabilistic reward learning, which appear to be related to decreased NAcc activity associated with reward prediction errors (but not necessarily reward predictions), which may result from reduced MPFC input into striatal circuits.
- Understanding how ageing variably influences brain function and structure may better inform targeted interventions designed to improve decision performance in individuals of all ages.

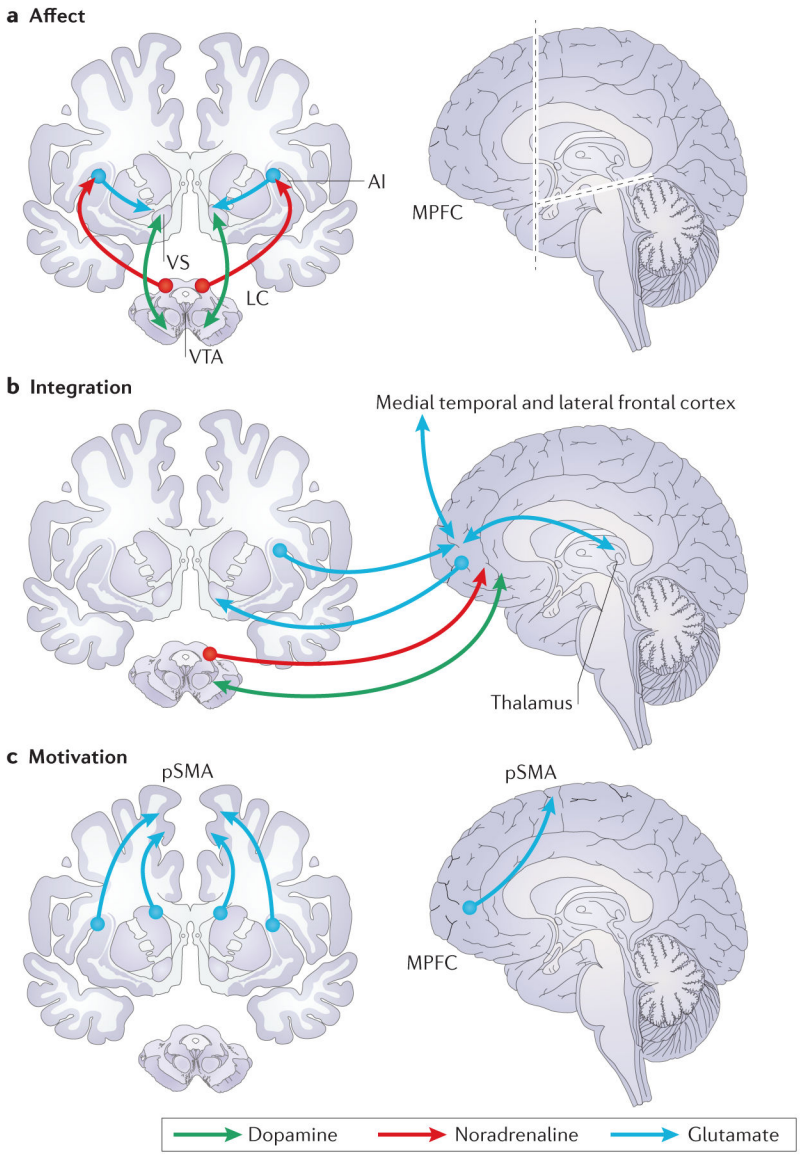

Figure 1. Critical components of the Affect-Integration-Motivation (AIM) framework

The AIM framework implies that three hierarchical and sequential processes can occur prior to and promote choice. a| Affect, in which ventral tegmental area (VTA) dopamine neurons project to the ventral striatum (VS, including the NAcc), locus coeruleus (LC) norepinephrine neurons project to the AI (AI), and AI glutamatergic neurons (blue) project to the VS, potentiating anticipation of gain and loss. b| Integration, in which VTA dopamine neurons and LC norepinephrine neurons modulate medial prefrontal cortex (MPFC) activity, VS indirectly projects to the MPFC via GABA connections in the pallidum (not depicted) and glutamate projections from the thalamus, AI projects to the MPFC, and MPFC glutamatergic neurons directly project back to the VS, facilitating integration of value and modulatory signals (for instance, from the medial temporal and lateral frontal cortical regions). c| Motivation, in which dorsal striatal and insular glutamatergic neurons project to the pre-supplementary motor area (pSMA), potentiating motor action. Healthy ageing is

predicted to degrade glutamatergic projections from the prefrontal cortex to the striatum, thus diminishing value integration (b), and compromising choice optimality.

