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Review

Neural responses to monetary incentives in younger and older adults

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ABSTRACT

Reward anticipation is associated with activity in the dopaminergic midbrain as well as the ventral striatum, amygdala, and medial prefrontal cortex. Dopaminergic neuromodulation declines with age, suggesting that incentive processing should also undergo age-related change. However, the literature is mixed, perhaps reflecting variation in the degree to which tasks made demands on learning and memory. Furthermore, the emphasis has been on the reward network, with few studies addressing reward-related activations in other brain regions. In the current study, 16 younger adults (mean age: 25.4) and 15 older adults (mean age: 69.0) underwent fMRI while completing a monetary incentive delay task. This task allowed the separate assessment of responses to gain and loss incentive cues while minimizing memory demands. We assessed incentive-related activations using mean-centered Partial Least Squares, a data-driven multivariate technique optimal for identifying spatiotemporal whole-brain activation patterns associated with variation in task conditions. The analyses yielded two significant latent variables representing distinct incentive-related activation patterns. The first pattern showed robust activation of the reward network and was not modulated by age. The second pattern, peaking ~10 s after cue onset, showed reduced deactivation of default-network regions, and increased activation of prefrontal cognitive-control regions in older adults, compared with younger adults. Neither pattern was modulated by incentive valence. Overall, these findings suggest that aging may not affect primary motivational signaling in the reward network, but may rather be associated with alterations in incentive-driven modulation of cortical networks that influence multiple cognitive domains.

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1. Introduction

Sensitivity to incentives is critical for goal-directed cognition and behavior throughout the lifespan. In order to adapt to changing environmental contingencies, individuals must continuously monitor and integrate information about stimuli that are predictive of reward and punishment. These motivational signals, in turn, bias executive control, learning and memory, and action selection. To date, only a small number of studies have examined how aging affects incentive processing, and several questions remain unanswered in this literature. There is no consensus on whether aging affects the relative salience of cues signaling the availability of reward versus punishment. It is also unclear how incentive-based modulation of cortical networks, critical for goal-directed cognition, changes with age. The current study was designed to fill these gaps by comparing neural responses to monetary incentive cues in younger and older adults.

1.1. *Incentive processing, dopamine, and aging*

The dopaminergic "reward network" plays a key role in incentive processing (Schultz, 1998). The network includes dopaminergic cells in the ventral tegmental area (VTA) and their projections in ventral and dorsal striatum, amygdala, and medial prefrontal cortex (Haber and Knutson, 2010). Functional magnetic resonance imaging (fMRI) has shown that these regions respond not only to the delivery of reward but also to its anticipation (Knutson et al., 2000), reflecting emotional arousal linked to the expectation of uncertain positive and negative outcomes (Knutson and Greer, 2008).

Age-related declines in dopaminergic neuromodulation are well-documented (for review, see Bäckman et al., 2010). Relative to younger adults, older adults show reduced D1 and D2 receptor density in striatal and extrastriatal regions, as well as reduced cortical D2 receptor binding (e.g., Kaasinen and Rinne, 2002; Rinne et al., 1990). Furthermore, aging is associated with deficits in the acquisition of stimulus-reward associations and in the monitoring of reward and punishment outcomes (for review, see Bäckman et al., 2010; Eppinger et al., 2011), as well as increased variability in activity in the ventral striatum during reward-based decision making (Samanez-Larkin et al., 2010). Correlational evidence from multimodal imaging research has linked these functional deficits to age-related dopaminergic decline (Dreher et al., 2008), and recent findings indicate that pharmacological manipulation of dopamine may reduce age-related deficits in reward-based learning, at least for older adults with low baseline levels of task performance (Chowdhury et al., 2013).

