# Neural Representations of Gain-Loss Frequency in Older and Younger Adults

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## 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. We scanned older and younger adults performing the Soochow Gambling task, which separates reward frequency from average reward. 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 lateral PFC. We also found broader recruitment of prefrontal and parietal regions in older adults, which may indicate compensation.


**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). 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). 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).

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 delta-like 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). This result highlights the need to potentially re-evaluate the neural architecture of value-based decision making – how they track reward frequency versus average reward – and how people's ability to use these aspects of reward history in decision making change as a function of healthy aging.

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 reward schedule for each deck 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 A and B, 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 Iowa Gambling Task (IGT; Bechara et al., 1994; 1997) 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).

The SGT may be useful for re-evaluating how frequency and average reward information are represented in regions of the brain associated with value-based decision making. For example, although the ventral striatum is known to track average reward, and prediction errors from average reward, it is less certain if and whether reward frequency information may affect value representations. Likewise, the lateral PFC is known to track uncertainty related to outcome variability (Kahnt, Heinzle, Park, & Haynes, 2011; Schonberg, Fox, & Poldrack, 2011), is involved in state change uncertainty signals (Worthy et al., 2016), and tracks individual differences in risk aversion (Christopoulos, Tobler, Bossaerts, Dolan, & Schultz, 2009). On a mechanistic level, the lateral PFC is thought to be involved in resolving conflicting information (e.g., outcome variability) in cases of higher uncertainty, 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). Finally, OFC is involved in controlling and suppressing responses to previous outcomes. Whether such control processes are primarily associated with average reward

or reward frequency remains an open question. Reward frequency tends to do a better job of predicting SGT behavior than average reward, and lateral PFC should thus be sensitive to people's use of frequency in decisions. Choices with lower frequency value (i.e., the good decks that yield losses more frequently) should also be associated with more conflict as they go against participants' preferences for more frequent reward, and thus we'd expect that lateral PFC would be negatively associated with frequency value.

In addition to the issue of reward frequency versus average reward, there is evidence that older adults are more responsive to recent events (Besedes, Deck, Sarangi, & Shor, 2012; Castel, Rossi, & McGillivray, 2012), 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 average of past rewards to guide choices (Worthy & Maddox 2012; Worthy, Otto & Maddox, 2012). Older adults are also more likely to use reactive, rather than proactive cognitive control (Karayanidis, Whitson, Heathcote & Michie, 2011). The use of simpler, reactive decision making strategies in older adults may compensate for deficits in sensitivity to long-term average reward. However, the precise neural and computational mechanisms associated with age-related differences in decision-making are still unclear.

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 |

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.

The current study therefore aimed to determine whether brain areas associated with average reward are associated with reward frequency, and to assess whether there are age-based differences in activation that reflect age-based differences in decision making strategies. We also aimed to determine whether there is evidence of compensation in either prefrontal or parietal regions in older adults. To achieve this aim, 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. 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. 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, we expected greater activation associated with expected values in the ventral striatum and PFC regions involved in value based decision making, as well as greater PE-related activation in the striatum (Hare et al., 2008; Rangel et al., 2008; Samanez-Larkin et al., 2014; Worthy et al., 2016).

# Results

## Behavioral results

Optimal choices (proportion of C and D deck choices) across four 25-trial blocks of the SGT are shown in Figure 1. Performance was analyzed with a 2 (age group) x 4 (block) mixed measures ANOVA. There was a significant linear effect of block, $F(1,101) = 14.52$, $p < .001$, $\eta^2_p = .126$, indicating an increase in optimal choices as the task progressed. There was no significant main effect of age group, $F(1,101) = .350$, $p = .555$, $\eta^2_p = .003$. However, there was a significant interaction between age group and the linear effect of block, $F(1,101) = 9.19$, $p = .003$, $\eta^2_p = .083$. 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 the younger adults, $F(1,49) = 14.19$, $p < .001$, $\eta^2_p = .225$, but this effect did not reach significance for the older adults, $F(1,52) = 0.724$, $p = .399$, $\eta^2_p = .014$. 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.

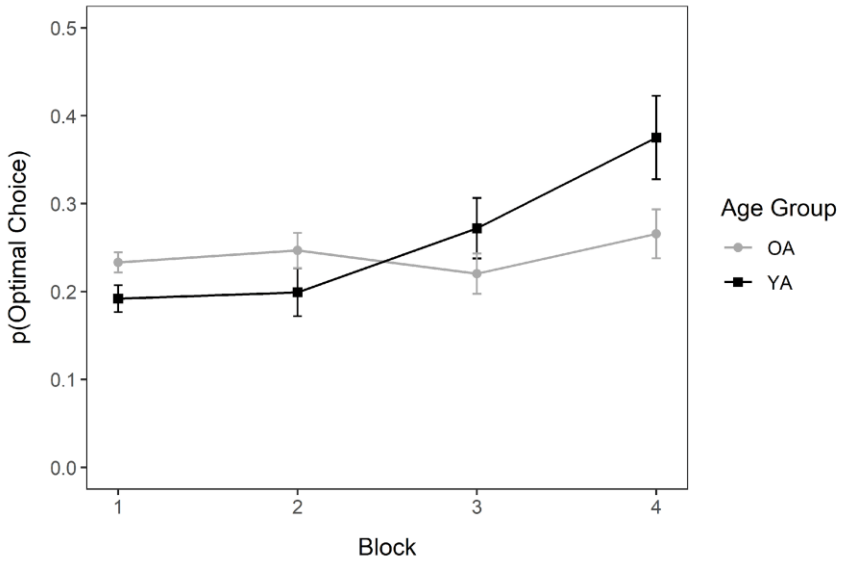


*Figure 1.* Mean optimal choices across four 25-trial blocks of the Soochow Gambling Task for older and younger adults. Younger adults (YA) show an improvement in optimal choices across the duration of the task, while older adults (OA) maintain suboptimal choices.

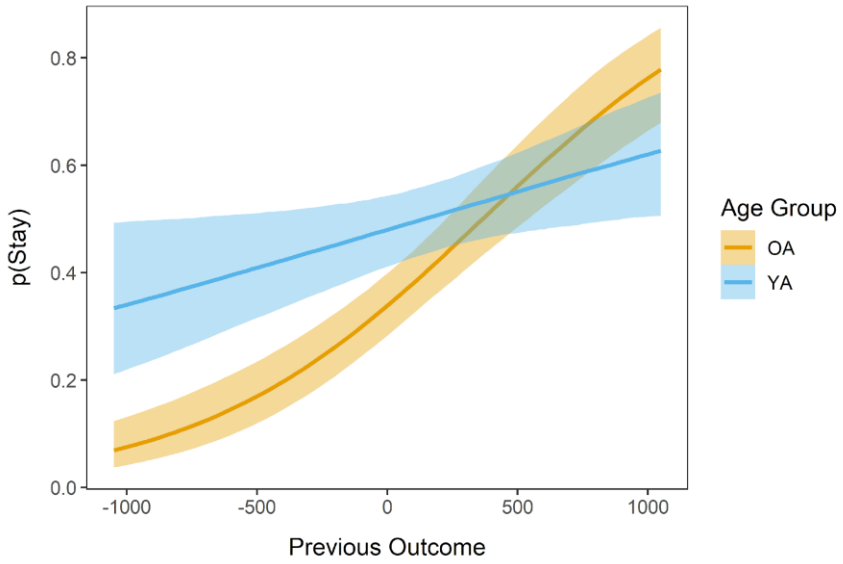


*Figure 2.* Probability of stay choices based on the outcome on the previous trial for younger adults (YA) and older adults (OA).

