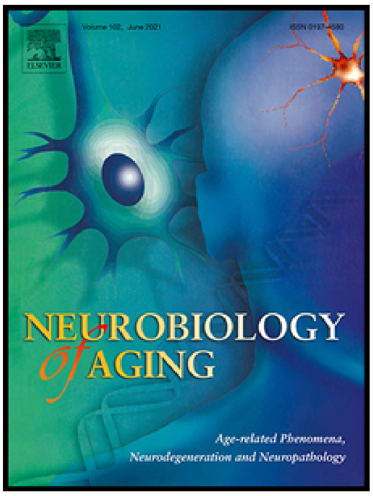
Journal Pre-proof

Neural regions associated with gain-loss frequency and average reward in older and younger adults

Hilary J. Don , Tyler Davis , Kimberly L. Ray , Megan C McMahon , Astin C. Cornwall , David M. Schnyer , Darrell A. Worthy



PII: S0197-4580(21)00305-5
DOI: https://doi.org/10.1016/j.neurobiolaging.2021.10.001
Reference: NBA 11258

To appear in: *Neurobiology of Aging*

Received date: 17 November 2020
Revised date: 4 October 2021
Accepted date: 5 October 2021

Please cite this article as: Hilary J. Don , Tyler Davis , Kimberly L. Ray , Megan C McMahon , Astin C. Cornwall , David M. Schnyer , Darrell A. Worthy , Neural regions associated with gain-loss frequency and average reward in older and younger adults, *Neurobiology of Aging* (2021), doi: https://doi.org/10.1016/j.neurobiolaging.2021.10.001

Highlights

- Choice in reward task better modeled by gain-loss frequency than average reward
- Older adults maintain suboptimal choices based on reward frequency
- Younger adults show greater activation in OFC related to average reward
- Older adults show greater frequency-based activation in DLPFC
- Similar brain regions sensitive to average and frequency-based prediction error

Neural regions associated with gain-loss frequency and average reward in older and younger adults

Hilary J. Don[1,*], Tyler Davis[2], Kimberly L. Ray[3], Megan C McMahon[3], Astin C. Cornwall[1], David M. Schnyer[3], & Darrell A. Worthy[1]

[1]Texas A&M University

[2]Texas Tech University

[3]University of Texas at Austin

[*]Correspondence concerning this article should be addressed to Hilary J. Don, who is now at Division of Psychology and Language Sciences, University College London, 26 Bedford Way, Bloomsbury, London WC1H 0AP, United Kingdom. h.don@ucl.ac.uk

Abstract

Research on the biological basis of reinforcement-learning has focused on how brain regions track expected value based on average reward. However, recent work suggests that humans are more attuned to reward frequency. Furthermore, older adults are less likely to use expected values to guide choice than younger adults. This raises the question of whether brain regions assumed to be sensitive to average reward, like the medial and lateral PFC, also track reward frequency, and whether there are age-based differences. Older (60-81 years) and younger (18-30 years) adults performed the Soochow Gambling task, which separates reward frequency from average reward, while undergoing fMRI. Overall, participants preferred options that provided negative net payoffs, but frequent gains. Older adults improved less over time, were more reactive to recent negative outcomes, and showed greater frequency-related activation in several regions, including DLPFC. We also found broader recruitment of prefrontal and parietal regions associated with frequency value and reward prediction errors in older adults, which may indicate compensation. The results suggest greater reliance on average reward for younger adults than older adults.

Keywords: decision-making; expected value; aging; compensation; model-based FMRI

Introduction

Decisions in every-day life often involve choosing amongst multiple options that each have potential for positive or negative outcomes. For example, deciding which stocks to invest in, which school to send your children to, or which property to buy all come with the possibility of good and bad outcomes. Making optimal choices is assumed by many researchers to require an estimation and comparison of the expected value (EV) of alternative choice options (Edwards, 1954; Rangel et al., 2008; Samanez-Larkin and Knutson, 2015). Several studies have found that, compared to younger adults, older adults are less sensitive to differences in EV, or less reliant on EV to make decisions (Brand & Markowitsch, 2010; Brand & Schiebener, 2013; Deakin, Aitken, Robbins, & Sahakian, 2004, Weller et al., 2011). For example, Weller, King, Figner and Denburg (2019) found that older adults were less likely to base decisions on expected value than younger adults in a risky decision-making task. Older adults used only a subset of information, adapting their choices based on probability information (presented as frequencies of losses), but not on the magnitude of gains and losses.

These declines in value-based decision-making performance appear to be due to changes in executive function and working memory (Li et al., 2001; Salthouse, 2004), changes in associated cognitive control regions in the lateral PFC (Braver et al., 2001; Sharp, Scott, Mehta, & Wise, 2006) as well as structural declines in striatal regions (Bäckman et al., 2006, Li et al., 2001) that are associated with processing reward (Hare et al., 2008; Pagnoni et al., 2002; Chowdhury et al., 2013). Age related changes may also be present in orbitofrontal cortex (OFC; Resnick, Lamar, & Driscoll, 2007), and the lateral OFC has been implicated in suppression of previously rewarded responses (Elliott, Dolan, & Frith, 2000).

Most prominent models of reinforcement learning assume that EV is based on the average reward provided by each option (e.g., delta models; Rescorla & Wagner, 1972; Widrow & Hoff, 1960; Williams, 1992). Extensive work on the role of prefrontal and striatal brain regions in value-based choice has focused on how these regions track average reward using predictions from these reinforcement learning models (Blair et al., 2006; Daw et al., 2006; Elliot, Dolan & Frith, 2000; Hare et al, 2008; Pagnoni et al., 2002; Pessiglione et al., 2006). However, there are many contexts in which people use sources of information other than average reward to inform their expectations (Estes, 1976; Einhorn & Hogarth, 1981). For example, people are often sensitive to the relative frequency of positive versus negative outcomes (e.g., Pang, Blanco, Maddox & Worthy, 2017). People also prefer choice options that have been frequently rewarded, even if they have lower average reward than an alternative (Don, Otto, Cornwall, Davis & Worthy, 2019). These results highlight the need to potentially re-evaluate the neural architecture of value-based decision making, to determine whether similar areas are involved in tracking reward frequency and average reward, and how people's ability to use these aspects of reward history in decision making change as a function of healthy aging.

The current study therefore aimed to investigate the neural regions associated with value-based decision-making in older and younger adults using model-based fMRI. We will compare a typical Delta rule model, which bases expected values on recency-weighted average rewards provided by each option, with the Prediction Error Decay (PE-Decay) model, which tracks the cumulative number of positive (rewards are greater than expected) versus negative (rewards are less than expected) prediction errors. Throughout this paper, we will use the term average reward to refer to the net amount of reward provided by each choice option, and gain-loss frequency to refer to the number of gains versus losses provided by each choice option. Options that provide a greater net reward will have higher average value than options that provide a smaller net reward overall. Options with a greater number of gains than losses will have higher frequency value than options with a greater number of losses than gains. While typically EV has been used to refer to average value, here, we assume expected values can be based on either average value (AV) or frequency value (FV), depending on the model.

Separating average reward and gain-loss frequency

One task that neatly dissociates average reward from gain-loss frequency, and thus can be useful for isolating these computations using neuroimaging, is the Soochow Gambling Task (SGT; Chiu et al., 2008). The SGT is an experience-based decision-making task in which participants choose between four decks of cards that each have different schedules of earning and losing points, where the goal is to maximize rewards received. The SGT was designed to tease apart the confounds of average reward and reward frequency in the Iowa Gambling Task (IGT; Bechara et al., 1994; 1997). In the IGT, healthy adults initially tend to prefer the high-gain-high-loss (bad) decks, but soon learn to choose the more advantageous low-gain-low-loss (good) decks. In the IGT, both good and bad decks provide a similar number of gains, but the good decks provide fewer losses. Thus, the good decks have both higher average reward and better gain-loss frequency relative to the bad decks, making it unclear which factor is responsible for improved performance across the IGT in healthy adults (Lin, 2007; Chiu et al., 2008). Some studies have found impaired IGT performance in older adults relative to younger adults (Beitz, Salthouse & Davis, 2014; Denburg, Tranel & Bechara, 2005; Fein, McGillivray, & Finn, 2007; Isella et al., 2008; Rogalsky et al., 2012), while others have shown equivalent performance, but using different strategies (Lamar & Resnick, 2004; MacPherson, Phillips, & Della Sala, 2002; Wood, Busemeyer, Koling, Cox, & Davis, 2005). It is yet to be determined whether similar results are found in the SGT.

The reward schedule for each deck in the SGT is shown in Table 1. Decks A and B are "bad decks" according to average reward, as they lead to long-term negative payoffs (-500 over 10 card draws). Decks C and D are "good decks", as they lead to long-term positive payoffs (+500 over 10 card draws). However, the bad decks provide small gains on 80% of trials, and large losses on 20% of trials, while the good decks provide small losses on 80% of trials, and large gains on 20% of trials. Optimal performance in this task therefore relies on participants using long-term payoffs to guide their choices. Healthy participants typically perform poorly in this task, continuing to prefer the bad decks, suggesting their decisions are guided more by gain-loss frequency than average reward (Chiu et al, 2008; Lin et al, 2009). This is further supported by work demonstrating that reinforcement learning models provide better fits to IGT and SGT data when using decay-reinforcement updating rules, which base expected value on reward frequency, than delta-reinforcement updating rules, which base expected value on average reward (Ahn et al., 2008; Dai et al., 2015).

