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The impact of natural aging on computational and neural indices of perceptual decision making: A review

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ABSTRACT

It is well established that natural aging negatively impacts on a wide variety of cognitive functions and research has sought to identify core neural mechanisms that may account for these disparate changes. A central feature of any cognitive task is the requirement to translate sensory information into an appropriate action - a process commonly known as *perceptual decision making*. While computational, psychophysical, and neurophysiological research has made substantial progress in establishing the key computations and neural mechanisms underpinning decision making, it is only relatively recently that this knowledge has begun to be applied to research on aging. The purpose of this review is to provide an overview of this work which is beginning to offer new insights into the core psychological processes that mediate age-related cognitive decline in adults aged 65 years and over. Mathematical modelling studies have consistently reported that older adults display longer non-decisional processing times and implement more conservative decision policies than their younger counterparts. However, there are limits on what we can learn from behavioural modeling alone and neurophysiological analyses can play an essential role in empirically validating model predictions and in pinpointing the precise neural mechanisms that are impacted by aging. Although few studies to date have explicitly examined correspondences between computational models and neural data with respect to cognitive aging, neurophysiological studies have already highlighted age-related changes at multiple levels of the sensorimotor hierarchy that are likely to be consequential for decision making behaviour. Here, we provide an overview of this literature and suggest some future directions for the field.

1. Introduction

Advances in modern medical science have led to an unprecedented growth in the world's aging population. The number of people aged 65 years or older is projected to rise from an estimated 617 million people, comprising 8.5% of the world's population, to approximately 1.6 billion older people sby 2050, representing 16.7% of the total population [1]. With this exceptional growth in the aging community it is becoming increasingly important to understand the cognitive changes associated with both normal and pathological aging. Such changes in our cognitive capacities have the potential to impact our ability to perform everyday tasks such as crossing the road, driving, activities relying on mobility, and all forms of social engagement. Indeed, older adults consider a decline in cognitive function to be one of the most debilitating aspects of growing old and fear the reduced quality of life that accompanies this decline [2].

Extensive research has already demonstrated that normal aging is accompanied by a gradual decline in many cognitive abilities including episodic memory (e.g. [3]), working memory (e.g. [4]), speed of processing (e.g. [5]) and task-switching (e.g. [6]) and the extent of this decline has been shown to predict the risk of progression to dementia [7]. In an effort to explain these wide-ranging changes, researchers have sought to identify core age-related processes that may cut across multiple domains of cognitive functioning (e.g. [5,8,9]). One common feature of any cognitive test is *perceptual decision making,* the process through which sensory information is translated into an appropriate action.The last twenty years have witnessed substantial advances in our understanding of the core neural mechanisms underpinning perceptual decision making. The development of a powerful set of computational models that parse the latent psychological processes guiding our decisions has provided the field with a common theoretical framework, while neurophysiological research has made it possible to directly observe and measure the unfolding neural decision process in a range of species including rodents, monkeys, and humans (see [10] for a recent review). Recent behavioural modelling and neurophysiological studies suggest that perceptual decision making is degraded by aging, a critical observation since this deterioration could potentially contribute to age-related decrements on a wide variety of perceptual and cognitive tasks s

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(e.g. [11–13]).

The aim of this paper is first to provide a brief overview of the key insights that have been garnered thus far from research on perceptual decision making. We will then examine how the resulting models and techniques are being applied to the study of aging. In so doing, we will first review behavioural modelling research examining the impact of aging on perceptual decision making and consider its strengths and limitations. Next, we will highlight the essential role that neural data can play in empirically validating mathematical models and in linking age-related model parameter differences to distinct levels of neural processing. Neurophysiological research examining aging effects on three of these levels (decision formation, sensory encoding, and motor processing) will then be reviewed.