To examine whether older adults were more reactive decision-makers than younger adults, we compared the probability of staying and switching based on the preceding outcome. We hypothesized that, in general, participants would be more likely to stay if they received a reward on the previous trial, and would be more likely to switch if they experienced a loss. If older adults are more reactive decision-makers, they may be more likely to switch following losses than younger adults.

To assess this hypothesis we estimated a mixed-effects model using the brms package in R (Bürkner, 2017; 2018) to predict the probability of repeating the same choice (stay vs. switch), based on the outcome of the previous trial, and age group. There was an overall tendency to repeat choices that had higher reward on the previous trial ($B$ = 0.002, odds ratio = 1.002; 95% CI = [0.001, 0.002]). Younger adults were also more likely to repeat previous choices than older adults ($B$ = 0.67, odds ratio = 1.956, 95% CI = [0.23, 0.95]). There was also an interaction between previous outcome and age group, indicating a greater responsivity to the previous

outcome in older adults than younger adults (B = -0.001, odds ratio = 0.999, 95% CI = -0.002, -0.0006). Examining Figure 2, it appears that older adults were more likely to switch their previous choice following larger losses than younger adults, and, to a lesser extent, more likely to stay with the same option following larger gains.

**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 EVs produced by these models were not highly correlated within-subjects ($r$ = .003, $p$ = .738, see Figure 3), and are therefore ideal as regressors for fMRI analyses. For consistency with previous research, we also fit two versions of the 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 Delta model than the EVs produced by the PE-Decay model.[1] The fits of these models are therefore reported in the Supplementary Material, but are not included as regressors in the fMRI analyses.

[1] 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.

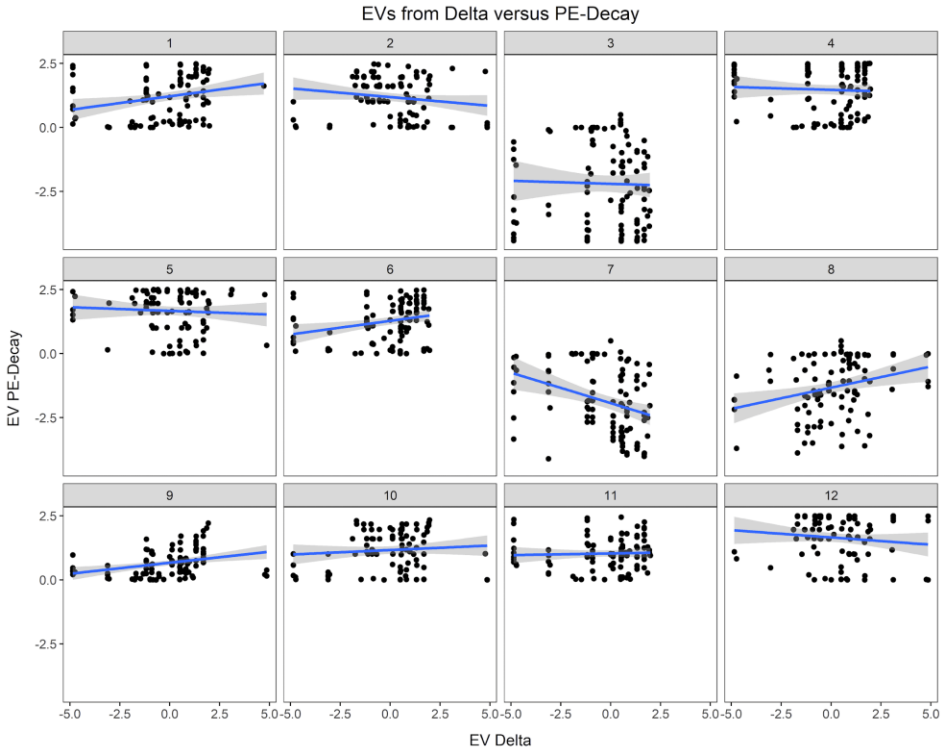


*Figure 3.* Correlations between expected values from Delta and PE-Decay models for 12 participants.

Table 2

*BIC values and best-fitting parameter values for Delta and PE-Decay models. Standard deviations are shown in brackets.*

| | Younger adults | Older adults | Average |
|---|---|---|---|
| *BIC values* | | | |
| Delta | 278.08 (8.34) | 274.56 (9.08) | 276.27 (8.86) |
| PE-Decay | 234.81 (31.37) | 237.49 (31.98) | 236.19 (31.56) |
| | | | |
| *Parameter estimates* | | | |
| Delta | | | |
| α | .37 (0.43)* | 0.67 (0.37)* | 0.53 (0.42) |
| c | .09 (0.12) | 0.22 (0.67) | 0.16 (0.49) |
| PE-Decay | | | |
| α | 0.43 (0.39) | 0.39 (0.35) | 0.41 (0.37) |
| λ | 1.29 (1.75)* | 2.05 (1.90)* | 1.68 (1.86) |
| c | 0.50 (0.33) | 0.48 (0.33) | 0.49 (0.32) |

*Note:* *significant age difference at p<.05.

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 ($\Delta BIC = 40.08$). From the behavioral data, it is clear that participants did not use the more optimal strategy represented by the Delta model. Figure 4 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. The best-fitting parameters derived from each model are shown in Table 2. This table also presents the best fitting parameters for older and younger adults separately. For the Delta model, the best-fitting parameter for learning rate ($\alpha$) was higher for older adults than younger adults, indicating a greater weight to recent outcomes in older adults. The same pattern was not evident in best-fitting decay rate parameters. However, older adults were more loss averse (mean $\lambda$ = 2.05) compared to younger adults (mean $\lambda$ = 1.29), $t(101) = 2.10$, $p = .038$, $d = .413$.

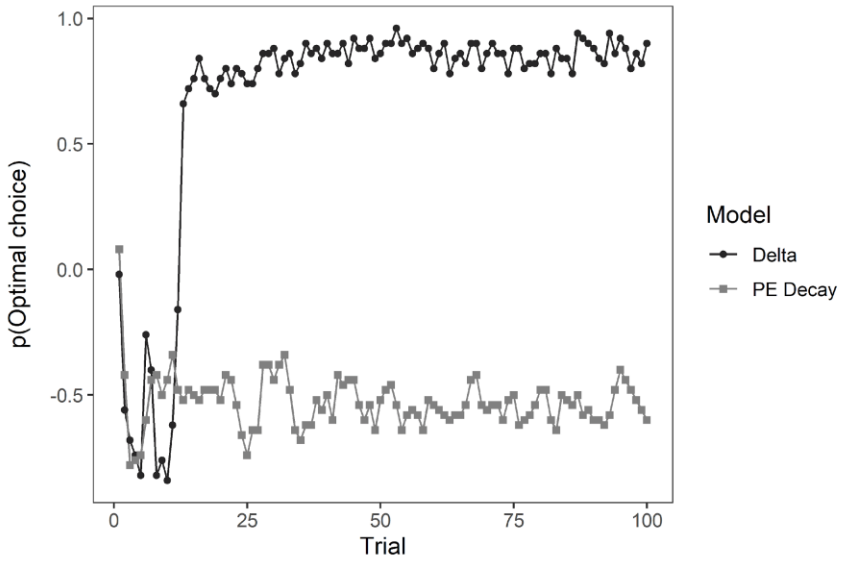


*Figure 4.* Simulated optimal choices across the SGT predicted by the Delta model and PE Decay model. The Delta model very quickly prefers the optimal decks after a large loss, while the PE Decay models predicts persistent choice of the suboptimal decks.