Table 1

Reward schedule for 10 trials of the Soochow Gambling Task.

	Bad decks		Good decks	
Draw from deck	Deck A	Deck B	Deck C	Deck D
1	200	100	-200	-100
2	200	100	-200	-100
3	200	100	-200	-100
4	200	100	-200	-100
5	-1050	-650	1050	650
6	200	100	-200	-100
7	200	100	-200	-100
8	200	100	-200	-100

9	200	100	-200	-100
10	-1050	-650	1050	650
Net payoff	-500	-500	500	500

Responsivity to recent events in older adults

In addition to the issue of reward frequency versus average reward, there is evidence that older adults are more responsive or reactive to recent events (Besedes, Deck, Sarangi, & Shor, 2012; Castel, Rossi, & McGillivray, 2012; Eppinger and Kray, 2011; Eppinger et al., 2011), particularly recent negative events. Older adults are more likely to switch choices following large losses or negative prediction errors than younger adults (Worthy et al., 2015; Worthy et al., 2016). They are also more likely to use a "win-stay-lose-shift" (WSLS) heuristic, in which choices are based only on the outcome of the previous trial. That is, choices are repeated if they provided reward on a previous trial, and switched if they were unrewarded (Worthy & Maddox 2012; Worthy, Otto & Maddox, 2012). In comparison, younger adults are more likely to use a recency-weighted[1] average of past rewards to guide choices (Worthy & Maddox 2012; Worthy, Otto & Maddox, 2012). In the IGT, older adults give greater weight to recent outcomes and show greater forgetting of past outcomes (Wood et al., 2005). Older adults also appear to display a loss frequency bias, showing a preference for options with a lower frequency of punishment (Beitz et al., 2014; MacPherson et al, 2002). Thus, younger adults may perform better in the SGT, and older adults may show more reactive choices, with a greater tendency to switch choices following losses. The use of simpler, reactive decision making strategies in older adults may compensate for deficits in

[1] In reinforcement learning models, recency-weighting is typically determined by a free parameter that determines how much influence recent outcomes have on value updating.

sensitivity to long-term average reward. However, the precise neural and computational mechanisms associated with age-related differences in decision-making are still unclear.

Neural regions associated with value-based decision-making

The SGT is a useful task for re-evaluating how reward frequency and average reward information are represented in regions of the brain associated with value-based decision making. The ventral striatum is known to track average reward, and prediction errors based on average reward (Schultz, 2002; Hare et al., 2008; Rangel et al., 2008; Worthy et al., 2016, Pagnoni et al., 2002; Pessiglione et al., 2006). It is less certain whether these areas also track reward frequency information, and prediction errors produced by models that base value on gain-loss frequency. We might also expect activation in the lateral PFC to be related to frequency information, as it is thought to be involved in resolving conflicting information in cases of higher uncertainty (see Kahnt, Heinzle, Park, & Haynes, 2011; Schonberg, Fox, & Poldrack, 2011; Worthy et al., 2016), due to its more general role as a center for cognitive control (Koechlin, Ody, and Kouneiher, 2003; Badre and D'esposito, 2009; Breukelaar et al., 2017). Good decks, which yield losses more frequently, should be associated with more conflict, as they go against participants' preferences for more frequent reward, and so we would expect lateral PFC to be negatively associated with reward frequency value. Finally, OFC is involved in controlling and suppressing responses to previous outcomes, and has been shown to be active following negative feedback (O'Doherty et al., 2001).

Neural compensation in older adults

Several studies have found evidence of increased activation in lateral and inferior prefrontal brain regions for older adults relative to younger adults in a variety of cognitive tasks. These prefrontal regions are often associated with executive function, and can be recruited adaptively to meet task demands. An increase in activation in these regions is suggested to compensate for age-related neural decline that may otherwise affect task performance (Cabeza, 2002; Cabeza et al, 2002; 2004; Cappell et al., 2010; Park & Reuter-Lorenz, 2009; Phillips & Andres, 2010; Reuter-Lorenz & Cappell, 2008; Reuter-Lorenz et al, 2000). Such compensatory activation should therefore be associated with improvement in task performance (Cabeza et al., 2002; 2018). There is also evidence of increased parietal activation in older adults in cognitively demanding tasks (e.g. DiGirolamo et al., 2001; Jimura & Braver, 2010, Nielson, Langenecker, & Garavan, 2002; Nielson et al., 2004; Vallesi, McIntosh, & Stuss, 2011; Zhu, Zacks, & Slade, 2010, Heuninckx, Wenderoth, Debaere, Peeters, & Swinnen, 2005; Heuninckx, Wenderoth, & Swinnen, 2008, Langenecker, Nielson, & Rao, 2004; Prakash et al., 2009; Zysset, Schroeter, Neumann, & Yves von Cramon, 2007). Huang, Polk, Goh & Park (2011) showed that this increase in activation serves a compensatory function, as it was associated with improved performance in resolving interference. We therefore also assessed whether there is evidence of compensation in older adults during the decision-making task.

Study aims

To summarize, the current study had three main aims, 1) to determine whether brain areas associated with average reward are also associated with reward frequency, 2) to assess whether there are age-based differences in activation that reflect age-based differences in decision making strategies, and 3) to determine whether there is evidence of compensation in either prefrontal or parietal regions in older adults. To achieve these aims, we used fMRI combined with model-based analyses to examine the neural bases of decision-making in older and younger adults while performing the SGT. The models value options based on average reward (Delta model) or gain/loss frequency (PE-Decay model), and are described in detail below. In a model-based fMRI analysis approach, reinforcement learning models are first fit to the behavioral data. Model-derived components such as EVs and prediction errors are then used as regressors in order to identify brain regions whose activity is associated with those components. The benefit of this approach over traditional fMRI is that it provides a theoretically grounded way of interpreting fMRI data, as it allows us to identify *how* cognitive processes are represented in specific brain regions, rather than simply identifying where in the brain these processes occur (O'Doherty, Hampton & Kim, 2007; Glascher & O'Doherty, 2010). Based on previous work, if average reward and gain-loss frequency rely on similar brain areas, we would expect greater activation in the ventral striatum and PFC regions involved in value-based decision making, as well as greater prediction error related activation in the striatum (Hare et al., 2008; Rangel et al., 2008; Samanez-Larkin et al., 2014; Worthy et al., 2016).

We expected that older adults would engage in more reactive decision-making behavior than younger adults. That is, older adults would be more likely to base their choices on the outcome they received on the previous trial, whereas younger adults would be more likely to base their choices on expected values integrated across a longer sequence of prior outcomes. This would be evident if older adults have a greater tendency to switch choices following losses and stay following rewards. We may observe differences in neural activation associated with expected value and prediction errors in older and younger adults. We also examined whether there is evidence for broader recruitment of prefrontal and parietal regions in older adults compared to younger adults, and whether this is associated with improved task performance, which would provide evidence of compensation.

Materials and methods

Participants

Healthy younger and older adults were recruited from the Austin, Texas area as part of a larger project, including a sleep study. Some method details are related to aspects of this larger project, but are not important for the study reported here. The study was advertised through posters, online forums, and recruitment events at aging conferences and senior recreation centers. Candidate participants were invited to participate in the study if they met the following inclusion criteria: 1) endorsed fewer than 8 items on the Pittsburgh Sleep Quality Inventory (PSQI), 2) endorsed fewer than 16 items on the Center for Epidemiological Studies Depression Scale (CESD) or fewer than 15 items on the Geriatric Depression Scale (GDS), 3) did not meet criteria for significant sleep disturbance or disorder, cardiovascular disease, and/or neurological or psychiatric disorders, and 4) were not currently taking sleep medication or psychoactive substances. Candidate participants were administered a neuropsychological battery assessing executive function and memory, and those who scored greater than two standard deviations from the age-adjusted norm were excluded from the study. Performance of older and younger adults in these assessments are reported in the Supplemental Materials.

The data from fifty-three older adults (*mean age* = 67.7, *SD* = 5.58, range: 60-81, 38 female) and 50 younger adults (*mean age* = 21.3, *SD* = 3.5, range: 18-30, 28 female) were analyzed. Three additional participants were recruited but were excluded from the analyses for not meeting the neuropsychological assessment criteria (1), or incomplete SGT data sets (2). Participants were compensated for their participation in the study. Ethical approval was received from The University of Texas at Austin Institutional Review Board and prior written consent was obtained from all participants.

Neuropsychological assessments

All candidate participants were administered an abbreviated neuropsychological battery, including the Wechsler Adult Intelligence Scale IV (WAIS-IV) Vocabulary and Digit Span subtest, Trail Making Test A and B, and Psychomotor Vigilance Test. Older adults were additionally administered the California Verbal Learning Test-II (CVLT-II) and Controlled Oral Word Association Test (COWAT-FAS).