2. Abstract decision models

Understanding how the brain allows us to select appropriate courses of action based on information that is almost always to some degree incomplete or unreliable has been the subject of a major multi-disciplinary research effort spanning several decades [14]. According to a highly influential set of 'sequential sampling' models [15–17], the brain can make decisions that are robust to sensory noise by accumulating relevant sensory information, or 'evidence', over time and withholding commitment until a predefined quantity has accrued in favour of one of the decision alternatives. These sequential sampling models have been shown to provide a highly detailed account of choice accuracy and response time distributions on a wide range of perceptual and cognitive tasks. Aside from their success in accounting for choice behaviour, a key advantage of these models is that they decompose behavioural data into a set of psychologically meaningful latent parameters such as the quantity of evidence needed to trigger commitment (the 'decision bound'), the quality of evidence entering the decision process (the 'drift rate') and processes not directly associated with evidence accumulation such as sensory encoding and motor execution (the 'non-decision time', see Fig. 1 for an overview of two of the main variants of sequential sampling models). The widespread adoption of sequential sampling models in decision neuroscience can also be attributed to the fact that they have received empirical validation from both direct and non-invasive electrophysiological recordings which have highlighted neural signals exhibiting choice-predictive dynamics that closely correspond to the theorised accumulate-to-bound processes ([14,18]; see '*Neurophysiological investigations of aging and decision making*' below for further discussion).

To date, most of the research in this field has focussed on highly simplified two-alternative sensorimotor tasks because they are computationally tractable, feasibly implemented in non-human animals, and facilitate the selection of candidate brain regions likely to trace decision formation in neurophysiological investigations. However, even though perceptual tasks act as the vehicle, it is assumed that they can expose a set of fundamental neural computations that apply to a far broader range of perceptual and cognitive tasks (e.g. [14]). Indeed, sequential sampling models have already been applied in investigations of response inhibition, response conflict, and item recognition [19]. The potential scope of these models is particularly underlined by the demonstration that even the memory retrieval process can be modelled as an evidence accumulation process [11,20–24]. Sequential sampling models have also played an important role in elucidating the impact of various contextual factors on decision making. For example, there is broad agreement across a range of studies that the speed-accuracy tradeoff is principally mediated by adjustments to the decision boundary such that the quantity of evidence required to trigger commitment is raised when accuracy is at a premium and lowered when time pressure increases [19,25–27]. The cumulative result of this research effort is that there now exists a powerful set of models, paradigms, and neural signals for probing decision making processes and these are increasingly being adopted for research on aging. Thus, establishing precisely how aging impacts on decision making mechanisms may take us a long way towards understanding age-related cognitive decline.

3. Modelling age-related changes in decision making behaviour

One of the most ubiquitous findings in research on aging is an age-related increase in response latencies during cognitive performance [5,28]. The task-independence of this effect has inspired a highly influential hypothesis that cognitive aging can be understood in terms of a general slowing of information processing due to increased neural noise [5,28,29]. However, a neurobiological constraint on the speed of information processing cannot readily explain age-related differences in accuracy which vary substantially across studies and appear to be highly task-dependent. Nor can it account for the fact that, with sufficient training, older adults are capable of achieving accuracy levels and response latencies that match those of younger adults (e.g. [30]). A number of studies have therefore turned to mathematical modelling techniques in order to obtain a unified view of the age-related processes driving changes in both choice accuracy and reaction time.

Thus far, only a relatively small number of modelling studies have examined the effects of aging on perceptual decision making, with the vast majority of these studies emanating from a single research group and employing the DDM ([17]; see Fig. 1A). Despite the fact that these studies employed a variety of different tasks, experimental manipulations and age groups, some consistent trends have already emerged. For instance, one consistent finding in these studies is an *increase* in decision threshold amongst older adults suggesting that their longer response times are in part due to a more cautious decision policy whereby a greater quantity of evidence is required in order to reach commitment (e.g. [11,20,22,23,12,24,30–34,35,36]). In a further exploration of this phenomenon using a different sequential sampling model (the LBA, see Fig. 1B), Forstmann et al. [13] asked young and old participants to perform a motion discrimination task in which they were randomly cued on a trial-to-trial basis to emphasise either speed or accuracy in their decision making. In addition to exhibiting higher decision boundaries overall, the elderly participants also made smaller boundary adjustments in response to the speed/accuracy cues. In another study by Ratcliff et al. [30], older and younger participants underwent training on brightness and letter discrimination tasks across four sessions. At the outset, the older group made more errors and responded more slowly than their younger counterparts. However, by the end of training these differences had disappeared for the brightness task and were substantially reduced for the letter task. Drift diffusion modelling indicated that these improvements in the older group were mediated by a gradual reduction in the decision threshold and an increase in drift rate. Taken together the findings of Forstmann et al. [13] and Ratcliff et al. [30] suggest that, while older individuals retain a substantial capacity for making decision threshold adjustments over time, their capacity for rapid, moment-to-moment adjustments may be comprised. An open question that arises from this work is whether these differences in boundary setting reflect a voluntary strategic preference and/or capacity limitations (see '*Neurophysiological investigations of aging and decision making*' for further discussion).