## Model-based fMRI analysis

For each of the models, 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. Activation correlated with expected value and prediction errors from each model are reported below.

## Expected value activation

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

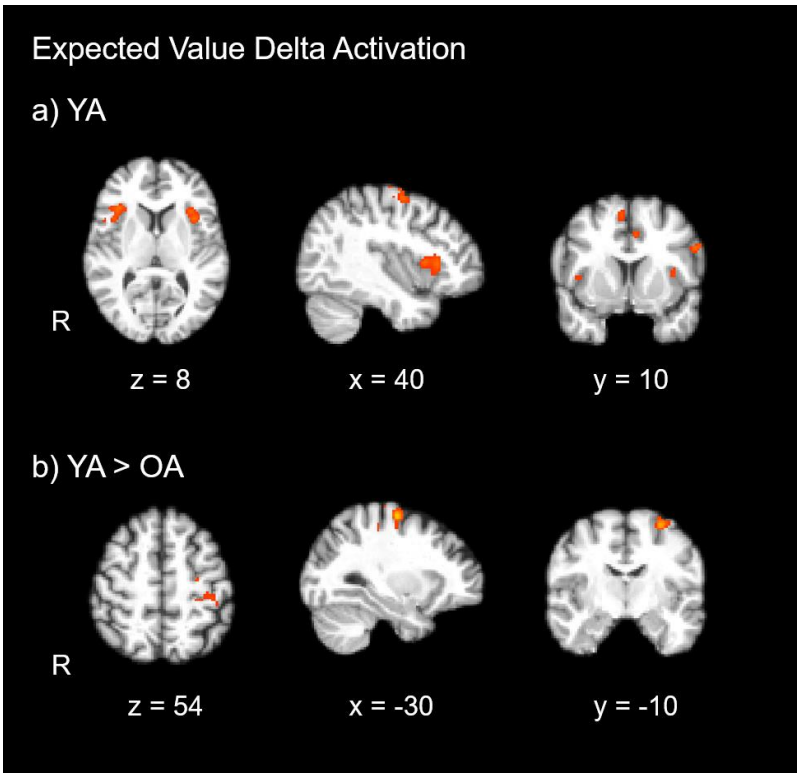


*Figure 5.* a.) YA activation correlated with expected values from the delta model. b.) YA activation greater than OA activation correlated with expected values from the delta model. The delta model represents an optimal strategy for the task.

Table 3

*Delta model expected value unique activation.*

| | | | | | Maximum z-score (mm) | | | |
|---|---|---|---|---|---|---|---|---|
| | Region | Cluster Index | Voxels | P | z-score | X | Y | Z |
| YA | L. precentral gyrus, post central gyrus | 6 | 1269 | < .001 | 6.36 | -32 | -12 | 62 |
| | Supplementary motor cortex | 5 | 526 | < .001 | 4.93 | -4 | -8 | 52 |
| | R. frontal operculum cortex, insula, OFC | 4 | 355 | < .001 | 4.55 | 36 | 20 | 12 |
| | L. OFC, insula, frontal operculum cortex | 3 | 214 | < .001 | 4.31 | -32 | 28 | 2 |
| | R. precentral gyrus | 2 | 197 | < .001 | 4.92 | 42 | -6 | 64 |
| | L. precentral gyrus | 1 | 179 | < .001 | 4.59 | -54 | 4 | 30 |
| YA>OA | L. postcentral gyrus | 2 | 244 | < .001 | 4.75 | -36 | -38 | 40 |
| | L. precentral gyrus | 1 | 116 | .005 | 5.61 | -32 | -12 | 64 |

Note: YA= younger adults; OA = older adults; R = right; L = left; Frontal orbital cortex functionally labeled as OFC.

**Delta model EV related activation.** Table 3 lists regions of activation in younger adults, and regions where activation was significantly greater for younger adults than older adults. 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 5a), Delta model expected values were associated with activation in regions involved in decision making, including the right and left orbital frontal cortex (OFC), operculum cortex and the insula. 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 5b).

**PE-Decay model EV related activation.** Figure 6 shows activation negatively correlated with expected values from the PE-Decay model for younger adults. These regions are listed in Table 4. There was significant deactivation in frontoparietal regions as a function of

expected value. That is, younger adults showed greater activation in these cognitive control regions when expected value for the PE-Decay model was low. The PE-Decay model's expected values will be lower for the good decks than the bad decks, as these decks provide more frequent losses than gains. Thus, these regions were active in younger adults when they were selecting from the good decks.

Table 4

*Expected value PE Decay negative correlation.*

| | | | | Maximum z-score (mm) | | | |
|---|---|---|---|---|---|---|---|
| | Region | Voxels | P | z-score | X | Y | Z |
| YA | Right inferior frontal gyrus, frontal orbital cortex, inferior frontal gyrus, insula | 8547 | < .001 | 7.68 | 46 | 24 | -2 |
| | Superior frontal gyrus, anterior cingulate gyrus, paracingulate gyrus | 4437 | < .001 | 7.42 | 4 | 16 | 64 |
| | Left inferior frontal gyrus, frontal orbital cortex, inferior frontal gyrus, insula | 2670 | < .001 | 7.33 | -30 | 18 | -14 |
| | Left angular gyrus, supramarginal gyrus, posterior parietal cortex | 2081 | < .001 | 6.71 | -62 | -60 | 24 |
| | Brain stem, left caudate, left thalamus | 916 | < .001 | 5.9 | 0 | -24 | -20 |
| | Left precuneus | 366 | < .001 | 5.23 | -22 | -60 | 4 |
| | Right precuneus | 224 | < .001 | 4.27 | 14 | -64 | 26 |
| | Left precuneus | 197 | < .001 | 4.86 | -6 | -60 | 36 |
| | Left superior temporal gyrus | 189 | < .001 | 5.69 | -50 | -28 | -4 |
| | Right precuneus | 172 | < .001 | 4.38 | 24 | -58 | 6 |
| | Superior frontal gyrus | 134 | 0.002 | 4.73 | 20 | 4 | 56 |
| | Right fusiform gyrus | 134 | 0.002 | 4.78 | 42 | -62 | -14 |
| | Left precuneus | 127 | 0.003 | 4 | -8 | -76 | 38 |
| | Left inferior frontal gyrus, middle frontal gyrus | 111 | 0.007 | 4.22 | -44 | 30 | 12 |
| | Left insula | 109 | 0.008 | 4.48 | -40 | -12 | -8 |
| | Right thalamus | 86 | 0.026 | 4.22 | 10 | -8 | 6 |
| | Right caudate | 81 | 0.035 | 4.53 | 8 | 10 | 8 |

Note: Frontal orbital cortex functionally labeled as OFC, middle frontal gyrus functionally labeled as DLPFC.