1.2. *fMRI studies of aging and incentive processing*

Despite the evidence for age-related reductions in dopamine, reward-based learning, and outcome monitoring, some aspects of incentive processing appear to be relatively stable in old age, at least when stimulus-reward associations do not have to be learned (cf. Schott et al., 2007). In several fMRI studies, learning-free variants of the monetary incentive delay task (MID task; Knutson et al., 2000) were employed to examine age differences in reward anticipation. In a seminal study by Samanez-Larkin et al. (2007), literal monetary cues ($0, $.50, $5.00) indicated the amount of money that could be earned by responding successfully on each trial of a button-press task in which difficulty was individually adjusted to yield a hit rate of 66%. The framing varied trial-by-trial, such that successful performance resulted either in gains or in avoided losses. In both age groups, affective ratings and striatal activation scaled to the magnitude of the anticipated gain, suggesting intact processing of positive incentives in older adults. However, there was an age-related reduction in the response to loss cues, with older adults failing to show a loss-magnitude effect in both self-reported affect and striatal activation – a finding interpreted as evidence for an age-related positivity effect in incentive processing (Mather and Carstensen, 2005). Rademacher et al. (2014) used an incentive delay paradigm to compare age differences in the neural response to anticipated monetary and social rewards. Social rewards were operationalized as the presentation of faces expressing varying degrees of positive emotion (versus

scrambled faces). Across the two reward types, younger and older adults showed a similar pattern of activation that included the ventral striatum, thalamus, and anterior cingulate. However, a region-of-interest analysis revealed an interaction of age and reward type within the right nucleus accumbens, with younger adults showing a stronger response to monetary reward and older adults to social reward, consistent with the idea that motivational priorities may shift across the lifespan (e.g., Carstensen, 2006).

A small set of fMRI studies have also examined neural responses to reward *outcomes* in younger and older adults. In both the aforementioned study by Samanez-Larkin et al. (2007) as well as in a more recent study employing the same learning-free MID paradigm (Samanez-Larkin et al., 2014), no age differences in outcome-related activity were found. Cox et al. (2008) examined neural responses to positive and negative outcomes in younger and older adults, using a card-guessing task in which correct guesses resulted in monetary gains and incorrect guesses resulted in monetary losses. Despite statistical trends suggesting possible age differences in spatial extent and time course of striatal activations, the primary finding was that younger and older adults showed a similar pattern, with differentiation between gain and loss outcomes in the caudate head and greater sustained activity for gains than for losses.

In summary, existing fMRI studies using incentive delay tasks indicate that reward-network responses during anticipation and outcome processing show relatively little age-related change, at least when demands on the acquisition of stimulus-reward associations are minimized. One study (Samanez-Larkin et al., 2007) indicated that older adults may be less sensitive to loss cues than younger adults. This finding is intriguing as it supports the idea of an age-related positivity shift (Mather and Carstensen, 2005), consistent with socioemotional selectivity theory (Carstensen, 2006). Interestingly, however, the finding of a reduced response to loss cues in older adults appears to conflict with the results of studies on reward-based learning. In those studies, older adults often show increased loss sensitivity or reduced reward sensitivity (for a review, see Eppinger et al., 2011), consistent with theoretical perspectives that postulate age-related increases in loss avoidance motivation (Baltes, 1997; Ebner et al., 2006). Considering the mixed evidence in the literature, then, one goal of the current study was to examine possible age differences in the brain response to gain and loss cues.

1.3. *Age-related changes in cortical networks*

An issue that has received relatively little attention in previous studies of age differences in incentive delay tasks is how reward cues affect activity of large-scale brain networks. Most previous studies (Cox et al., 2008; Rademacher et al., 2014; Samanez-Larkin et al., 2007; but see Samanez-Larkin et al., 2014) have focused on the discussion of age differences in the ventral striatum, even when reporting whole-brain analyses. However, a growing literature documents systematic age-related changes in the recruitment of distributed cortical networks during cognitive tasks that draw on high-level cognitive functions such as attention and memory. It is therefore important to investigate how aging may affect incentive-based modulation of distributed cortical systems. Such modulations have previously been documented in studies with younger adults, for example in tasks of working memory (e.g., Jimura et al., 2010) and long-term memory (e.g., Adcock et al., 2006). Of particular interest in the current context are the default network (Raichle et al., 2001) as well as networks associated with cognitive control (e.g., Vincent et al., 2008), both of which are known to undergo functional changes with age.