Aside from elevated decision thresholds, the other consistent observation across modelling studies has been that older adults display longer non-decision components across a range of different tasks indicating delays in sensory encoding and/or motor execution [11,20–22,30,31,33,37]. In contrast, the effects of age on drift rate are much less consistent, depending more on the task at hand. For instance, whereas older and younger adults accumulated sensory information at a similar rate on a signal detection task [31], older adults accumulated evidence at approximately half the rate of younger adults on a letter discrimination task [33] and at a faster rate than younger adults on a motion discrimination task [13]. This task dependency suggests that aging does not lead to a fundamental decline in information processing,

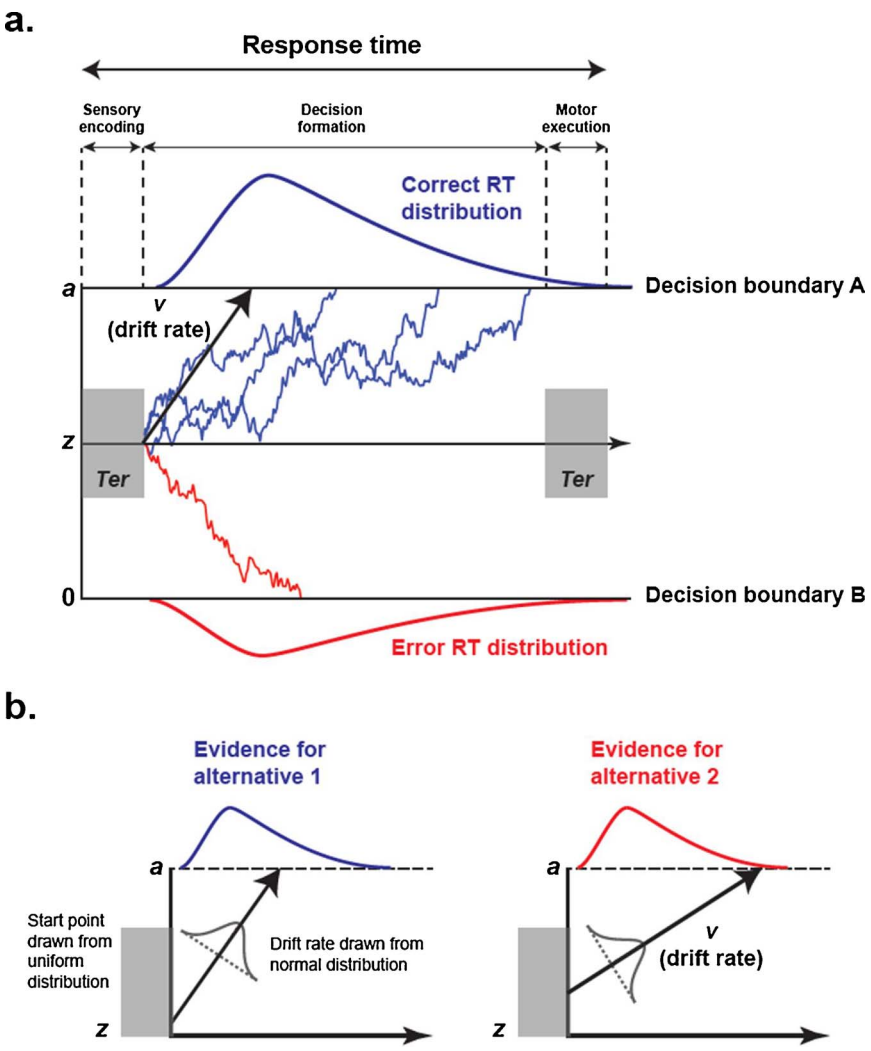

Fig. 1. Schematic depicting decision trajectories from two of the most popular variants of sequential sampling models - (a) the Drift Diffusion Model (DDM; [17]), and (b) the Linear Ballistic Accumulator Model (LBA; [162]). 1(a). The diffusion process begins at starting point (*z*) located between the decision boundaries and noisy evidence is accumulated over time with average drift rate (*v*) until one of the boundaries is crossed leading to a response. Traces are shown for correct (blue) and incorrect (red) responses and probability density plots represent cumulative boundary-crossing times for the two responses. Non-decision time (*Ter*) incorporates processing delays associated with sensory encoding and motor execution. The simulated response time is the sum of the diffusion process and the non-decision time. 1(b). The LBA assumes that evidence accumulation for different choice alternatives occurs in separate and independent accumulators (allowing for the modelling of multi-alternative decisions, by simply increasing the number of integrators). The evidence for each decision is integrated as a separate total, and the various totals (two in the case of Fig. 1B) race against each other. The ultimate choice is dependent on which of the integrators reaches its threshold first. The LBA shares the majority of its parameters with the DDM, but is different in that, while drift rate variability is included, within-trial noise is not. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

as predicted by the general slowing hypothesis [5], but rather impacts on certain aspects of sensory processing (see '*Aging and sensory encoding*' for further details).

3.1. Behavioural modelling: Summary and evaluation

In contrast to unitary explanatory accounts, such as the general slowing hypothesis, mathematical modelling studies of decision making point to a more multifaceted view of cognitive aging by highlighting the important influence of altered decision making strategies as well as task-specific differences in evidence accumulation rates and task-independent increases in non-decisional processing times. Nevertheless, it is important to stress that the mathematical modelling literature on decision making in older age is still in relative infancy and several important phenomena await examination. For example, we still know very little about how computational indices of decision making are impacted by age-related differences in risk aversion, temporal discounting, valuation, and in the learning of stimulus probabilities (see Sparrow and Spaniol [38] for review). In addition, sequential sampling models come in many forms, often containing fundamentally different algorithmic elements, yet the studies conducted to date have implemented a single model variant in isolation. Studies that formally compare the relative ability of alternative models to quantitatively account for age-related changes in decision making behaviour have yet to be conducted.