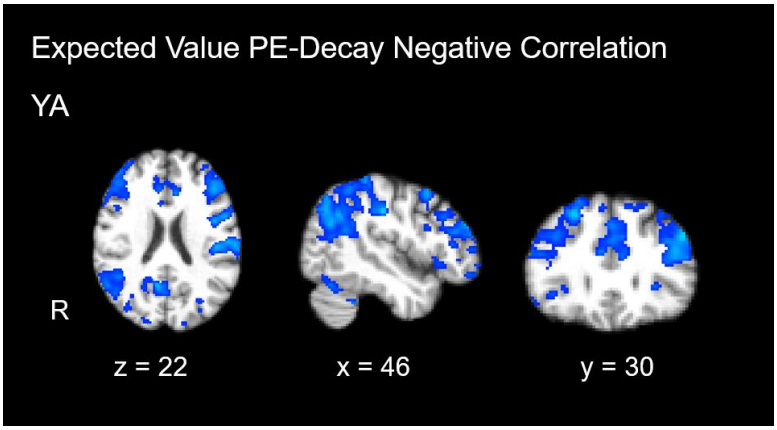


*Figure 6.* YA activation negatively correlated with expected values from the PE-Decay model. The PE-Decay model represents a sub-optimal strategy for the task. Thus, these regions were active when young adults made choices inconsistent with the sub-optimal, frequency-based strategy.

Table 5 lists regions where PE-Decay model EV related activation was greater for older adults than younger adults, including greater bilateral activation in the DLPFC (see Figure 7). Older adults also showed greater activation in the right and left frontal pole, left inferior frontal gyrus, insula, and OFC than younger adults. This activation, combined with the negative correlation with activation in younger adults, suggests that older adults may have been engaging these regions to track which options had recently given gains versus losses.

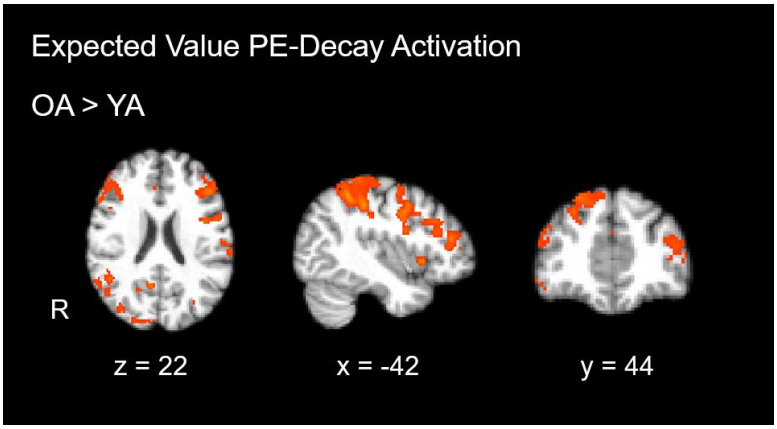


*Figure 7.* Greater activation for OA than for YA correlated with expected values from the PE-Decay model.

Table 5

*PE-Decay model expected value unique activation.*

| | | | | | Maximum z-score (mm) | | | |
|---|---|---|---|---|---|---|---|---|
| | Region | Cluster Index | Voxels | P | z-score | X | Y | Z |
| OA>YA | Precuneus, lateral occipital complex (superior division), posterior parietal cortex | 20 | 4872 | < .001 | 5.19 | 2 | -58 | 58 |
| | L. precentral gyrus, DLPFC, post central gyrus | 19 | 1896 | < .001 | 4.74 | -38 | -4 | 64 |
| | R. frontal pole, DLPFC | 18 | 1430 | < .001 | 5.38 | 22 | 40 | 50 |
| | R. angular gyrus, lateral occipital cortex (superior division) | 17 | 851 | < .001 | 4.35 | 46 | -64 | 26 |
| | Lingual gyrus, occipital pole | 16 | 565 | < .001 | 4.68 | 0 | -90 | -6 |
| | L. inferior frontal gyrus, frontal operculum cortex, OFC, insula | 15 | 313 | < .001 | 4.59 | -44 | 16 | -4 |
| | R. frontal pole (rostral) | 14 | 309 | < .001 | 4.78 | 14 | 68 | 2 |
| | R. superior frontal gyrus | 13 | 276 | < .001 | 4.43 | 22 | 0 | 54 |
| | R. middle temporal gyrus | 12 | 229 | < .001 | 4.15 | 66 | -52 | 0 |
| | Superior frontal gyrus, paracingulate gyrus | 11 | 160 | < .001 | 4.33 | -6 | 24 | 44 |
| | R. supramarginal gyrus | 10 | 144 | .001 | 4.31 | 50 | -22 | 34 |
| | Cerebellum | 9 | 140 | .001 | 4.3 | 26 | -52 | -28 |
| | Posterior cingulate gyrus | 8 | 138 | .001 | 4.36 | 4 | -30 | 30 |
| | Occipital pole | 7 | 135 | .002 | 4.12 | 16 | -94 | 24 |
| | R. frontal pole (lateral) | 6 | 125 | .003 | 4.06 | 48 | 38 | -2 |
| | L. fusiform gyrus | 5 | 116 | .004 | 4.02 | -24 | -74 | -14 |
| | Anterior cingulate gyrus | 4 | 114 | .005 | 4.01 | 4 | 36 | 10 |
| | R. inferior temporal gyrus | 3 | 98 | .011 | 4.4 | 56 | -22 | -26 |
| | Lingual gyrus | 2 | 76 | .037 | 4.03 | 4 | -70 | -12 |
| | R. middle temporal gyrus | 1 | 73 | .044 | 4.03 | 60 | -6 | -28 |

Note: YA= younger adults; OA = older adults; R = right; L = left; Frontal orbital cortex functionally labeled as OFC, middle frontal gyrus functionally labeled as DLPFC.

**Prediction error related activation**

Prediction errors produced by the Delta and PE-Decay models were substantially overlapping, $r = .85$, $p < .001$. Figure 8 shows correlations between the models' prediction errors for several participants. Table 6 lists regions of activation associated with Delta model prediction errors and Table 7 lists regions of activation associated with PE-Decay model prediction errors. In younger adults (Figure 9a, Figure 10a), 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. Table 8 shows activation negatively correlated with prediction error from the Delta model (see Figure 11). Younger adults showed a similar pattern of deactivation in frontoparietal areas with increasing prediction error to that seen with PE-Decay expected value.