Procedure

Enrolled participants were administered a neuropsychological battery comprising assessments designed to test executive function and memory and a psychomotor vigilance task to measure arousal and attention. Eligible participants first completed a sleep study for 10 days, which is not of interest to the current study. Following this period, participants underwent MRI scanning, during which T1w structural images and functional images were collected.

MRI acquisition

Imaging data were collected using a Siemens Skyra 3T scanner (TIM Systems, Siemens Medical Solutions, Erlangen, Germany) with a 32-channel head coil at the Biomedical Imaging Center at The University of Texas at Austin. Anatomical MRI volumes were acquired for co-registration with functional data using a 3D Multi-echo MPRAGE T1-weighted (T1w) sequence with the following parameters: TR=2530.0 ms, TE=1.69, 3.55, 5.41, and 7.27 ms, T1=1100 ms, FOV=256 mm^2, 176 coronal slices, voxel size 1.0 mm^3. Participants viewed the stimuli via a back project screen and a mirror mounted on top of the head coil and responded with two four-button MR-compatible optical transmission devices, one held in each hand. Functional gradient echo EPI images were collected during two runs of the SGT task (TR = 1500 ms, TE = 30ms, 65 axial slices oriented for best whole head coverage, acquisition voxel size = 2 x 2 x 2 mm^3, FOV 220x200 mm).

Behavioral Task

Participants completed two 50-trial scanning runs of the SGT. The reward structure for each option is shown in Table 1. Participants were instructed that they would repeatedly select from one of four decks of cards, and that they could gain or lose points on each draw. They were given 2000 points to begin, and their goal was to try to finish with at least 2500 points. Participants were told to do their best to maximize their gains and minimize their losses. On each trial, four colored rectangles representing decks of cards were presented horizontally aligned on the screen (See Figure 1), accompanied with the prompt “PICK A CARD”. The point goal and the point total were presented on the right side of the screen. Participants selected a deck by pressing a corresponding number key. If participants responded within 2 s, this was followed by a variable fixation, feedback presented for 2 s, and a variable inter-trial interval (ITI). During feedback, the selected deck was presented in white, with the number of points gained or lost displayed on the card. Gains were presented in black text, and losses presented in red text. If participants responded slower than 2 s, the fixation was replaced with the instruction “You must respond sooner” and the feedback screen displayed only the point goal and total.

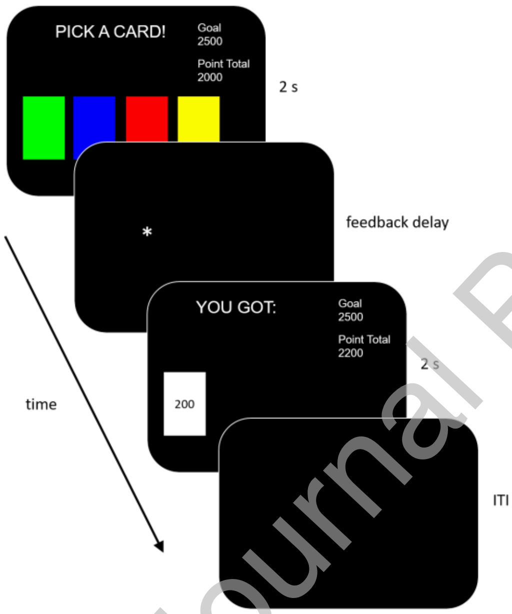


Figure 1. Schematic of the trial structure of the Soochow Gambling Task. Participants selected a card by pressing a corresponding key. This was followed by a variable delay before presenting feedback. The selected card was presented in white, and the number of points gained or lost were displayed on the card. The point goal and point total were displayed throughout the entirety of the task on choice and feedback screens. There was a variable inter-trial interval (ITI). If participants did not select a card within 2000 ms, the fixation screen was replaced with “You must respond sooner”, and no card was shown on the feedback screen.

Models

We fit participants' behavioral data with two reinforcement learning models, a Delta model, and a PE-Decay model, in order to dissociate expected values that were computed based on average reward and expected values based on the frequency of positive versus negative outcomes. The Delta model (Rescorla & Wagner, 1972; Widrow & Hoff, 1960; Williams, 1992) updates expected values based on prediction error: the difference between what was expected and what was received in a given instance. Delta model expected values will therefore approximate the average reward associated with each option.

Delta model. Expected values in the delta rule model are calculated as:

$$AV_j(t+1) = AV_j(t) + \alpha \cdot (r(t) - AV_j(t)) \cdot I_j \tag{1}$$

where I_j is an indicator value that is set to 1 if option j is selected on trial t, and 0 otherwise. Rewards (r) are the points earned on trial t. Prediction error is represented by the portion of Equation 1 in parentheses, and is modulated by a learning rate parameter $(0 \leq \alpha \leq 1)$. Higher values of α indicate greater weight to recent outcomes, while lower values indicate less weight to recent outcomes. When α = 0 no learning takes place and expected values remain at their starting points, and when α = 1 expected values are equal to the last outcome received for each option. The predicted probability that option *j* is chosen on trial t is calculated using a Softmax rule:

$$p\left|C_j(t)\right| = \frac{e^{\beta \cdot AV_j(t)}}{\sum_1^{N(j)} e^{\beta \cdot AV_j(t)}} \tag{2}$$

where $\beta = 3^c - 1$, and $(0 \leq c \leq 5)$ is a log inverse temperature parameter that determines how consistently the option with the higher expected value is selected (Yechiam & Ert, 2007). Lower values of *c* provide more random choices, and as c increases the option with the highest expected value is selected most often. Defining β in this way allows it to take on a very large range of values (0-242), and is equivalent to setting a prior on beta with a truncated exponential distribution.

PE-Decay model. The PE-Decay model tracks the cumulative instances of positive and negative prediction errors, and does not consider the magnitude of rewards or losses. The PE-Decay model used here is similar to that used in Pang et al. (2017). In the PE-Decay model, a prediction error (PE) is first computed as the difference between the reward given on trial t, *r(t)*, and the expected value for the chosen option, *i*:

$$PE = r(t) - EV_i(t) \tag{3}$$

The prediction error is then used to update expected values for each j option on trial t+1:

$$EV_j(t+1) = EV_j(t) + \alpha \cdot PE \cdot I_j \tag{4}$$

Here, $(0 \leq \alpha \leq 1)$ is a learning rate parameter, where higher values indicate greater weight to more recent events. *I* is a dummy variable coded as 1 if the option was chosen, or 0 otherwise, such that only expected values for the chosen option is updated. Note that EV is updated in the same way as AV in the Delta model, but expected value is only used to determine if the prediction error is positive or negative. Frequency value (FV) is then updated and incremented based on expected value and prediction error:

$$FV(t+1) = \begin{cases} FV(t) \cdot (1-\alpha) + 1, & \text{if } PE > 0 \\ FV(t) \cdot (1-\alpha) - \lambda, & \text{if } PE < 0 \end{cases} \tag{5}$$

Such that FV would increment by 1 if prediction errors were positive, and would decrease by a loss aversion parameter $(0 \leq \lambda \leq 5)$ if prediction errors were negative. The inclusion of this parameter allows losses to have either more or less of an effect than gains. The PE-Decay model therefore simply tracks the cumulative instances of positive and negative prediction errors, and does not consider the magnitude of rewards or losses. That is, a loss of 100 points will be treated in the same way as a loss of 1,000 points. Frequency value is modulated by a decay rate parameter, $(1-\alpha)$. Having the decay rate represented as $(1-\alpha)$ allows for alpha to be interpreted similarly to learning rate in the Delta model, where higher values of α indicate a higher rate of decay, and therefore greater weight to more recent events. Choice probabilities are calculated by entering FVs into the Softmax rule.

$$p\left|C_j(t)\right| = \frac{e^{\beta \cdot FV_j(t)}}{\sum_1^{N(j)} e^{\beta \cdot FV_j(t)}} \tag{6}$$

fMRI Processing and Analysis.

Pre-processed data (Esteban et al., 2018) were analyzed using a standard three-level general linear model (GLM) analysis implemented in FSL's FEAT. The first-level models tested the effect of task-related variables within single functional runs. All task related models included constant EVs for the effect of choice and feedback parts of a trial and nuisance regressors for the 6 realignment parameters and their temporal derivatives. Trial-by-trial model-based measures were included in first-level models as parametric modulators of choice (for AV and FV) and feedback (for PE). For prediction errors from the PE-Decay model, we took the difference between the reward received and the frequency value from Equation 5 on each trial. Although the PE-Decay model uses prediction errors from a Delta rule to determine how to update frequency-value representations, we regressed neural activation on prediction errors based on the difference between reward and FV so that these prediction errors would be distinct from delta-model prediction errors. However, these prediction errors were strongly correlated with the delta model's prediction errors because in both cases, rewards that were positive tended to elicit positive prediction errors, and rewards that were negative tended to elicit negative prediction errors.