A more fundamental point is that, while mathematical modelling techniques offer deeper insights into the impact of aging on decision making processes, there are limits on what can be gleaned from behavioural modelling alone. For instance, it is difficult to ascertain whether age-related differences in drift rate reflect differences in the way that sensory information is encoded, differences in the way that sensory information is readout at the level of decision formation, or differences in the recruitment of other supportive processes, such as attention. Similarly, neurophysiological studies are increasingly highlighting the multi-level nature of the brain's neural architecture for implementing even the most elementary sensorimotor decisions [18,26,39]. A behavioural modelling approach alone cannot necessarily disentangle the effects of aging on these distinct processing levels.

A more technical point concerns the use of scaling parameters in sequential sampling models. If all the parameters in the model are free to vary, there is an infinite number of possible parameter values with the result that the model cannot converge on a solution. To get around this issue, one parameter value must remain fixed and all other parameters are interpreted with respect to this scaling parameter. By convention, the parameter usually fixed in the DDM is within-trial noise [40]. However, the use of within-trial noise as a scaling parameter in aging research is complicated by the fact that there is ample psychophysical and neurophysiological research to suggest that a key consequence of aging is a significant increase in neural noise (see '*Aging and sensory encoding*'). Despite this, the vast majority of aging studies that have employed the DDM have fixed this within-trial noise parameter to be the same for the young and older groups, potentially leading to misleading estimates of the unconstrained parameters.

Relatedly, recent studies have suggested that the full DDM may be

more complex than required and that its power in identifying between-group effects can be enhanced by eliminating or constraining some of its parameters [41–43]; however, determining which parameters should be constrained is not straightforward. Analysis of the neurophysiological signals that reflect the key neural computations underpinning decision formation processes could provide a principled way of determining which model parameters should be constrained to be equal between age groups. Thus, as we will highlight in the following section, there is much to be gained from considering neurophysiological data alongside mathematical models.

4. Neurophysiological investigations of aging and decision making

While computational models demonstrate that sensorimotor transformations can be reduced to a one-dimensional computation, the reality is that the brain forms decisions within multi-layered, hierarchical networks that perform at least three essential processing steps: the encoding of sensory evidence, the translation of that evidence into a decision to act, and the implementation of that action. In the following sections we outline the psychophysical and neurophysiological studies that have examined the impact of aging on each of these components.