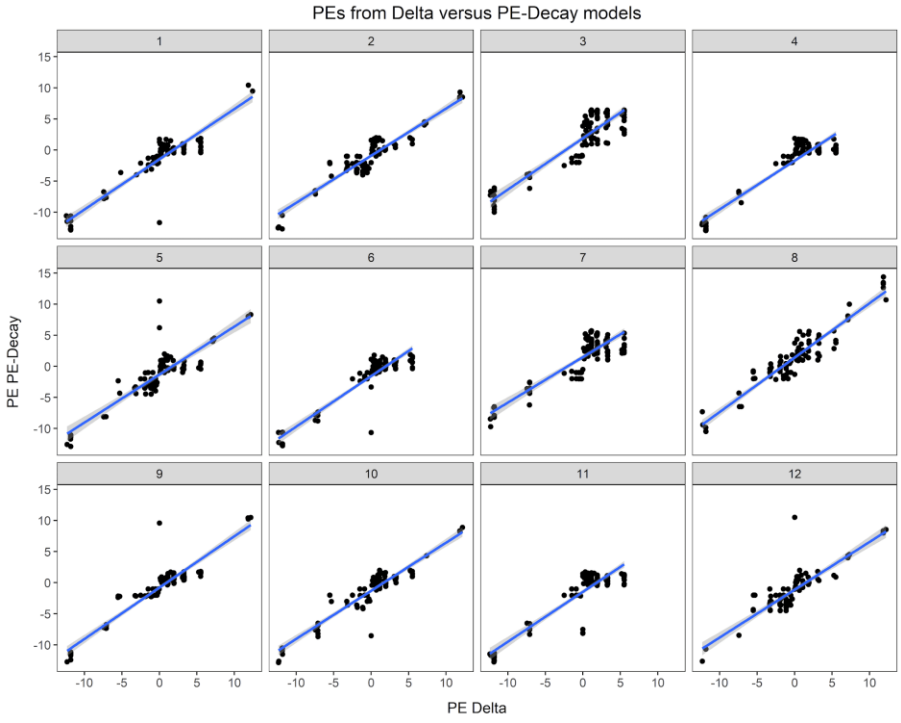


*Figure 8.* Correlations between Delta model prediction errors and PE-Decay model prediction errors for 12 random subjects.

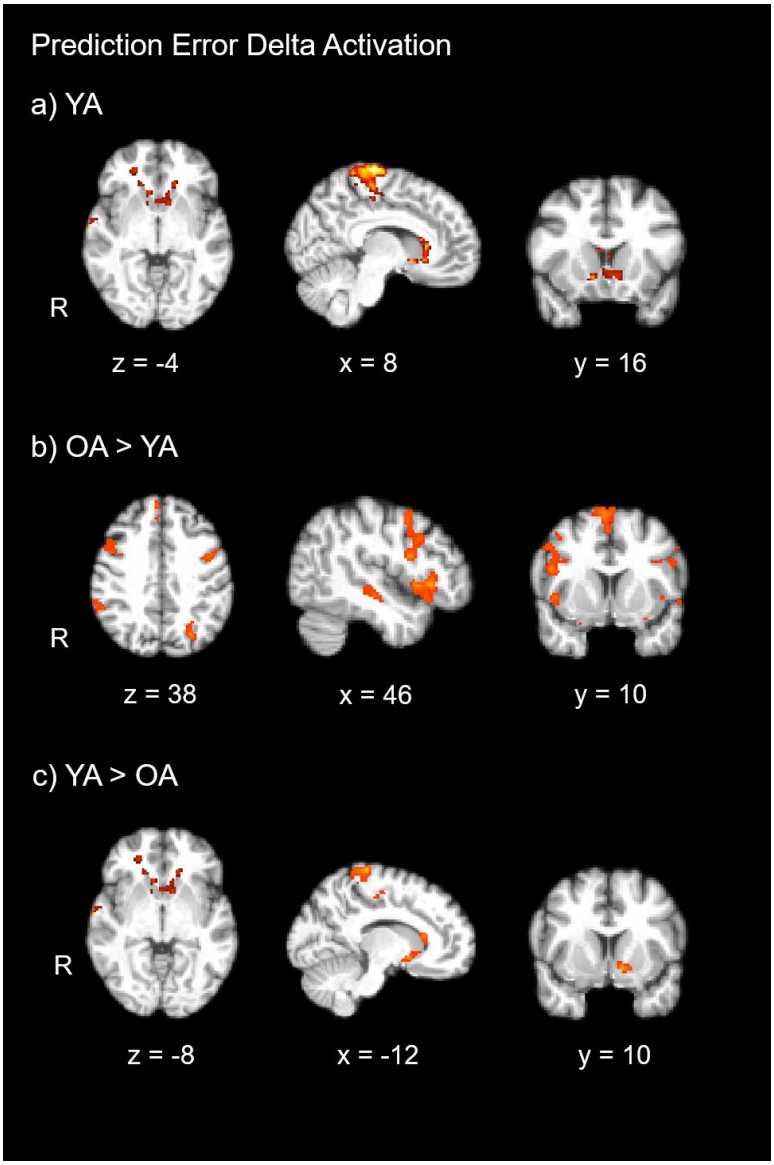


*Figure 9.* Prediction error related activation for the delta model. a.) younger adults. b.) older adults greater than younger adults. c.) younger adults greater than older adults.

Table 6

*Delta model prediction error activation.*

| | | | | | Maximum z-score (mm) | | | |
|---|---|---|---|---|---|---|---|---|
| | Region | Cluster Index | Voxels | P | z-score | X | Y | Z |
| YA | Precentral gyrus, postcentral gyrus | 10 | 2323 | < .001 | 7.15 | 2 | -26 | 64 |
| | Nucleus accumbens, putamen, caudate | 9 | 991 | < .001 | 6.08 | 12 | 10 | -8 |
| | R. precentral gyrus, superior parietal lobule | 8 | 612 | < .001 | 5.67 | 36 | -22 | 58 |
| | Tail of caudate, right ventricle | 7 | 344 | < .001 | 4.75 | 16 | -36 | 22 |
| | Tail of caudate, left ventricle | 6 | 229 | < .001 | 4.57 | -28 | -16 | 32 |
| | Tail of caudate, left ventricle | 5 | 214 | < .001 | 5.1 | -22 | -36 | 16 |
| | Superior temporal gyrus | 4 | 129 | 0.003 | 5.29 | 66 | -8 | -2 |
| | Occipital pole | 3 | 112 | 0.007 | 4.34 | 20 | -90 | 20 |
| | Occipital pole | 2 | 96 | 0.015 | 4.24 | -24 | -92 | 14 |
| | Frontal pole | 1 | 80 | 0.037 | 4.72 | -8 | 70 | 10 |
| OA>YA | Superior frontal gyrus, paracingulate cortex | 11 | 1522 | < .001 | 5.46 | 4 | 14 | 64 |
| | R. OFC, insula, frontal operculum, inferior frontal gyrus | 10 | 928 | < .001 | 5.25 | 52 | 18 | 0 |
| | L. OFC, insula, frontal operculum, inferior frontal gyrus | 9 | 647 | < .001 | 5.34 | -30 | 20 | -14 |
| | R. DLPFC, inferior frontal gyrus, precentral gyrus | 8 | 546 | < .001 | 5.08 | 42 | 6 | 48 |
| | R. middle temporal gyrus, superior temporal gyrus | 7 | 354 | < .001 | 5.08 | 48 | -20 | -10 |
| | R. angular gyrus, supramarginal gyrus | 6 | 264 | < .001 | 5.06 | 62 | -52 | 24 |
| | L. DLPFC, inferior frontal gyrus, precentral gyrus | 5 | 224 | < .001 | 4.48 | -46 | 2 | 40 |
| | L. lateral occipital cortex, superior division | 4 | 142 | 0.002 | 4.51 | -28 | -72 | 38 |
| | L. angular gyrus, supramarginal gyrus | 3 | 117 | .005 | 4.94 | -60 | -58 | 26 |
| | Brainstem | 2 | 113 | .006 | 4.99 | -2 | -28 | 0 |
| | L. middle temporal gyrus, superior temporal gyrus | 1 | 76 | .046 | 4.44 | -50 | -26 | -4 |
| YA>OA | Precentral gyrus, postcentral gyrus | 5 | 1215 | < .001 | 5.94 | 2 | -26 | 62 |
| | Precentral gyrus | 4 | 279 | < .001 | 4.72 | 38 | -22 | 58 |
| | L. nucleus accumbens, putamen | 3 | 204 | < .001 | 4.82 | -12 | 10 | -8 |
| | Caudate | 2 | 115 | .006 | 4.29 | 12 | 26 | 4 |
| | Superior temporal gyrus | 1 | 88 | .024 | 5.1 | 66 | -8 | -2 |

Note: YA= younger adults; OA = older adults; R = right; L = left; Frontal orbital cortex functionally labeled as OFC, middle frontal gyrus functionally labeled as DLPFC.