The default network is a set of functionally connected regions that are activated during spontaneous cognition and deactivated during externally-constrained, goal-directed thought. It includes medial prefrontal cortex, posterior cingulate, inferior parietal lobule, as well as lateral and medial temporal lobes (for a review, see Buckner et al., 2008). Compared with younger adults, older adults show reduced task-related deactivation and reduced functional connectivity within the default network (e.g., Andrews-Hanna et al., 2007; Campbell et al., 2013; Grady et al., 2010; Lustig et al., 2003). These changes are associated with negative consequences for older adults' memory (e.g., Miller et al., 2008) and executive function (e.g., Andrews-Hanna et al., 2007). How motivational signals influence default-network activity in younger and older adults has not been examined to date.

A pervasive finding in neuroimaging studies with younger and older adults, across a variety of cognitive tasks, is age-related overrecruitment of prefrontal regions associated with cognitive control (e.g., Davis et al., 2008; Grady et al., 1994). The functional significance of this overrecruitment has been a matter of some debate (for a review, see Grady, 2012), but it appears to be compensatory (i.e., beneficial) in at least some circumstances. A variety of cognitive-control functions with separate behavioral and neuroanatomical signatures have been identified (e.g., Badre and D'Esposito, 2007; Corbetta and Shulman, 2002; Miller and Cohen, 2001; Koechlin et al., 2003). For example, the dorsal attention system (Corbetta and Shulman, 2002) supports externally-directed spatial attention, whereas a frontoparietal control system (Vincent et al., 2008) that includes lateral anterior prefrontal cortex, anterior cingulate, and inferior parietal lobule supports integration of internal and external cognition. Incentive-based modulation of cognitive processing involves changes in cognitive control (e.g., Jimura et al., 2010), but it is unknown how this modulation may change with age.

1.4. *The current study*

In the current study, we used a learning-free version of the MID task (Knutson et al., 2000; Samanez-Larkin et al., 2007) to examine brain responses to monetary gain and loss cues in younger and older adults. Similar to prior research by Samanez-Larkin et al. (2007) and Rademacher et al. (2014), the current study focused on the *anticipation* of gains and losses, rather than on *outcome* processing. The novel element of the current study was the application of a data-analytic approach (PLS; McIntosh, 1999; McIntosh et al., 1996, 2004) that prioritized the examination of whole-brain activation patterns rather than a-priori regions of interest.

In line with previous literature, we expected to see similar reward-network activity in younger and older adults. Given