4.1. Impact of aging on decision signals

To date, there have been very few neurophysiological investigations that have explicitly examined the impact of aging on the decision formation stage of processing. In the only study of aging thus far to combine computational modelling with neurophysiological data, Forstmann et al. [13] examined relationships between age-related decline in decision boundary setting abilities and structural connectivity. In previous work involving a younger cohort, Forstmann et al. [44] had demonstrated that individuals who showed greater flexibility in adjusting their decision thresholds had stronger structural connections between the pre-SMA and striatum, consistent with the proposal that corticostriatal pathways serve to regulate the balance between risky and cautious response styles [45,46]. As previously mentioned, Forstmann et al. [13] had found that elderly participants exhibited a diminished capacity for flexibly adjusting their decision bounds in the face of rapidly changing speed versus accuracy demands compared to younger participants. The same cohort exhibited a reduction in white matter integrity within this same pathway suggesting that age-related differences in decision policy adjustments do not purely reflect voluntary strategic preferences but likely arise, at least in part, from a structural limitation of the aging brain.

While techniques such as functional magnetic resonance imaging (fMRI) are well-suited to pinpointing spatial locations associated with perceptual tasks, the comparatively poor temporal resolution of such methods means that they can provide only limited insight into the dynamic evolution of neural signals across time. It is only within the last ten years that electrophysiological signatures of evidence accumulation have been identified in the human brain (e.g. [47–52]). These signals have been shown to exhibit the same decision-predictive dynamics observed in single-unit recordings [14] including a gradual build-up whose rate is inversely proportional to the difficulty of the perceptual task (consistent with evidence accumulation) and a fixed amplitude immediately prior to the decision report (consistent with a threshold-crossing effect). These decision signals fall into two functionally distinct categories: effector-selective signals that reflect the translation of cumulative sensory evidence into a specific action plan (e.g. [27,48–50]) and a domain-general signal, known as the centro-parietal positivity (CPP), that traces cumulative evidence irrespective of the particular sensory or motor demands of the task [49–51,53].

While aging effects on these signals have yet to be directly examined in the context of the evidence accumulation tasks typically employed in research on perceptual decision making (e.g. random dot motion discrimination), it has recently been demonstrated that the CPP is functionally equivalent to the classic P300 or 'P3b' potential [54] which has been extensively studied in research on aging (e.g. [55–57]). The P300 is one of the most robust psychophysiological markers of aging [58] and age-related pathologies such as Alzheimer's Disease [59]. Studies with large normative samples spanning the lifespan show that P300 amplitude decreases and its peak latency increases linearly from adolescence to senescence [55,60]. In addition, the aging process is reliably associated with a marked anterior shift in P300 topography that has been proposed to arise from the compensatory activation of frontal regions [61,62]. The P300 and CPP have been shown to share the same polarity, topography, relationship with response time, and contingency on goal-relevance [49,50] but while the P300 is typically evoked using tasks involving discrete, briefly presented stimuli and short response times, the CPP has typically been examined in the context of tasks that involve difficult perceptual detections or discriminations that require relatively long periods of deliberation. Nevertheless, when Twomey et al. [54] analysed data from a classic oddball paradigm they found that, if aligned to the timing of response execution, the P300 exhibited the same build-to-threshold dynamics as the CPP.

If the P300 traces the evolution of a decision then the observation that its peak latency is delayed in older adults could point to a delay in decision formation as a contributing factor in their slowed response times. Meanwhile, the decrease in its peak amplitude could indicate that older adults set lower boundaries on the quantity of evidence required to commit to a decision. This latter result is clearly at odds with the findings from numerous computational modelling studies which consistently report elevated decision boundaries in older age. However, there are several potential explanations for this apparent discrepancy that will need to be explored. First, as already mentioned, the tasks used to elicit the P300 in aging research are markedly different to those employed in mathematical modelling studies. Consequently it is unclear whether these modelling and electrophysiological results are genuinely discrepant or if age-related influences on decision making manifest differently across these paradigms. Ultimately, studies that measure behavioural and neural indices of decision formation within the same paradigm will be required. Second, the P300 is typically measured in terms of its peak amplitude in stimulus-aligned averages. If the P300 does indeed index the decision formation process then its stimulus-aligned peak amplitude and latency will increase in inverse proportion to response time variability. In other words, between condition or group differences in stimulus-locked P300 amplitude can potentially arise purely from differences in RT dispersion in the absence of any change in amplitude at the single-trial level (for illustration see Fig. 2C of Twomey et al. [54]). These concerns can be potentially addressed by analyzing response-aligned amplitudes or single-trial peak measurements. It is noteworthy, however, that one study, which did correct for trial-to-trial variations in peak latency when measuring P300 amplitudes, still found reduced amplitudes in older versus younger adults [63]. A third concern is that the rapid stimulus onsets that are typically used to elicit the P300 also evoke a number of other spatially and temporally overlapping components, several of which are known to be affected by aging. Amongst these is the occipito-parietal N1 component which has been consistently found to increase with age (e.g. [50,64]) and could contribute to smaller parietal P300 amplitudes. Recent work has shown that decision signals can be better isolated via pattern classification techniques (e.g. [52,65]) and by avoiding sudden stimulus changes or intensity transients (e.g. [49,51]).