Table 7

*PE-Decay model prediction error activation.*

| | Region | Cluster Index | Voxels | P | Maximum z-score (mm) z-score | X | Y | Z |
|---|---|---|---|---|---|---|---|---|
| YA | Precentral gyrus, post central gyrus | 10 | 4133 | < .001 | 6.98 | 0 | -26 | 66 |
| | R. nucleus accumbens, caudate | 9 | 869 | < .001 | 5.94 | 12 | 10 | -8 |
| | R. occipital pole | 8 | 237 | < .001 | 4.76 | 22 | -92 | 18 |
| | L. cerebral white matter | 7 | 214 | < .001 | 4.66 | -28 | -14 | 32 |
| | R. superior temporal gyrus | 6 | 179 | < .001 | 5.9 | 64 | -4 | -2 |
| | L. superior temporal gyrus | 5 | 155 | .001 | 5.59 | -64 | -14 | 4 |
| | R. cerebral white matter | 4 | 133 | .003 | 4.38 | 22 | -28 | 24 |
| | R. precentral gyrus | 3 | 123 | .005 | 4.7 | 52 | 0 | 28 |
| | L. cerebral white matter, putamen | 2 | 120 | .005 | 4.57 | -32 | -14 | 12 |
| | R. cerebral white matter, caudate | 1 | 95 | .019 | 4.27 | 18 | -6 | 28 |
| OA>YA | Superior frontal gyrus | 8 | 717 | < .001 | 5.02 | 2 | 12 | 68 |
| | R. inferior frontal gyrus, insula, OFC | 7 | 384 | < .001 | 4.37 | 44 | 12 | -2 |
| | L. OFC, frontal operculum cortex | 6 | 282 | < .001 | 4.45 | -30 | 18 | -14 |
| | R. middle temporal gyrus | 5 | 239 | < .001 | 4.84 | 54 | -20 | -10 |
| | Superior frontal gyrus | 4 | 98 | .016 | 4.12 | 6 | 50 | 36 |
| | Thalamus, brain stem | 3 | 95 | .019 | 4.2 | -2 | -28 | 0 |
| | R. DLPFC | 2 | 93 | .021 | 4.06 | 38 | 2 | 46 |
| | R. angular gyrus | 1 | 91 | .023 | 4.14 | 62 | -50 | 26 |
| YA>OA | Precentral gyrus, post central gyrus | 5 | 1431 | < .001 | 5.89 | 12 | -22 | 74 |
| | Post central gyrus | 4 | 476 | < .001 | 4.82 | 38 | -22 | 58 |
| | L. nucleus accumbens | 3 | 236 | < .001 | 4.83 | -12 | 10 | -10 |
| | R. nucleus accumbens | 2 | 128 | .004 | 6.62 | 12 | 10 | -8 |
| | Superior temporal gyrus | 1 | 100 | .015 | 5.31 | 64 | -6 | -2 |

Note: YA= younger adults; OA = older adults; R = right; L = left; Frontal orbital cortex functionally labeled as OFC, middle frontal gyrus functionally labeled as DLPFC.

Table 8

*Prediction error PE Decay negative correlation.*

| | | | | Maximum z-score (mm) | | | |
|---|---|---|---|---|---|---|---|
| | Region | Voxels | P | z-score | X | Y | Z |
| YA | Right/Left post central gyrus, Right/Left supramarginal gyrus, Right/left posterior parietal lobe | 25818 | < .001 | 6.55 | -44 | -34 | 46 |
| | Right frontal pole, middle frontal gyrus, inferior frontal gyrus | 5748 | < .001 | 6.25 | 22 | 40 | 50 |
| | Anterior cingulate gyrus, paracingulate gyrus | 1710 | < .001 | 5.58 | -8 | 22 | 44 |
| | Left inferior frontal gyrus, insula | 769 | < .001 | 4.9 | -50 | 18 | -2 |
| | Right middle temporal gyrus | 392 | < .001 | 4.42 | 60 | -56 | 0 |
| | Right inferior frontal gyrus, insula | 347 | < .001 | 4.48 | 34 | 24 | -4 |
| | Right putamen, caudate | 282 | < .001 | 4.22 | 24 | 12 | 4 |
| | Left thalamus | 259 | < .001 | 4.78 | -12 | -18 | 10 |
| | Right middle temporal gyrus | 209 | < .001 | 5.7 | 62 | -4 | -26 |
| | Right thalamus | 94 | 0.0145 | 4.3 | 22 | -30 | 8 |

Note: Frontal orbital cortex functionally labeled as OFC, middle frontal gyrus functionally labeled as DLPFC.

For Delta model prediction error, there was greater left nucleus accumbens activation in younger adults than older adults. For PE-Decay prediction error, there was greater bilateral activation of nucleus accumbens in younger adults than older adults (Figure 10c). In older adults, there was greater activation in more lateral PFC and posterior parietal regions compared to younger adults (Figure 9b), 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 12). 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.