Five separate first-level models were run: one with average value and frequency value simultaneously modeled as modulators of choice, one model where each of average value and frequency value were modeled separately as modulators of choice, and two models where PE from each model were modeled separately as modulators of feedback. Second level models averaged effects of task variables across individual runs within each participant using a fixed effects model. Third-level models tested whether task variables were significant across participants using a mixed effects model for population inference. Final statistical maps were corrected for multiple comparisons at $p < .05$ using a Gaussian Random Field Theory-based correction with a primary (cluster-forming) threshold of $z = 3.1$ ($p = .001$, one-tailed).

Results

Behavioral results

We examined younger and older adults' performance on the SGT. Younger adults missed responding on 4% of trials, and older adults on 8% of trials. Optimal choices (proportion of C and D deck choices) across four 25-trial blocks of the SGT are shown in Figure 2a. Performance was analyzed with a 2 (age group) x 4 (block) mixed measures ANOVA. There was a significant linear effect of block, $F(1,101) = 12.28$, $p = .001$, $\eta^2_p = .108$, indicating an increase in optimal choices as the task progressed. There was no significant main effect of age group, $F(1,101) = .015$, $p = .903$, $\eta^2_p < .001$. However, there was a significant interaction between age group and the linear effect of block, $F(1,101) = 10.56$, $p = .002$, $\eta^2_p = .095$. To further examine this interaction, we separately assessed the effect of block for each age group. There was a significant linear effect of block for younger adults, $F(1,49) = 14.54$, $p <. 001$, $\eta^2_p = .229$, but this effect did not reach significance for older adults, $F(1,52) = 0.066$, $p = .799$, $\eta^2_p = .001$. This indicates that younger adults learned to select the optimal options more frequently as the task progressed, whereas older adults did not show much improvement.

To examine whether older adults were more reactive decision-makers than younger adults, we compared the probability of staying based on the preceding outcome. We estimated a mixed-effects model using the brms package in R (Bürkner, 2017; 2018) to predict the probability of repeating the same choice (p(stay)), based on the outcome of the previous trial, and age group. A higher probability of staying indicates greater repetition of the same choice, and a lower probability of staying indicates greater switching. Across all participants, there was a higher probability of staying when the previous trial had a higher reward (*B* = 0.002, odds ratio = 1.002; 95% CI = [0.001, 0.003]), suggesting that participants tended to continue selecting decks that yielded a higher reward on the previous trial. Younger adults were also more likely to stay than older adults (*B* = 0.57, odds ratio = 1.775, 95% CI = [0.19, 0.92]). There was also an interaction between previous outcome and age group, indicating a greater reactivity to the previous outcome in older adults than younger adults (B = -0.001, odds ratio = 0.999, 95% CI = -0.002, -0.0007). Examining Figure 2b, it appears that older adults were less likely to stay following larger losses than younger adults, and, to a lesser extent, more likely to stay following larger gains.

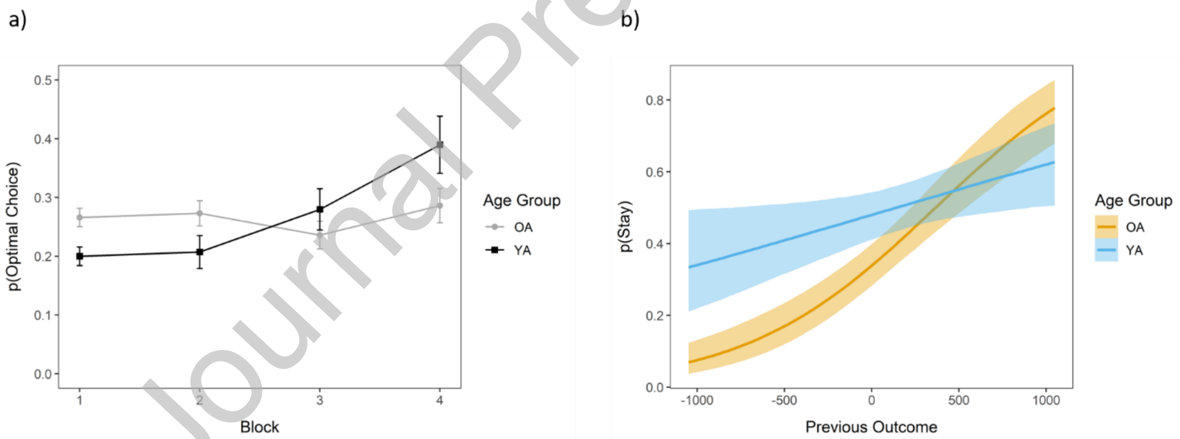


Figure 2. a) Mean optimal choices across four 25-trial blocks of the Soochow Gambling Task for older and younger adults. Younger adults (YA) show an improvement in optimal choices across the duration of the task, while older adults (OA) maintain suboptimal choices. b) Probability of stay choices based on the outcome on the previous trial for younger adults (YA) and older adults (OA).

Modeling results

We focused on the comparison of Delta and PE-Decay models in order to dissociate expected values that were computed based on average rewards and expected values based on the frequency of positive and negative outcomes. The Delta model represents a more optimal strategy, as it bases expected values on the average payoffs provided by each option. The PE-Decay model represents a sub-optimal strategy, in which only the frequency of gains and losses is considered, and magnitude of gains and losses is ignored. The AVs and FVs produced by these models were not highly correlated within-subjects (r = .003, p = .738, see Supplemental Material for example correlations for several participants), and are therefore ideal as regressors for fMRI analyses.[2]

We fit each model to each individual participant's data by maximizing the log-likelihood of the model's next step ahead predictions, and used Bayesian Information Criterion (BIC; Schwarz, 1978) to compare model fits. Overall, the PE-Decay model provided a much better fit than the Delta model (ΔBIC = 40.08). From the behavioral data, it is clear that participants did not use the more optimal strategy represented by the Delta model. Figure 3 shows simulated optimal choices predicted by each model. The Delta model predicts a preference for the good decks that emerges quickly, while the PE-Decay model predicts persistent choice of the bad decks. For the Delta model, the best-fitting parameter for learning rate (α) was higher for older adults (.67) than younger adults (.37), indicating a greater weight to recent outcomes in older adults. The same pattern was not evident in best-

[2] For consistency with previous research, we also fit two versions of the Prospect Valence Learning (PVL) model, using both a delta-reinforcement updating rule (PVL-delta) and a decay-reinforcement updating rule (PVL-decay). These models did not fit the data as well as the PE-Decay model, and the EVs produced by the PVL-Decay model were more highly correlated with the AVs produced by the Delta model than the FVs produced by the PE-Decay model.[2] The fits of these models are therefore reported in the Supplementary Material, but are not included as regressors in the fMRI analyses. The reason we did not compare the PVL-Decay model to the PVL-Delta model is that both of these models have a shape parameter that allows for exponential discounting of reward magnitudes. This means both models can account for choice behavior that is driven only by the frequency of reward provided by each option, and not the magnitude. The basic Delta model does not have a shape parameter, and the magnitude of past rewards is not discounted. This makes the basic Delta model a valuable comparator against models that assume that the magnitude of rewards is discounted, and choices are based primarily on the frequency of gains versus losses.

fitting decay rate parameters (older adults .39, younger adults .43). However, older adults were more loss averse (mean λ = 2.05) compared to younger adults (mean λ = 1.29), $t(101) = 2.10$, $p = .038$, $d = .413$. See Supplementary Material for a full table of best-fitting parameter values.

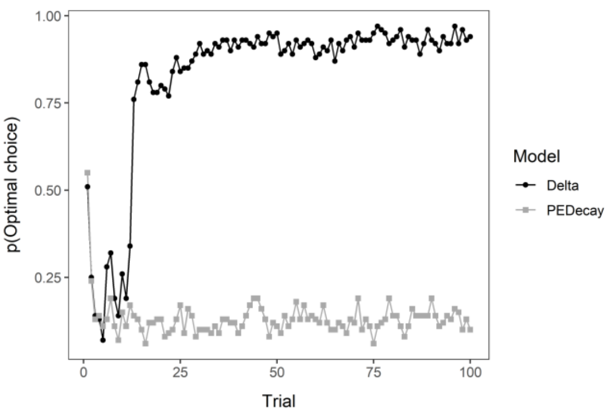


Figure 3. Simulated optimal choices across the SGT predicted by the Delta model and PE Decay model. The Delta model very quickly prefers the optimal decks after a large loss, while the PE Decay models predicts persistent choice of the suboptimal decks.

Model-based fMRI analysis

For each model, we computed expected values for the chosen option, as well as prediction errors (the difference between outcomes received and the expected value), using each model's best-fitting parameters. When expected values were used as regressors, we took the difference in expected value between the chosen and unchosen decks, such that it reflects expected value for the chosen deck, relative to the unchosen decks. In the Delta model, expected value will reflect the recency weighted average reward provided by each option. In the PE-Decay model, expected value will reflect the gain-loss frequency provided by each option. Activation correlated with expected value and prediction errors from each model are reported below. For all results, we first present activation associated with Delta model regressors, as this is the prominent model in the literature, followed by activation associated with PE-Decay model regressors. For each regressor, we analyzed correlations with activation for younger adults alone, older adults alone, for younger adults greater than older adults, and for older adults greater than younger adults. Only significant correlations are reported. Tables of regions of activation are presented in the Supplemental Material.