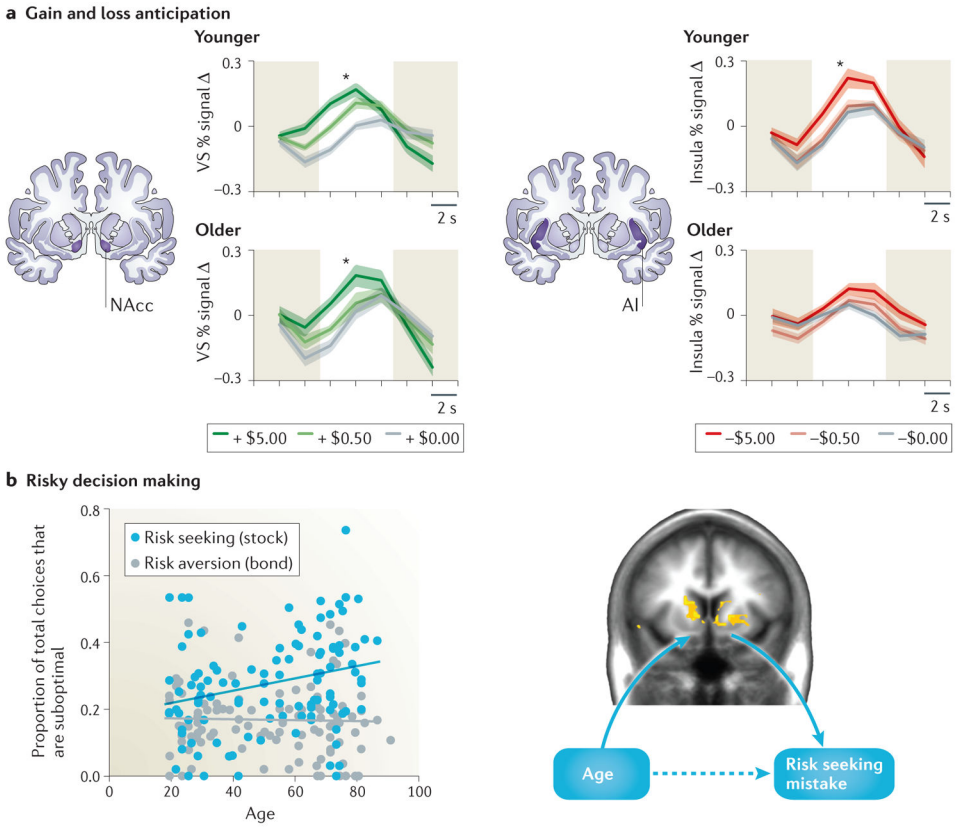

Figure 2. Age-related differences in incentive anticipation and risky decision making

a| In an incentive anticipation task in which subjects saw cues signalling the potential gain or loss of varying amounts of money, gain anticipation increased nucleus accumbens (NAcc) activity in both younger (ages 19–27) and older (ages 65–81) adults (left panels). Loss anticipation, however, increased AI activity in younger, but not older, adults (right panels). Shaded error bars indicate standard error of the group mean. Y-axis represents percentage FMRI activity change in the ventral striatum (VS, including the NAcc).b| In a financially risky choice task, older adults make more mistakes than younger adults when seeking risk (selection of stocks) but not when avoiding risk (selection of bonds) (left panel). Age-related differences in behaviour (ages 19–85) were associated with age-related increased variability in striatal activity, including the NAcc (right panel; coloured areas overlaid on the brain are voxels for which a statistical test of the linear effect of age exceeded $p < .0001$, uncorrected). This increased variability mediated the association between increased age and risky stock (RS) mistakes. Figures in part a adapted from [49]. Figures in part b adapted from [54].