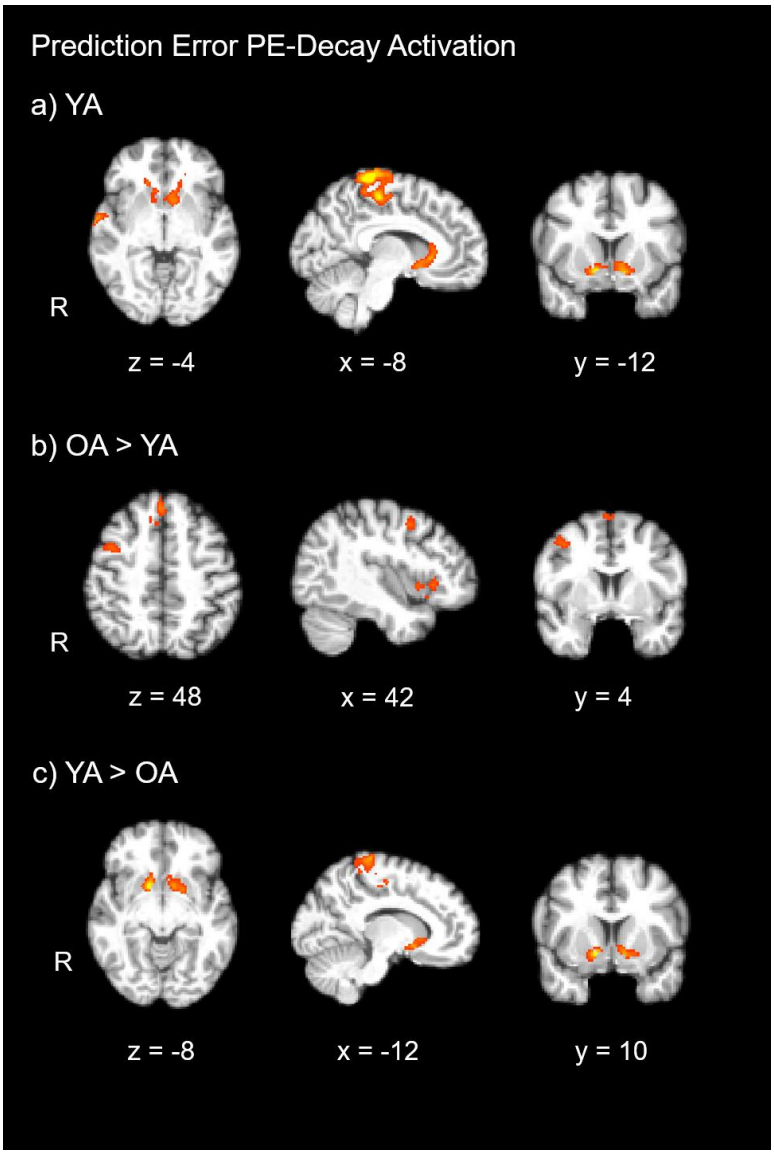


*Figure 10.* Prediction error related activation for the PE-Decay model. a.) younger adults. b.) older adults greater than younger adults. c.) younger adults less than older adults.

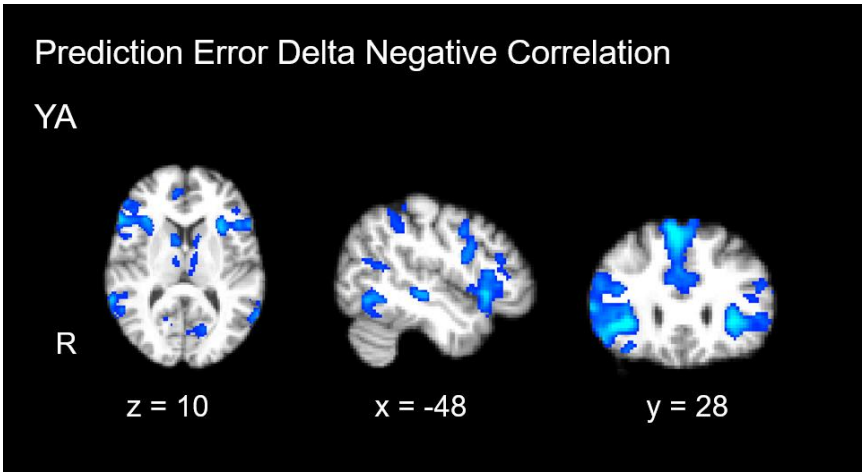


*Figure 11. Negative correlation with prediction errors from Delta model for younger adults.*

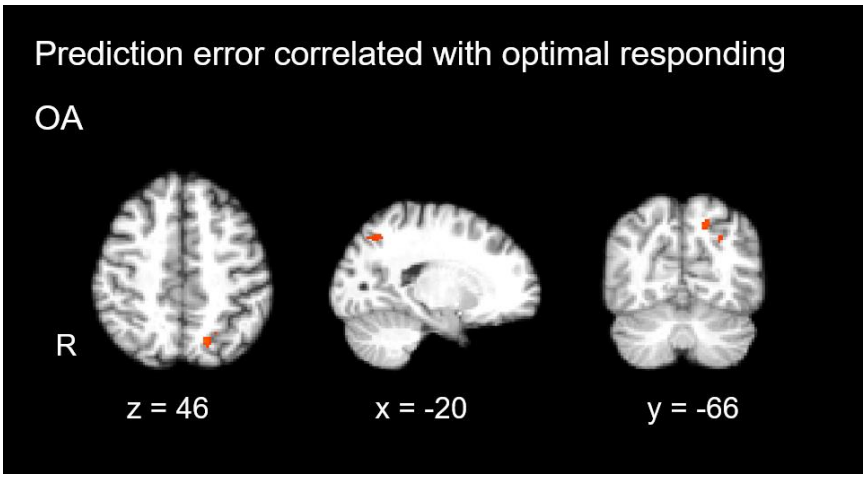


*Figure 12.* Prediction error related activation from the Delta model correlated with optimal responding

## Discussion

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 based on average reward with experience. Older adults appeared to be more reactive to recent outcomes than younger adults. Younger adults engaged cognitive control networks to suppress negative prediction errors that resulted from picking the good decks, which gave frequent losses. This may be why younger adults were less reactive to recent events compared to younger adults, and why they showed better learning across the task.

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).

Consistent with previous research, older adults also appeared to be more reactive to recent outcomes. In particular, older adults were more likely to switch 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 best-fitting loss aversion parameters in the PE-Decay model were also higher for 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). However, unlike Wood et al., we saw both a difference in strategy and in performance.

Model-based fMRI analyses also indicate differences in activation associated with expected values and prediction errors for older and younger adults. In younger adults, delta model expected values, which predict more optimal responding, were associated with areas implicated in decision making, including bilateral OFC, operculum cortex and insula. OFC has been implicated in suppression or responses to previous outcomes, and this is consistent with younger adults' reduced sensitivity to previous outcomes compared to older adults (Elliott et al., 2000). Several regions showed greater activation associated with PE decay expected values for older adults than younger adults. The PE-Decay model represents a sub-optimal strategy, based on the frequency of gains versus losses, which fits closely with the pattern of behavior shown by older adults in the task. Consistent with this result, older adults showed greater activation in DLPFC associated with PE-Decay expected values, in accord with the hypothesis that DLPFC is involved in accumulating information about past positive outcomes associated with each option. This finding is consistent with prior studies in decision making (Worthy et al., 2016) and working memory (Cappell et al., 2010; Hillary et al., 2006; Park & Reuter-Lorenz, 2009). This pattern of activation is also consistent with the idea that older adults are using short-term memory strategies in which they remember which options led to gains and losses on recent trials, and use this to guide their choices. However, 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 will have lower PE-Decay model expected values and prediction errors, as they provide more frequent losses. Thus, the increased activation in these regions for

older adults compared to younger adults may actually be due to younger adults tracking expected value and prediction error to a greater extent than older adults, with younger adults using more controlled processes on low expected value and prediction error 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.

The results for prediction error related activation in younger adults are particularly noteworthy. Previous studies have found activation in the ventral striatum related to Delta model prediction errors (Blair et al., 2006; Daw et al., 2006; Elliot e al., 2000; Hare et al, 2008; Pagnoni et al., 2002; Pessiglione et al., 2006). This has been taken as tacit neurobiological support for the Delta model's assumptions and predictions about behavior. Here, we also found activation in the ventral striatum associated with Delta model prediction errors. However, activation in this area was also associated with prediction errors from the PE-Decay model, and prediction errors produced by the PE-Decay model were highly correlated with those produced by the Delta model. Although the prediction errors were highly correlated, the expected values produced by the models were not strongly associated, and each model made distinct predictions about behavior in the SGT. We found that 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.