Expected value activation

To assess activation uniquely associated with each model's expected values, we entered both as regressors in the fMRI regression model simultaneously. Note that the results are very similar when EVs for each model were entered into separate regression models (see Supplementary Material).

Delta model AV related activation. In the Delta model, expected value will be higher for the good decks than the bad decks. Figure 4A-D shows regions of activation associated with Delta AVs. As the Delta model represents the more optimal strategy, these are the regions that are most active when selecting the optimal options. In younger adults (Figure 4A), Delta model AVs were associated with activation in the right and left orbital frontal cortex (OFC), operculum cortex and the insula, regions involved in decision-making. There was also associated activation in motor/pre-motor regions, including the precentral and post-central gyrus, and supplementary motor cortex. Younger adults showed greater activation in the left precentral and postcentral gyrus than older adults (Figure 4C).

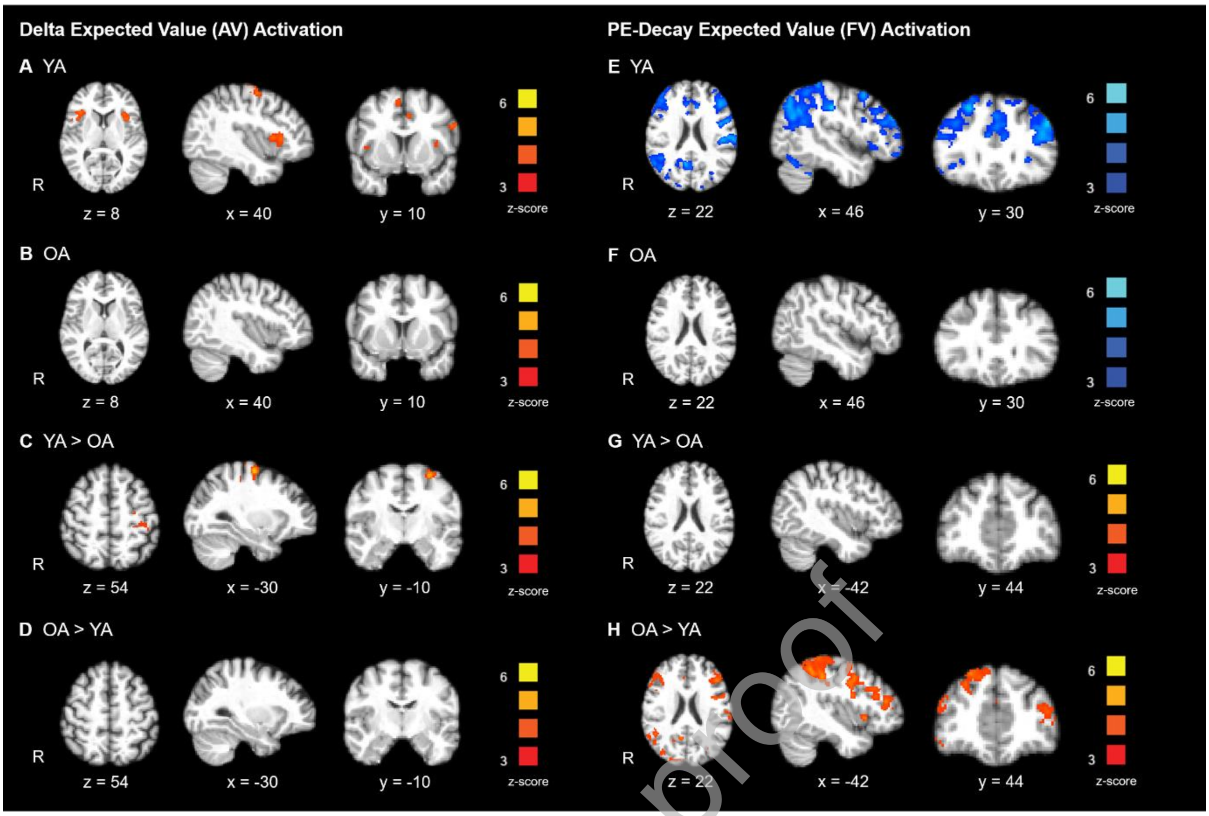


Figure 4. Activation correlated with expected values. Panels A-D show activation correlated with expected values from the delta model. Panels E-H show activation correlated with expected values from the PE-Decay model; panels A and E indicate regions of activation for younger adults, Panels B and F indicate regions of activation for older adults; panels C and G indicate regions of activation that were greater for younger adults than older adults; and panels D and H indicate regions of activation that were greater for older adults than younger adults. Blank brains indicate there were no significant regions of activation.

PE-Decay model FV related activation. In the PE-Decay model, expected values will be lower for the good decks than the bad decks, as the good decks provide more frequent losses than gains. Figure 4E-H shows activation correlated with expected values from the PE-Decay model. Younger adults showed greater activation in frontoparietal regions, which are associated with cognitive control, when PE-Decay expected value was low. Thus, these regions were active in younger adults when they were selecting from the good decks.

Figure 4H shows regions where PE-Decay model EV related activation was greater for older adults than younger adults. Older adults showed greater bilateral activation in the DLPFC, and greater activation in the right and left frontal pole, left inferior frontal gyrus, insula, and OFC than younger adults. As older adults did not have any significant activation alone for this regressor, and younger adults showed negative correlations in these areas, this might simply mean that older adults are not engaging cognitive control for good decks as younger adults are.

Prediction error related activation

Prediction errors produced by the Delta and PE-Decay models were substantially overlapping, $r = .85$, $p < .001$ (see Supplemental Material for correlations between the models' prediction errors for several participants). Regions of activation associated with Delta model prediction errors are shown in Figure 5A-C , and PE-Decay model prediction errors in Figure 5E-H. In younger adults, for both Delta and PE-Decay prediction errors, there was activation in the ventral striatum (caudate, nucleus accumbens and putamen), which are regions typically found to be activated in response to prediction error (Rodriguez, Aron, & Poldrack, 2006). There was also activation in the precentral and postcentral gyrus.

For PE-Decay prediction error, there were significant correlations for younger adults > older adults, and older adults > younger adults. There was greater bilateral activation of nucleus accumbens in younger adults than older adults (Figure 5G). In older adults, there was greater activation in more lateral PFC and posterior parietal regions compared to younger adults (Figure 5H), indicating that older adults may not be tracking prediction error as well as younger adults in the ventral striatum. This activation in lateral posterior parietal cortex also correlated with optimal responding in the task within older adults (Figure 6). Regions of activation that were greater for older adults than younger adults were similar to those associated with PE-Decay model expected values, including right DLPFC, bilateral OFC and insula. This is consistent with the idea that older adults are using short-term, working memory strategies to remember which options recently led to positive versus negative prediction errors, while activation in the ventral striatum in younger adults indicate that they are using prediction errors to update long-term expected values.

Figure 7 shows activation negatively correlated with prediction error from the Delta model. Younger adults showed a similar pattern of deactivation in frontoparietal areas with increasing prediction error to that seen with PE-Decay expected value. There was greater left nucleus accumbens activation in younger adults than older adults.