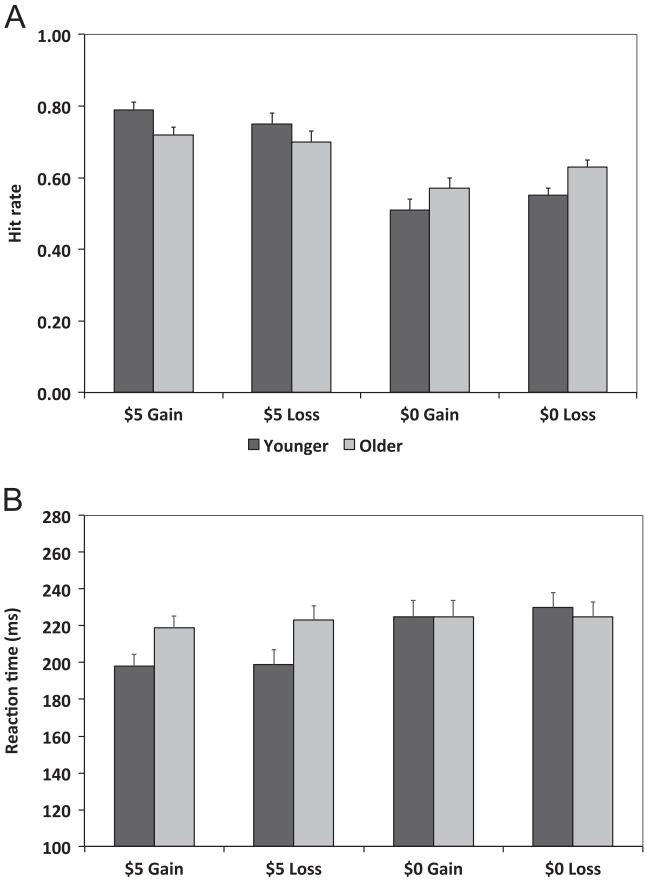

Fig. 1 – Behavioral performance. (A) Hit rate as a function of age group and task condition. (B) Reaction time (in ms) on hit trials as a function of age group and task condition. Error bars show standard errors of the mean.

that age × valence effects had been reported in only one prior fMRI study (Samanez-Larkin et al., 2007), with other studies either not including loss conditions (Rademacher et al., 2014) or finding no age × valence effects (Cox et al., 2008; Samanez-Larkin et al., 2014), the first goal of the current study was to examine whether patterns of activity within the reward network and beyond would respond differently to gain and loss cues in younger and older adults. Whereas reduced loss sensitivity in older adults would provide support to socioemotional selectivity theory (Carstensen, 2006), increased loss sensitivity, sometimes observed in the reward-based learning literature (Eppinger et al., 2011), would be consistent with the view that aging is associated with a shift towards loss prevention goals (e.g., Baltes, 1997; Ebner et al., 2006).

The second major objective of the current study was to shed light on incentive-based modulation of distributed activity in cortical regions. We hypothesized that incentives would produce alterations in cortical activity in both age groups, and that these alterations would be associated with enhanced task performance. However, in light of the aforementioned literatures documenting functional age-related changes in large-scale cortical networks (notably, the default network and networks subserving cognitive control), we hypothesized that the nature of incentive-based modulation would dissociate in younger and older adults. A simple reaction-time task such as the MID was well-suited for capturing age differences in incentive effects on cortical networks. This is because the MID task makes minimal a-priori demands on attention, learning, and cognitive control, thereby reducing the risk of confounding age differences in incentive effects with age differences in other aspects of task performance.

2. Results

2.1. Behavioral results

Cumulative earnings on the MID task were significantly higher for younger adults (M=$56.56, SD=$11.06) than for older adults (M=$44.33, SD=$15.10), $t(29)=2.58$, $p=.015$, $\eta^2=.19$. Hit rates and hit-trial reaction times (RTs) are presented in Fig. 1. Younger adults' higher earnings resulted from a greater modulation of performance in response to the incentive magnitude ($5 vs. $0), compared with older adults. This was borne out by ANOVAs on hit rates and hit-trial reaction times (RTs).

Averaging across conditions, both age groups had the same hit rate (M=.65, SD=.03), indicating that the algorithm that regulated average individual hit rates by adjusting the target duration was successful. However, the conditions differed in average hit rates. A mixed ANOVA on hit rates, with factors group (younger vs. older), cue value ($5 vs. $0), and valence (gain vs. loss) showed a significant effect of magnitude, $F(1, 29)=47.65$, $p<.001$, $\eta_p^2=.62$. Hit rates were higher for $5 trials ($M$=.74, SD=.06) than for $0 trials ($M$=.57, SD=.08). The main effect of magnitude was qualified by a significant age × magnitude interaction, $F(1, 29)=6.33$, $p=.018$, $\eta_p^2=.43$. Separate ANOVAs conducted for each age group indicated that the effect of magnitude on the hit rate was significant in both age groups, but it was larger for younger adults ($5: M=.77, SD=.05; $0: M=.53, SD=.06), $F(1, 15)=87.41$, $p<.001$, $\eta_p^2=.85$, than for older adults ($5: M=.71, SD=.07; $0: M=.60, SD=.10), $F(1, 14)=6.18$, $p=.026$, $\eta_p^2=.31$. No effects involving valence were significant.