Prediction error activity also 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 were 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) criterion of improved performance may be good in some cases good performance is clearly defined, it's important to note that defining what is optimal in a given task is not always easy, 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 in their reply to Cabeza et al.'s 2018 paper. They view compensation as one of the many ways *cognitive reserve* can be implemented, and note that the success of compensation can be modulated by lifestyle variables. As we note above, the success of compensation may be related to task, or other environmental variables as well. Older adults may recruit a broad number of brain regions when implementing a sub-optimal cognitive strategy. Whether this strategy is successful seems irrelevant to whether the enhanced neural activation is viewed as evidence for neural compensation. 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.

The SGT was designed to tease apart the confounds of average reward and gain-loss frequency in the IGT (Bechara et al., 1994; 1997). In the IGT, healthy adults initially tend to first prefer the high-gain-high-loss decks, but soon learn to choose the more advantageous low-gain-low-loss decks. In this task, both good and bad decks provide a similar number of gains, but the good decks provide fewer losses. Thus, it is unclear whether improved performance across the IGT in healthy adults is guided by EV or gain-loss frequency (Lin, 2007; Chiu et al., 2008). 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. This is important because it makes age-related differences in performance on the IGT difficult to interpret. 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). In particular, older adults show greater recency biases, with 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).

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 of 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 examine 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 RL 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.

# Materials and methods

## Participants

Healthy younger and older adults were recruited from the Austin, Texas area. 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.

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 following assessments: 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 were fitted with an actigraph watch, which was worn on the left wrist for a minimum of 10 days. Participants also completed daily sleep surveys to document bed time, wake time, sleep quality, and any instances in which they removed the actigraph. All behavioral data were collected and managed using REDCap electronic data capture tools hosted at The University of Texas at Austin. Following the actigraphy period, participants underwent MRI scanning, during which T1w structural images and functional images were collected.

## MRI acquisition

Imaging data was 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 13), 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.

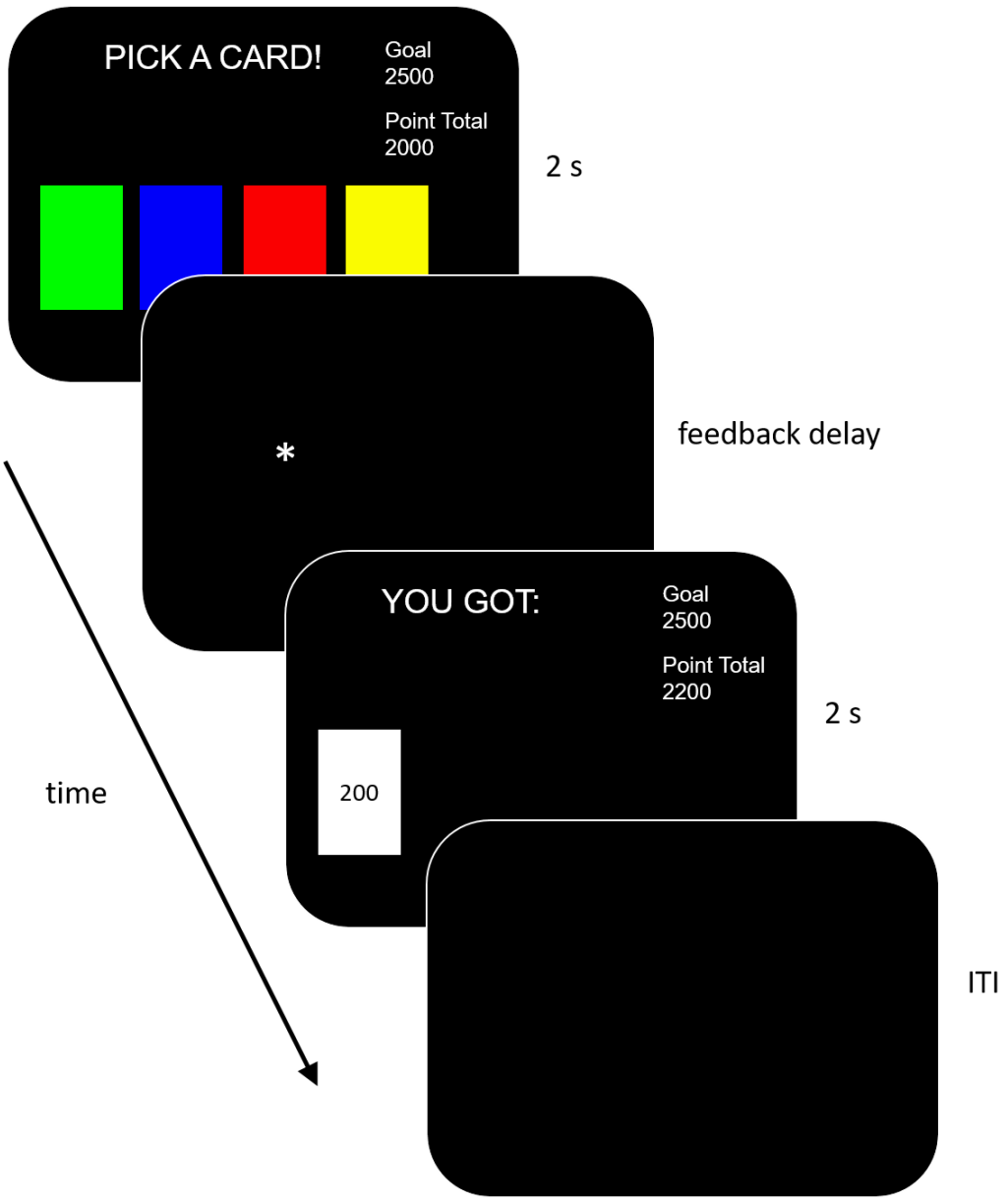


*Figure 13.* Schematic of the trial structure of the Soochow Gambling Task. Participants selected a card by pressing a corresponding key. This was followed by a variable delay before presenting feedback. The selected card was presented in white, and the number of points gained or lost were displayed 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 Prediction-Error Decay model (PE-Decay), 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. Expected values (EV) in the delta rule model are calculated as:

$$EV_j(t+1) = EV_j(t) + \alpha \cdot (r(t) - EV_j(t)) \cdot I_j \quad (1)$$

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 $\alpha$ indicate greater weight to recent outcomes, while lower values indicate less weight to recent outcomes. When $\alpha$ = 0 no learning takes place and expected values remain at their starting points, and when $\alpha$ = 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:

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

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.

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. 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 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, $(1-\alpha)$, where higher values of $\alpha$ indicate a higher rate of decay, and therefore

greater weight to more recent events. Choice probabilities are calculated by entering FVs into Equation 2 in place of EVs.

**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. Model-based measures were included in first-level models as parametric modulators. Five separate first-level models were run: one with expected value and frequency value simultaneously modeled as modulators of choice, one model where each of expected 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).

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## Author Contributions

H.J. Don helped design the study, analyzed the data, and wrote the paper; T. Davis analyzed the data and edited the paper; K.L. Ray collected and analyzed the data, and edited the paper; M.C. McMahon collected and analyzed the data, and edited the paper; A.C. Cornwall helped design the study, programmed the study, and edited the paper; D.M. Schnyer helped designed the study, oversaw data collection, and edited the paper. D.A. Worthy helped design the study, analyzed the data, and edited the paper.

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