4.2. Aging and sensory encoding

Our ability to make accurate perceptual decisions is heavily dependent on the quality of sensory evidence entering the decision process. Accordingly, when assessing the effects of aging on perceptual decision making, it is also important to consider how aging affects sensory processing. As outlined above in *Modelling age-related changes in*

decision making behaviour, computational modelling studies suggest that the degree to which aging impacts the quality of sensory information entering the decision process is highly dependent on the task at hand and that this task dependency speaks against the idea that senescence simply leads to a general slowing of information processing. Consistent with this view, psychophysical studies suggest that although some aspects of visual perception are compromised by normal aging, other visual abilities are spared (reviewed in [66–68]). For instance, examples of perceptual tasks that appear to remain intact throughout adulthood include orientation discrimination [69], contrast discrimination of suprathreshold stimuli [70,71], blur perception [72,73] and colour perception [74,75]. On the other hand, visual acuity [76], spatial and temporal contrast sensitivity [77–79], motion perception [80,81], binocular vision [82] and visual processing speed [5,66] have all been shown to decline with age.

While some of these impairments may be attributable to changes in the eye, optical factors alone cannot fully explain the extent of these sensory deficits [83–85]. Indeed, single-unit recordings in senescent monkeys and cats suggest that age-related impairments are the result of changes in the response characteristics of neurons located in a number of early visual regions. These studies have shown that although the effects of aging in the lateral geniculate nucleus (LGN) are minor [86], neurons in primary visual cortex (V1; [87,88]), visual area V2 [89] and the middle temporal area (MT; [90]) are subject to a variety of functional changes with age. These changes include reduced orientation and direction selectivity, higher rates of spontaneous neural activity and decreased signal-to-noise ratios [87,90,91]. Moreover, subsequent studies have linked these results from animal neurophysiology to the age-related perceptual deficits observed in humans through simulations from simple models of sensory processing. For instance, Bennett et al. [81] developed a model of motion processing, consisting of a population of evenly distributed directionally-selective mechanisms, to simulate motion detection and discrimination performance in young and older adults. While the model could successfully recreate performance for both tasks and age groups, a substantial increase in internal noise was required to reproduce the older group's data. As previously mentioned (see '*Modelling age-related changes in decision making behaviour*'), evidence of increased neural noise in older age is problematic for sequential sampling models of perceptual decision making, which typically fix within-trial noise as a scaling parameter that cannot vary between age groups.

While there is good agreement between different animal neurophysiology studies regarding the effects of age on sensory encoding, the findings across human neuroimaging studies have been less consistent. One controversy, for example, surrounds whether the structure of early visual cortex is affected by aging and whether any such changes can account for the behavioural effects reported in psychophysical studies. Whereas some structural magnetic resonance imaging (MRI) studies report prominent age-related atrophy in primary visual cortex (e.g. [92,93]), other research suggests that occipital areas are largely preserved from the effects of age (e.g. [94,95]). Similar discrepancies exist in the results of fMRI studies, with some suggesting that there are no age-related changes in the size of V1 (e.g. [96]), while others indicate significant changes in areal size (e.g. [97]). One consistent finding, however, is that of lower blood-oxygen-level-dependent (BOLD) activity in the foveal representation of V1 in older adults compared to their younger counterparts [96,98]. Furthermore, using fMRI population receptive field modelling methods [99], Brewer and Barton [98] revealed an increase in the population receptive field size in the same foveal region in older adults and suggested that these neural changes may contribute to well-established effects of aging on vision, such as impairments in visual acuity and reduced contrast sensitivity at high spatial frequencies [77,100].