An ANOVA on hit RT yielded a similar pattern. The effect of incentive magnitude was significant, $F(1, 29)=22.22$, $p<.001$, $\eta_p^2=.43$, with shorter RTs following $5 cues ($M$=210 ms, SD=26 ms) than following $0 cues ($M$=226 ms, SD=32 ms). The main effect of cue value was qualified by a significant age × magnitude interaction, $F(1, 29)=12.68$, $p=.001$, $\eta_p^2=.30$. Separate ANOVAs conducted for each age group revealed that the effect of magnitude on hit RT was significant for younger adults, $F(1, 15)=28.76$, $p<.001$, $\eta_p^2=.66$, with shorter hit RTs following $5 cues ($M$=198 ms, SD=23 ms) than following $0 cues ($M$=228 ms, SD=36 ms). For older adults, there was no significant effect of magnitude on hit RT, $F(1, 14)=.86$, $p=.371$, $\eta_p^2=.06$, with similar RTs following $5 cues ($M$=221 ms, SD=30 ms) and $0 cues ($M$=225 ms, SD=27 ms). No effects involving valence were significant.

Finally, we conducted a mixed ANOVA of group, magnitude, and valence on target duration (M=278 ms, SD=49 ms),

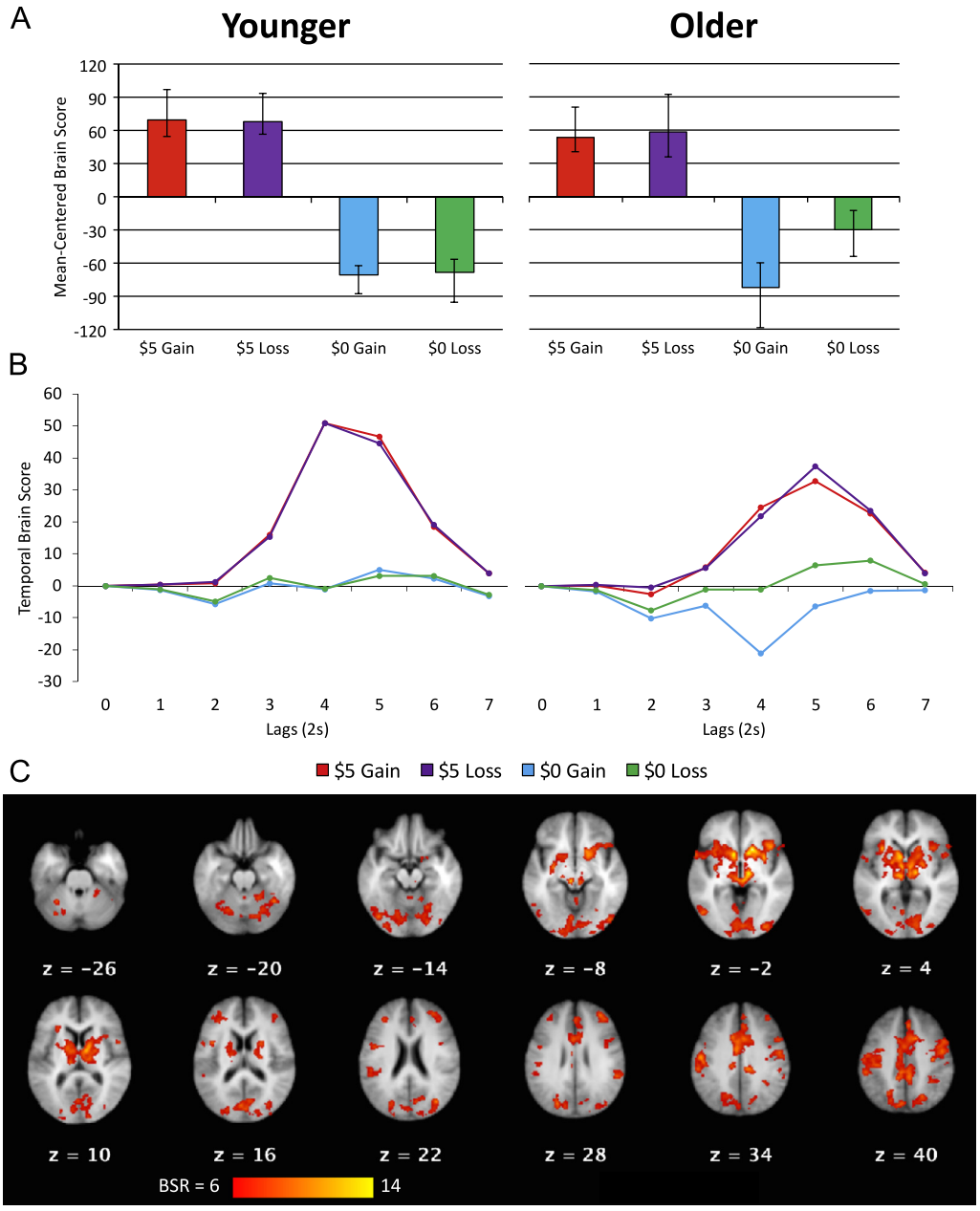

Fig. 2 – Latent Variable 1. (A) Mean-centered brain scores (averaged over all time points) for each age group and condition. Error bars are the 95% confidence interval around each mean. (B) Temporal brain scores for each group and condition. (C) Brain areas showing differences in activity as a function of reward magnitude ($5 vs. $0), from Lag 4 (8 s after cue onset). Significant clusters contained at least 80 voxels exceeding a bootstrap ratio of 6 ($p < .0001$). Warm-colored areas had positive bootstrap ratios, indicating more activity following $5 cues compared with $0 cues. The left hemisphere is shown on the left side. z-coordinates are in MNI space. The activation map is superimposed on the average anatomical scan for all 31 participants.

which was adjusted dynamically throughout the experiment to produce average hit rates at ~66% for all participants. The analysis yielded no significant effects (each $p \geq .13$).