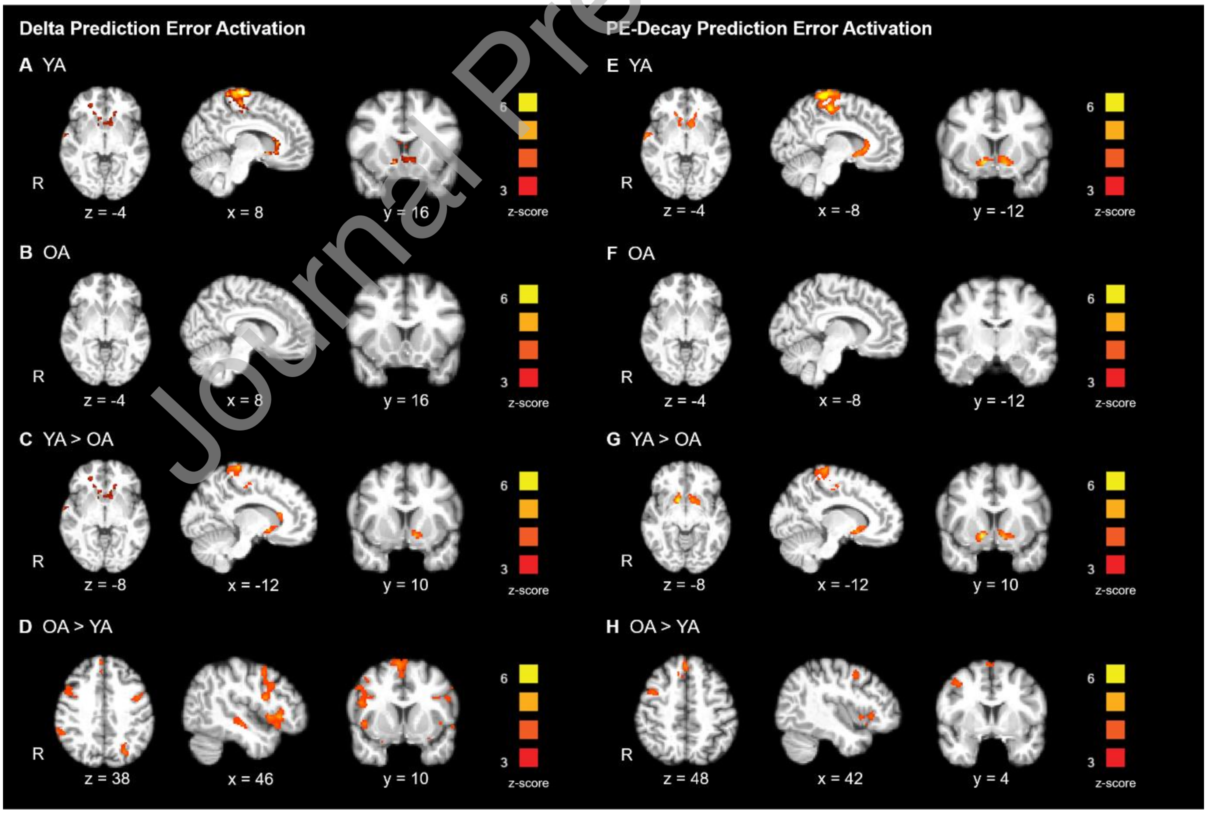


Figure 5. Activation correlated with prediction error. Panels A-D show activation correlated with prediction error from the delta model. Panels E-H show activation correlated with

prediction error from the PE-Decay model; panels A and E indicate regions of activation for younger adults, Panels B and F indicate regions of activation for older adults; panels C and G indicate regions of activation that were greater for younger adults than older adults; and panels D and H indicate regions of activation that were greater for older adults than younger adults. Blank brains indicate there were no significant regions of activation.

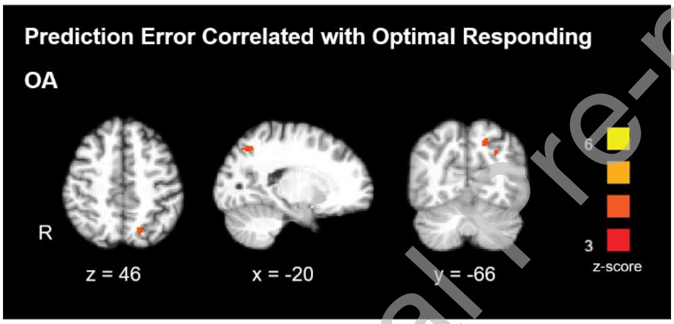


Figure 6. Prediction error related activation from the Delta model correlated with optimal responding

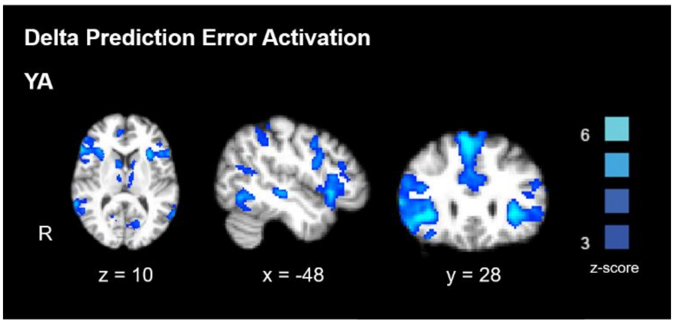


Figure 7. Negative correlation with prediction errors from Delta model for younger adults.

Discussion

The current study had three main aims. 1) to determine whether brain areas associated with average reward are also associated with gain-loss frequency, 2) to assess whether there are age-based differences in activation that reflect age-based differences in decision-making strategies, and 3) to determine whether there is evidence of compensation in either prefrontal or parietal regions in older adults. We will first discuss behavioral performance in the task, before discussing each of these aims.

Task performance

We compared performance of older and younger adults in a decision-making task that dissociates average reward from frequency of gains versus losses. Overall, participants performed poorly in this task, preferring the decks that provided small frequent gains but large infrequent losses, which resulted in a negative net payoff. However, younger adults showed an improvement in optimal choices across the duration of the task, while older adults maintained their preference for the sub-optimal decks. This pattern of results suggests that younger adults were better able to adjust their choices with experience based on average reward. Older adults appeared to be more reactive to recent outcomes than younger adults, and were more likely to switch their choices following losses than younger adults. This is in keeping with previous findings that older adults show greater avoidance of negative outcomes and greater focus on negative feedback (Eppinger, Hammerer, & Li, 2011; Eppinger & Kray, 2011; Frank & Kong, 2008; Hämmerer, Li, Muller, & Lindenburger, 2011; Simon, Howard, & Howard, 2010). The finding that healthy older adults are more sensitive to recent outcomes and continue to prefer the bad decks in the SGT suggests that gain-loss frequency is driving their decision-making. The best-fitting loss aversion parameters in the PE-Decay model were higher for older adults than younger adults, indicating that losses had greater relative influence on older adults than younger adults. Our results therefore indicate a difference in behavioral strategy between older and younger adults in the SGT, similar to those found in some studies of the IGT (Wood et al., 2005).

It is worth noting that there is good evidence that older adults tend to perseverate more on tasks such as the Wisconsin Card-Sorting Task (WCST; Ridderinkhof et al., 2002), and reversal learning tasks (Eppinger et al., 2011), which is seemingly incongruent with the finding that older adults are also more reactive in decision making tasks. Arguably, reversal learning tasks are more comparable to the current task than is the WCST. While poorer performance in reversal learning tasks by older adults could be due to greater perseveration, there is evidence that it may instead be due to greater randomness of choice (e.g., switching; Eppinger et al., 2011; Mell et al., 2005). Mell et al (2005) found that while older adults performed more poorly on reversal learning tasks, there was no significant difference in perseverative errors between older and younger adults. In addition, Vo et al. (2018) found that older adults showed a higher probability of switching after misleading error feedback in a reversal learning task, indicating a lose-shift response, which is in line with our findings that older adults are more reactive decision-makers.

The data from both younger and older adults in this task were better fit by the PE-Decay model than the Delta model. The PE-Decay model tracks the number of positive versus negative prediction errors, and will therefore value options with frequent gains more highly than frequent losses, such that it predicts suboptimal performance in the task. In contrast, the Delta model predicts more optimal performance based on average reward magnitude. The modeling results suggest that decisions were based more on the frequency of positive versus negative outcomes provided by each option, rather than the magnitude of outcomes, which resulted in poor performance in the task. This is consistent with previous research that shows the SGT is better fit by models that use decay updating rules (Ahn et al., 2008; Dai et al., 2015).

Neural activation associated with expected value and prediction error

To compare whether expected value based on average reward and gain-loss frequency engage similar brain regions, we will consider expected value-related activation for AV and FV in younger adults alone. Note that AV will generally be higher for good decks and FV will generally be higher for bad decks, but were uncorrelated. Overall, FV provided a better account of choice behavior, and thus we also see a broader range of choice-related regions associated with FV than those associated with AV.

Previous studies have found activation in the ventral striatum related to Delta model prediction errors (Blair et al., 2006; Daw et al., 2006; Elliot et al., 2000; Hare et al, 2008; Pagnoni et al., 2002; Pessiglione et al., 2006) which has been taken as tacit neurobiological support for the Delta model's assumptions and predictions about behavior. Here, we found that activation in the ventral striatum was associated with prediction errors produced by both the Delta model and PE-Decay model, which were highly correlated with each other. However, the expected values produced by the models were not strongly associated, and each model made distinct predictions about behavior in the SGT. Human behavior was more closely aligned with the predictions made by the PE-Decay model than those of the Delta model. Thus, the striatal activation related to Delta model prediction errors in previous studies does not necessarily support the idea that the Delta model is an accurate model of human decision-making. Instead, such activation may be indicative of prediction error related activation produced by applying a decay model. Support for computational models should therefore come from multiple sources, such as behavior, fMRI, and physiological responses as two models may be highly correlated on one metric such as prediction errors, but uncorrelated on another metric like expected value.

Differences between older and younger adults

Model-based fMRI analyses indicate differences in activation associated with expected values and prediction errors for older and younger adults. In younger adults, expected values based on average reward were associated with bilateral OFC, operculum cortex and insula, areas implicated in decision-making. OFC has been implicated in suppression or responses to previous outcomes, and this is consistent with younger adults' reduced reactivity to previous outcomes compared to older adults (Elliott et al., 2000).