Elsewhere, numerous studies have examined the effects of age on early sensory-evoked potentials of the electroencephalogram (EEG). Consistent with the age-dependent increase in non-decision times reported by the DDM, the majority of these studies have reported an increase in the latencies of early visual evoked potentials with age, suggestive of delays in early sensory processing ([64,101–105]; but see [106]). Surprisingly, however, many of these studies have also reported that older adults exhibit significantly *larger* signal amplitudes than younger individuals. The functional significance of these changes remain unclear and their interpretation is complicated by the fact that the precise functional role of these signals has yet to be established. In particular, it is not known to what degree these signals index the quality of the sensory evidence on which the decisions are actually based versus task-irrelevant stimulus features. The presentation of any stimulus is likely to elicit a range of sensory signals, many of which may be irrelevant to the task at hand. The key defining characteristics that distinguish sensory evidence signals from other sensory activity is that they co-vary with a decision-relevant stimulus feature and also that they predict the timing and/or accuracy of the observer's choices in a stimulus-independent fashion. A challenge for future work will be to examine the impact of aging on such sensory evidence signals (see Kelly and O'Connell [18] for further discussion).

4.3. Aging and motor processes

A variety of age-related changes in the motor domain have been documented which could potentially account for some of the age-associated variance in performance on perceptual and cognitive tasks. A consistent finding in this literature is that older adults are slower and more variable in movement initiation and execution (e.g. [28,107–112]). In addition, older people perform more poorly on tasks that require trajectory corrections [113], inhibition of primed motor plans in favour of novel ones [114], and utilise slower and more variable force when executing motor responses relative to younger participants [115].

Several studies have examined age-related changes in non-invasive electrophysiological signatures of motor-level processing including contralateral mu and beta frequency band (11–33 Hz) desynchronisation (e.g. [116,117]), the lateralized readiness potential (LRP), which indexes preparation of unilateral hand or arm movements (e.g. [118–120]), the contralateral movement-related potential (MRP) which reflects the final stages of cortical response activation (e.g. [102,121]) and electromyography (EMG) which indexes the activation of the response executing muscle (e.g. [115]). This work has demonstrated that older adults have stronger movement-related mu/beta desynchronisation than younger groups [122,123] as well as increased MRP amplitudes [102]. Despite previous research indicating that older adults have more variability in their force output during voluntary motor responses (e.g. [124]), neither EMG activity nor response force differed between age groups in the studies of Falkenstein et al. [103] and Yordanova et al. [102]. Sosnoff and Newell [115] obtained similar findings, with a group of 20 year olds showing similar levels of force variability to a group of 60 year olds, although significant reductions in EMG activity were observed in a group of 70 year olds. Taken together these results suggest that older individuals may require greater cortical motor processing in order to execute a given movement, consistent with fMRI findings indicating that older adults show increased and more widespread activation of contralateral primary motor cortex during performance of a simple, voluntary motor response task [125].

Several studies have also presented evidence that motor preparation may be initiated more slowly with age. Falkenstein et al. [103] found that the onset latencies of both the LRP and MRP were delayed in older relative to younger adults as was the onset latency of the MRP. Yordanova et al. [102] observed no differences in LRP onset but did observe MRP delays. The MRP delays were only apparent on a choice reaction task and not in a simple reaction task suggesting that these motor processing differences arise from a functional dysregulation of motor processes, rather than a fundamental neurobiological one [102].

Thus the literature highlights a number of age-related changes in

motor preparation and execution. Precisely how these changes impact on decision making behaviour has yet to be determined. One obvious impact of deficient processing at the motor-level would be to introduce a longer delay between the time that commitment is reached and the execution of the decision-reporting action, which in mathematical modelling studies would manifest as an increase in the non-decision time parameter. However, neurophysiological data indicate that evidence accumulation dynamics are also apparent in brain regions involved in motor preparation [27,51,126], suggesting that motor-level changes have the potential to impact on decision accuracy as well as response times. A further consideration is that, given the hierarchical nature of decision networks, certain changes in motor processing might in fact reflect the knock-on consequences of changes at upstream processing levels. These uncertainties underscore the need for studies that can simultaneously probe multiple levels of the sensorimotor hierarchy and that link neurophysiological changes to changes in behaviour.