2.2. *fMRI results*

fMRI data analyses with mean-centered PLS (McIntosh, 1999; McIntosh et al., 1996, 2004; see Section 4.4 for details) yielded two significant latent variables (LVs). The first LV ($p < .001$, accounting for 58.39% of the covariance) showed increased activity for $5 cues relative to $0 cues. Inspection of the mean-centered brain scores (Fig. 2 A) confirmed that this pattern was similar for gain and loss cues and showed no age differences, as indicated by the overlap in confidence intervals. For both age groups, activation peaked at lags 4–5 (i.e., 8–10 s after cue onset; Fig. 2B). The spatial pattern associated with LV1 was dominated by reward-network regions, including a large cluster that extended from midbrain regions (ventral tegmental area/substantia nigra) to thalamus,

Table 1 – Latent Variable 1: Peak coordinates of clusters sensitive to cue value ($5>$0) in both age groups.

Region	BA	X	Y	Z	BSR	Cluster size
R caudate head		16	16	−2	13.11	5074
L medial frontal gyrus	6	−4	−10	54	12.65	13,990
R precuneus	31	36	−72	20	10.2	417
L fusiform gyrus	19	−40	−72	−14	9.24	1176
R culmen		40	−52	−20	9.12	567
R middle frontal gyrus	9	34	44	26	9.08	327
R inferior occipital gyrus	18	34	−86	−2	8.92	346
R inferior parietal lobule	40	56	−38	28	8.87	138
L insula	13	−42	6	16	8.84	151
R culmen		20	−46	−22	8.75	177
R precentral gyrus	44	52	8	6	8.61	80
R inferior parietal lobule	40	32	−46	36	8.24	159
R culmen		2	−50	−6	7.93	85
L middle frontal gyrus	9	−32	36	20	7.66	216

Key: BA, Brodmann area; BSR, bootstrap ratio; L, left; R, right. Peak MNI coordinates are listed in descending order of bootstrap ratio. All coordinates had positive saliences, indicating greater activation in response to $5 cues than to $0 cues. Results from Lag 4 (i.e., 8 s after cue onset) are shown. For italicized regions, percent signal change is shown in Fig. 3.