Several regions showed greater activation associated with expected values based on gain-loss frequency for older adults than younger adults. Older adults showed greater activation in DLPFC associated with PE-Decay expected values than younger adults, which is consistent with prior studies in decision-making (Worthy et al., 2016). DLPFC is implicated in working memory (Cappell et al., 2010; Hillary et al., 2006; Park & Reuter-Lorenz, 2009), and is involved in accumulating information about past positive outcomes associated with each option (Lin et al., 2020; Philiastides et al., 2011; Teslovich et al., 2014). Thus, this pattern of activation might indicate that older adults are relying on short-term memory strategies, remembering which options led to gains and losses on recent trials, to guide their choices.

Younger adults showed a negative association between frontoparietal activity and both prediction error and PE-Decay model expected values. That is, there was greater activation in these regions when expected value and prediction error was low (the good decks, which have frequent losses). These regions are implicated in cognitive control, which could indicate that younger adults are using more controlled processes on these trials to select the good decks, even though they frequently provide losses resulting in negative prediction errors. Suppressing these negative prediction errors may have led to younger adults' better learning across the task, and less reactivity to recent events. This negative association, paired with the finding that OA have greater positive activation associated with FV in these areas than younger adults could indicate that older adults are using these controlled processes to a lesser extent than younger adults. Overall, it appears that younger adults use long-term expected value more than older adults, which requires averaging rewards over many trials, rather than heavily weighting prediction errors from the most recent trials.

Neural compensation in older adults

Prediction error activity differed between older and younger adults. We found evidence of broader recruitment of prefrontal and parietal regions in older adults than younger adults. Activation in parietal regions was associated with optimal responding in the task, providing further evidence that activation in this area serves a compensatory function in older adults (Huang et al., 2012). Cabeza and colleagues (2018) have argued that increased activation in older versus younger adults must correlate with better performance on the task for the activation to be considered age-related neural compensation. Based on that criterion the enhanced prediction error related activity in parietal regions in older adults may be considered compensatory because it was correlated with performance. This enhanced prediction-error related activation may have led some older adults to use prediction errors more effectively to learn the long-term average rewards associated with the different choice options.

While Cabeza et al.’s (2018) compensation criterion of improved performance may be useful in cases where optimal performance is clearly defined, it is not always easy to define optimal performance, particularly in decision-making tasks (Einhorn & Hogarth, 1982). For example, one could design a task where attending to frequent rewards is the optimal strategy. In that case older adults’ tendency to focus on frequency of reward more than younger adults might lead to broader activation of frontal parietal regions than younger adults as well as improved performance. We might interpret the increased activation in older adults related to implementing a frequency-based strategy as compensatory in that task, while in the current task we would not since attending to frequency is sub-optimal. Thus, older adults might be engaging in the same activation related to their strategy use, but whether it leads to improved performance is dependent on the optimal strategy in the task.

Stern and colleagues made a similar point, suggesting that Cabeza et al.’s notion of compensation is one of the many ways *cognitive reserve* can be implemented, and note that the success of compensation can be modulated by lifestyle variables. Compensation should arguably be viewed as the recruitment of a broader brain regions in the service of a cognitive strategy regardless of whether that strategy is actually successful or optimal. Model-based fMRI, similar to what we have conducted in this paper, may help identify the types of strategies that younger and older adults are using, and exactly what brain regions younger and older adults are recruiting to implement those strategies.

Future directions and conclusions

A key note to take from the current results is that studies that track one construct (like delta rule prediction errors) and find reliable concordance with activation in a particular region may give misleading confirmation that the model is correct. The finding that there is strong overlap with brain regions associated with Delta and PE-Decay prediction errors, but little correlation between model expected values, suggests that this approach may not paint an accurate picture, and that studies require evidence from multiple sources. Along with the previous studies, the results we report in the present study suggest that older adults are consistently more reactive to recent outcomes when making decisions. Whether this can be characterized as an age difference in strategy use with older adults employing a win-stay-lose-shift type strategy, changes in working memory capacity, or differences in in selective attention to different features of the task such as gain-loss frequency are questions that could be more directly examined in future studies. Many previous studies have focused only on one or a few metrics of performance such as optimal choices, but there has been extensive progress made in recent years on methods for reinforcement learning and mixed effects modeling, and these types of analyses can answer additional questions or corroborate conclusions based on other measures. Our behavioral, modeling and fMRI results suggest that older adults may have a tendency to focus mainly on the most recent outcomes, particularly recent losses. This tendency could be a common cause for suboptimal decision-making behavior as people age.

Verification

We confirm that this work has not been published previously, that it is not under consideration for publication elsewhere, that its publication is approved by all authors and by the responsible authorities where the work was carried out, and that, if accepted, it will not be published elsewhere in the same form, in English or in any other language, including electronically without the written consent of the copyright-holder.

Dr Hilary J Don

Acknowledgements

This work was supported by NIA grant AG043425 to DMS and DAW. The authors declare no conflicts of interest.

Author Statement

Hilary J. Don: Conceptualization, Formal Analysis, Visualization, Writing - Original Draft; **Tyler Davis:** Formal Analysis, Visualization, Writing - Review & Editing; **Kimberly L. Ray:** Investigation, Writing - Review & Editing; **M.C. McMahon:** Investigation, Writing - Review & Editing; **A.C. Cornwall:** Conceptualization, Methodology, Writing - Review & Editing; **D.M. Schnyer:** Conceptualization, Supervision, Writing - Review & Editing. **D.A. Worthy:** Conceptualization, Supervision, Formal Analysis, Writing - Review & Editing.

References

Blair, K., Marsh, A. A., Morton, J., Vythilingam, M., Jones, M., Mondillo, K., ... & Blair, J. R. (2006). Choosing the lesser of two evils, the better of two goods: specifying the roles of ventromedial prefrontal cortex and dorsal anterior cingulate in object choice. *Journal of Neuroscience, 26*, 11379-11386.

Braver, T.S., Barch, D.M., Keys, B.A., Carter, C.S., Cohen, J.D., Kaye, J.A., Janowsky, J.S., Taylor, S.F., Yesavage, J.A., && Mumenthaler, M.S. (2001). *Journal of Experimental Psychology: General,, 130*(4), 746-763.

Breukelaar, I.A., Antees, C., Grieve, S.M., Foster, S.L., Gomes, L., Williams, L.M., & Korgaonkar, M.S. (2017). Cognitive control network anatomy correlates with neurocognitive behavior: a longitudinal study. *Human Brain Mapping, 38*(2), 631-643.

Bürkner P (2017). brms: An R Package for Bayesian Multilevel Models Using Stan. *Journal of Statistical Software, 80*, 1–28.

Bürkner P (2018). Advanced Bayesian Multilevel Modeling with the R Package brms. *The R Journal, 10*, 395–411.

Cabeza, R., Albert, M., Belleville, S., Craik, F., Duarte, A., Grady, C., Lindenberger, U., Nyberg, L., Park, D., Reuter-Lorenz, P.A., Rugg, M., Steffener, J., & Rajah, M.N. (2018). *Nature Reviews Neuroscience, 19*(11), 701-710.

Cabeza, R., Anderson, N.D., Locantore, J.K., McIntosh, A.R. (2002). Aging gracefully: Compensatory brain activity in high-performing older adults. *NeuroImage, 17*, 1394-1402.

Cabeza, R. (2002). Hemispheric asymmetry reduction in older adults: The HAROLD model. *Psychology and Aging, 17,* 85-100.

Cabeza, R., Daselaar, S.M., Dolcos, F., Prince, S.E., Budde, M., & Nyberg, L. (2004). Task-independent and task-specific age effects on brain activity during working memory, visual attention, and episodic retrieval. *Cerebral Cortex, 14,* 364-375.

Cappell, K.A., Gmeindl, L., & Reuter-Lorenz, P.A. (2010). Age differences in prefrontal recruitment during verbal working memory maintenance depend on memory load. *Cortex, 46,* 462-473.

Chiu, Y. C., Lin, C. H., Huang, J. T., Lin, S., Lee, P. L., & Hsieh, J. C. (2008). Immediate gain is long-term loss: Are there foresighted decision makers in the Iowa Gambling Task?. *Behavioral and Brain Functions, 4,* 13.

Daw, N. D., O'Doherty, J. P., Dayan, P., Seymour, B. & Dolan, R. J. (2006). Cortical substrates for exploratory decisions in humans. *Nature*, *441*, 876–879.

D'Esposito, M., Postle, B. R., Ballard, D., & Lease, J. (1999). Maintenance versus manipulation of information held in working memory: an event-related fMRI study. Brain and cognition, 41, 66-86.

Don, H. J., Otto, A. R., Cornwall, A. C., Davis, T., & Worthy, D. A. (2019). Learning reward frequency over reward probability: A tale of two learning rules. *Cognition*, *193*, 104042.

Einhorn, H.J., & Hogarth, R.M. (1981). Behavioral decision theory: Processes of judgment and choice. *Annual Review of Psychology, 32*, 53-88.

Elliot, R., Dolan, R.J., & Frith, C.D. (2000). Dissociable functions in the medial and lateral orbitofrontal cortex: Evidence from human neuroimaging studies. *Cerebral Cortex, 10*, 308-317.