4.4. Neurophysiological studies: Summary and evaluation

Neurophysiological studies of the aging brain highlight significant changes at each of the processing levels considered above. Very little work has yet been done to directly examine neural signatures of evidence accumulation in older age, but research on the P300 strongly indicates that there are prominent aging effects at this processing level. Research on sensory processing highlights modality-dependent aging effects which tally with cognitive modelling studies reporting task-dependent effects on drift rate. Aging effects have also been consistently reported at the level of motor preparation, but more research will be required to determine the degree to which these differences reflect altered processing at the level of motor processing or the consequence of alterations at upstream processing levels. In particular, the above review underlines the need for aging research to apply mathematical models in tandem with neural recordings to enable age-related changes in neural activity to be linked to specific computations underpinning decision formation.

5. Outstanding questions

Decision making mechanisms do not operate within a vacuum but rather are heavily dependent on the support of other brain systems. Age-related changes in these systems could potentially contribute to decision making deficits, or alternatively these systems could be recruited to compensate for and mask deficits in core components of the decision network. For example, most perceptual decision making experiments involve performance of many trials and thus place emphasis on the participant's ability to sustain goal-directed attention over time. The capacity to maintain vigilance over the duration of a trial (even one lasting a relatively short amount of time), or to maintain this vigilance over the course of a whole experiment is known as sustained attention, and is heavily dependent on the functioning of the frontal lobes [127–129], a region known to be disproportionately affected by aging. However, research on sustained attention in older age has yielded inconsistent results with some studies showing a decline in these abilities with age [130,131], and other studies showing no change [132,133], or even an improvement [134]. One complicating factor in synthesising these results is the variation in the tasks used across studies. Age-related decrements in sustained attention may only manifest under certain conditions. For example, a review by Zanto and Gazzaley concluded that age-related deficits in attentional engagement do become apparent under higher levels of task difficulty [135]. There is also some evidence to suggest that sustained attention may undergo a more rapid decline after the age of 70 [136]. Given the tendency to employ difficult perceptual tasks in research on decision making, further investigation of the behavioural influence of age-related differences in attentional engagement will be necessary.

A recent study has also indicated that target selection mechanisms play a far more general role in facilitating perceptual decisions than previously thought. Loughnane et al. [137] isolated an early target selection signal whose amplitude predicted the onset and rate of evidence accumulation signals. This relationship was observed even when sensory evidence was presented at an already attended location (e.g. coherent dot motion at fixation) and in the absence of any distracting information. Several studies have reported that target selection signals are delayed and attenuated in older adults [138,139] suggesting that target selection mechanisms are also affected by the aging process which may have knock-on consequences for evidence accumulation processes.

Another understudied question is how aging impacts on the ability to monitor and evaluate decisions i.e. metacognition, a highly important faculty for detecting errors and optimizing decision policies. No consensus has yet been reached on the precise mechanisms underlying metacognition in general (for a review see Yeung and Summerfield [140]), however, recent reports suggest that aging impacts on conscious error detection rates (e.g. [141]) and post error slowing [142], highlighting that further research is required in this area.

Finally, it has yet to be determined whether the performance of older adults in highly simplified laboratory-based perceptual decision making tasks correlates with decision making behaviour in real world settings. Do poorer perceptual decision making abilities under experimental settings indicate reduced functioning more generally?

6. Conclusions

The last two decades have witnessed substantial advances in our understanding of the neural principles and processes that enable decision making which have yielded a powerful set of experimental scenarios, mathematical models, and neural signals for probing the distinct components of decision making. Although still at a relatively early stage, research on perceptual decision making is providing important new insights into the manner in which natural aging impacts on cognitive functioning. The results discussed above illustrate that aging effects on choice behaviour are multifaceted and likely reflect a combination of strategic differences and compensatory adjustments, as well as information processing decrements at distinct levels of the sensorimotor hierarchy. However, there are many fundamental questions remaining to be addressed regarding the impact of aging on decision making and we highlight some prominent examples in the section above. There is also a clear dearth of studies that seek to draw correspondences between mathematical models and neural data. A key goal for future work, therefore, is to assess how decision-relevant signals in older adults differ from those measured in younger adults and to identify correspondences between these age-related differences and those derived from modelling studies. Together, these techniques will help to determine the key adaptations that occur in perceptual decision making with advancing age.

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