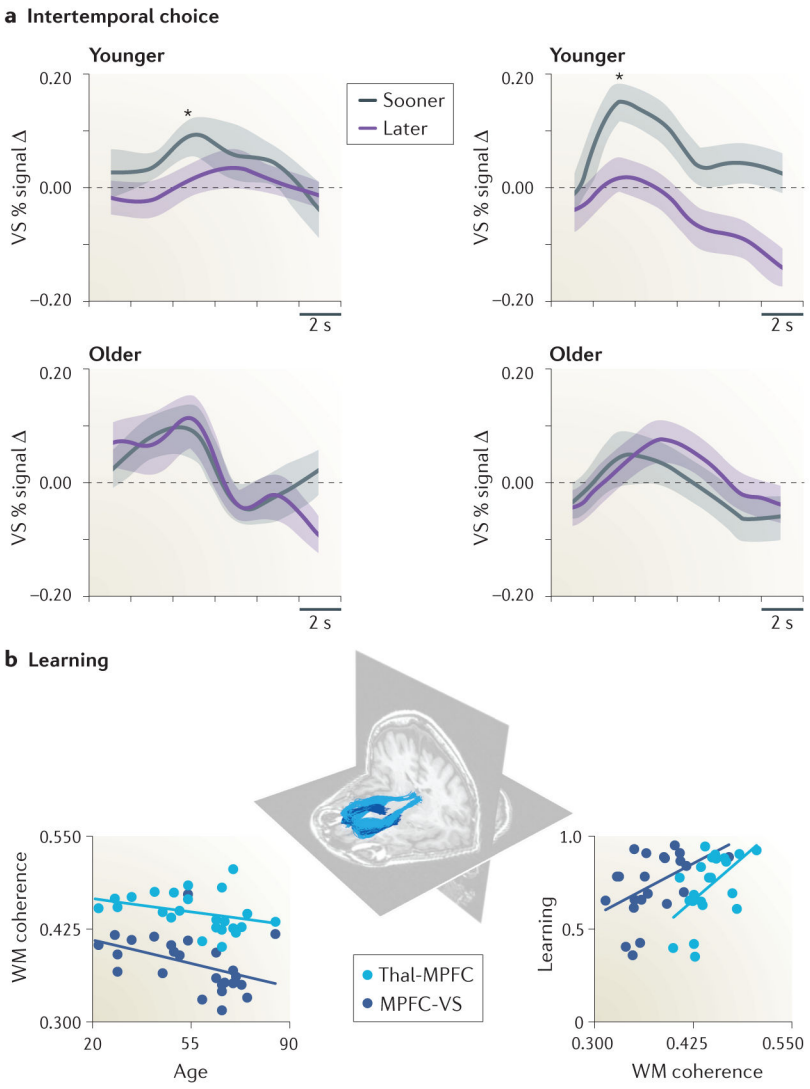

Figure 3. Age-related differences in temporal decision making and value learning

a| Younger adults show reduced NAcc activity for rewards available at longer (grey line) versus shorter (orange line) time delays, but older adults show comparable activity for both short and long delays. Shaded error bars indicate standard error of group means. Y-axis represents percentage FMRI activity change in the ventral striatum (VS, including the NAcc). b| Structural coherence along a frontostriatal axonal tract extending from the dorsomedial nucleus of the thalamus (Thal) to the medial prefrontal cortex (MPFC; light blue) and from the MPFC to the ventral striatum (dark blue) was reduced in older age but associated with better learning. White matter coherence was indexed by measuring fractional anisotropy. Individual differences in learning were calculated as the percentage of choices of the higher expected value option. Left panels in part a adapted from [95]. Right panels in part a adapted from [94]. Figure in part b adapted from [108].