Eppinger, B., Hammerer, D., & Li, S.C. (2011). Neuromodulation of reward-based learning and decisionmaking in human aging. *Annals of the New York Academy of Sciences, 1235*, 1-17.

Esteban, O., Markiewicz, C. J., Blair, R. W., Moodie, C. A., Isik, A. I., Erramuzpe, A., ... & Oya, H. (2019). fMRIPrep: a robust preprocessing pipeline for functional MRI. *Nature methods, 16*, 111-116.

Estes, W.K. (1976). Some functions of memory in probability learning and choice behavior. In G.H. Bower (Ed.), *The Psychology of Learning and Motivation* (Vol. 10). New York: Academic Press.

Hare, T.A., O'Doherty, J., Camerer, C.F., Schultz, W., & Rangel, A. (2008). Dissociating the role of the orbitofrontal cortex and the striatum in the computation of goal values and prediction errors. *The Journal of Neuroscience, 28*, 5623-5630.

Hillary, F. G., Genova, H. M., Chiaravalloti, N. D., Rypma, B., & DeLuca, J. (2006). Prefrontal modulation of working memory performance in brain injury and disease. *Human brain mapping, 27*, 837-847.

Karayanidis, F., Whitson, L. R., Heathcote, A., & Michie, P. T. (2011). Variability in proactive and reactive cognitive control processes across the adult lifespan. *Frontiers in psychology, 2*, 318.

Li, S. C., Biele G., Lindenberger, U., & Sikstrom, S. (2001). Aging cognition: from neuromodulation to representation. *Trends in Cognitive Sciences, 5*, 97-111.

Lin, Z., Nie, C., Zhang, Y., Chen, Y., & Yang, T. (2020). Evidence accumulation for value computation in the prefrontal cortex during decision making. *Proceedings of the National Academy of Sciences, 117*, 30728-30737.

Mather, M. (2006). A review of decision making processes: Weighing the risks and benefits of aging. In L.L. Carstensen & C.R. Hartel (Eds.), When I'm 64: Committee on aging frontiers in social psychology, personality, and adult developmental psychology (pp. 145-173). Washington, DC: National Academic Press.

Mell, T., Heekeren, H.R., Marschner, A., Wartenburger, I., Villringer, A., & Reischies, F.M. (2005). Effects of aging on stimulus-reward association learning. *Neuropsychologia, 43*, 554-563.

Mohr, P.N.C., Li, S.C., & Heekeren, H.R. (2010). Neuroeconomics and aging: Neuromodulation of economic decision-making in old age. *Neuroscience and Biobehavioral Reviews, 34*, 678-688.

O'Doherty, J. P., Hampton, A., & Kim, H. (2007). Model- based fMRI and its application to reward learning and decision making. Annals of the New York Academy of sciences, 1104(1), 35-53.

O'Doherty, J. P., Kringelbach, M. L., Rolls, E. T., Hornak, J., & Andrews, C. (2001). Abstract reward and punishment representations in the human orbitofrontal cortex. *Nature neuroscience, 4*, 95-102.

Pagnoni G., Zink C. F., Montague P. R., and Berns G. S. (2002). Activity in the human ventral striatum locked to errors of reward prediction. *Nature Neuroscience, 5*, 97–98.

Park, D.C., & Reuter-Lorenz, P. (2009). The adapting brain: aging and neurocognitive scaffolding. *Annual Review of Psychology, 60,* 173-196.

Pessiglione, M., Seymour, B., Flandin, G., Dolan, R. J., and Frith, C. D. (2006). Dopamine-dependent prediction errors underpin reward seeking behavior in humans. *Nature, 442*, 1042–1045.

Philiastides, M. G., Auksztulewicz, R., Heekeren, H. R., & Blankenburg, F. (2011). Causal role of dorsolateral prefrontal cortex in human perceptual decision making. *Current biology, 21,* 980-983.

Phillips, L.H., & Andres, P. (2010). The cognitive neuroscience of aging: New findings on compensation and connectivity. *Cortex, 46*, 421-424.

Peters, E., Hess, T.M., Vastfjall, D., & Auman, C. (2007). Adult age differences in dual information processes: Implications for the role of affective and deliberative processes in older adults' decision making. *Perspectives on Psychological Science, 2,* 1-23.

Rangel, A., Camerer, C., & Montague, P.R. (2008). A framework for studying the neurobiology of value-based decision making. *Nature Reviews Neuroscience, 9,* 545-556.

Raz, N. (2000). *Aging of the brain and its impact on cognitive performance: integration of structural and functional findings*. In The Handbook of Aging and Cognition, ed. F. Craik, T.A. Satlhouse, pp. 1-90. Hilsdale, NJ: Erlbaum.

Raz. N., Linberger, U., Rodrique, K.M., Kennedy, K.M., Head, D., Williamson, A., Dahle, C., Gerstorf, D., & Acker, J.D. (2005). Regional brain differences in aging healthy adults: General trends, individual differences and modifiers. *Cerebral Cortex, 15,* 1676-1689.

Rescorla, R.A., & Wagner, A.R. (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and non-reinforcement. In A.H. Black & W.F. Prokasy (Eds.) *Classical conditioning II: Current research and theory.* New York: Appleton-Century-Crofts.

Resnick, S.M., Lamar, M., & Driscoll, I. (2007). Vulnerability of the orbitofrontal cortex to age-associated structural and function brain changes. *Annals of the New York Academy of Sciences, 1121,* 562-575.

Reuter-Lorenz, P.A., & Cappell, K.A. (2008). Neurocognitive aging and the compensation hypothesis. *Current Directions in Psychological Science, 17,* 177-182.

Reuter-Lorenz, P.A., Jonides, J., Smith, E., Hartley, A., Miller, A., Marshuetz, C., & Keoppe, R. (2000). Age differences in the frontal lateralization of verbal and spatial working memory revealed by PET. *Journal of Cognitive Neuroscience, 12,* 174-187.

Rodriguez, P.F., Aron, A.F., & Poldrack, R.A. (2006). Ventral-striatal/nucleus-accumbens sensitivity to prediction errors during learning. *Human Brain Mapping, 27,* 306-313.

Samanez-Larkin, G.R., Wagner, A.D., & Knutson, B. (2011). Expected value information improves financial risk taking across the adult life span. *SCAN, 6*, 207-217.

Schott, B.H., Niehaus, L., Wittman, B.C., Schutze, H., Seidenbecher, C.I., Heinze, H.J., & Duzel, E. (2007). Ageing and early-stage Parkinson's disease affect separable neural mechanisms of mesolimbic reward processing. *Brain, 130*, 2412-2424.

Shultz, W. (2002). Getting formal with dopamine and reward. *Neuron, 36 (2),* 241-263.

Sharp, D.J., Scott, S.K., Mehta, M.A., & Wise, R.J. (2006). The neural correlating of declining performance with age: Evidence for age-related changes in cognitive control. *Cerebral Cortex, 16*(12), 1739-1749.

Stern, Y. et al. (2019). Mechanisms underlying resilience in ageing. *Nature Review Neuroscience, 20,* 246.

Teslovich, T., Mulder, M., Franklin, N. T., Ruberry, E. J., Millner, A., Somerville, L. H., Simen, P., Durston, S., & Casey, B. J. (2014). Adolescents let sufficient evidence accumulate before making a decision when large incentives are at stake. *Developmental Science, 17,* 59-70.

Widrow, B., & Hoff, M.E. (1960). Adaptive switching circuits. *1960 WESCON Convention Record Part IV,* 96-104.

Williams, R.J. (1992). Simple statistical gradient-following algorithms for connectionist reinforcement learning. *Machine Learning, 8,* 229-256.

Worthy, D. A., Davis, T., Gorlick, M. A., Cooper, J. A., Bakkour, A., Mumford, J. A., Poldrack, R. A., & Maddox, W. T. (2016). Neural correlates of state-based decision-making in younger and older adults. *Neuroimage, 130,* 13-23.

Worthy, D.A., Gorlick, M.A., Pacheco, J.L., Schnyer, D.M., & Maddox, W.T. (2011). With age comes wisdom: Decision-making in younger and older adults. *Psychological Science*, *22*, 1375-1380.

Worthy, D. A., & Maddox, W. T. (2012). Age-based differences in strategy use in choice tasks. *Frontiers in neuroscience, 5*, 145.

Worthy, D. A., Otto, A. R., Doll, B. B., Byrne, K. A., & Maddox, W. T. (2015). Older adults are highly responsive to recent events during decision-making. *Decision, 2*, 27.

Worthy, D. A., Otto, A. R., Cornwall, A. C., Don, H. J., & David, T., (2018). A case of divergent predictions made by delta and decay rule learning models. In T. T. Rogers, M. Rai, X.

Yechiam, E., & Ert, E. (2007). Evaluating the reliance on past choices in adaptive learning models. *Journal of Mathematical Psychology*, *51*, 75-84.

Zhu, & C. W. Kalish (Eds.) Proceedings of the 40th Annual Conference of the Cognitive Science Society (pp.1175-1180). Madison, Wisconsin: Cognitive Science Society.