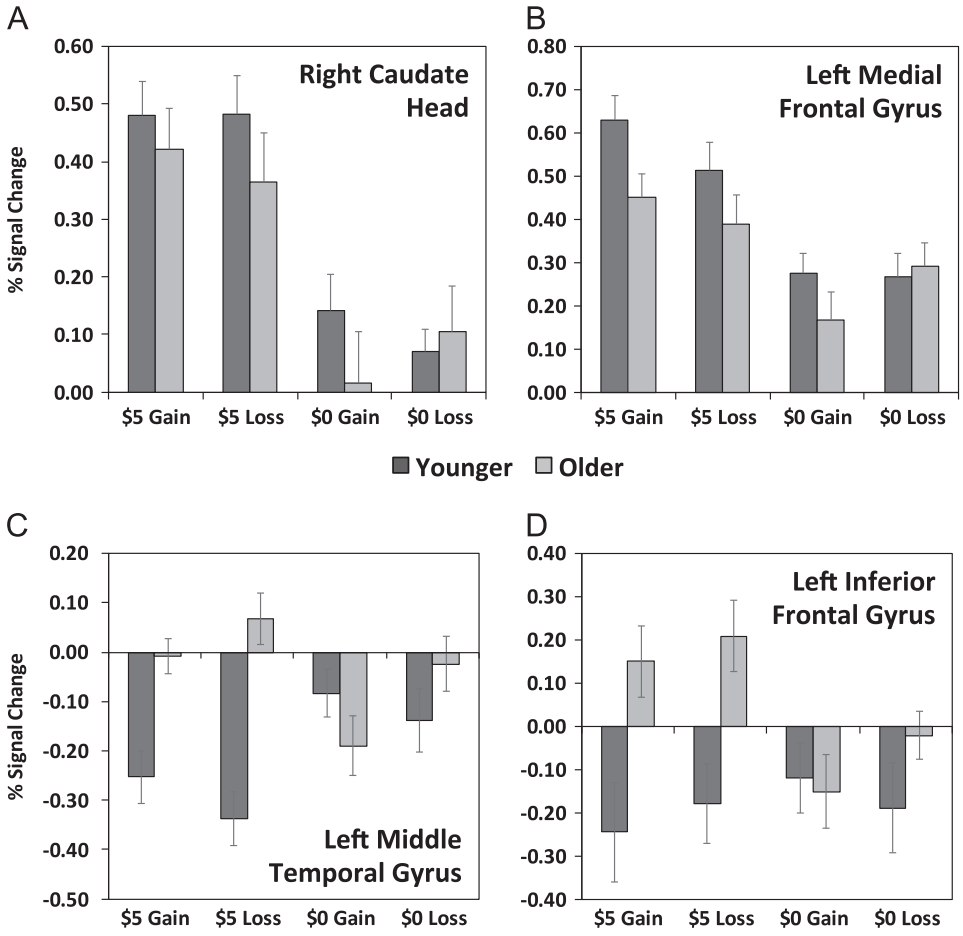

Fig. 3 – Percent signal change (relative to Lag 0) in 2 representative regions from both latent variables (LVs). MNI coordinates are provided in Tables 1 and 2 (italicized regions). Data are group means from Lag 4 (A and B) or Lag 5 (C and D). Error bars show standard errors of the mean.

bilateral ventral and dorsal striatum, and bilateral insula. Neocortical activations included a large bilateral cluster of dorsomedial frontoparietal regions, bilateral dorsolateral prefrontal cortex, right inferior parietal lobule, cerebellum, as well as visual processing areas such as fusiform gyrus and cuneus, extending to lingual gyrus (Table 1, Fig. 2C). Examples of regions showing this pattern are presented in Fig. 3(A and B).

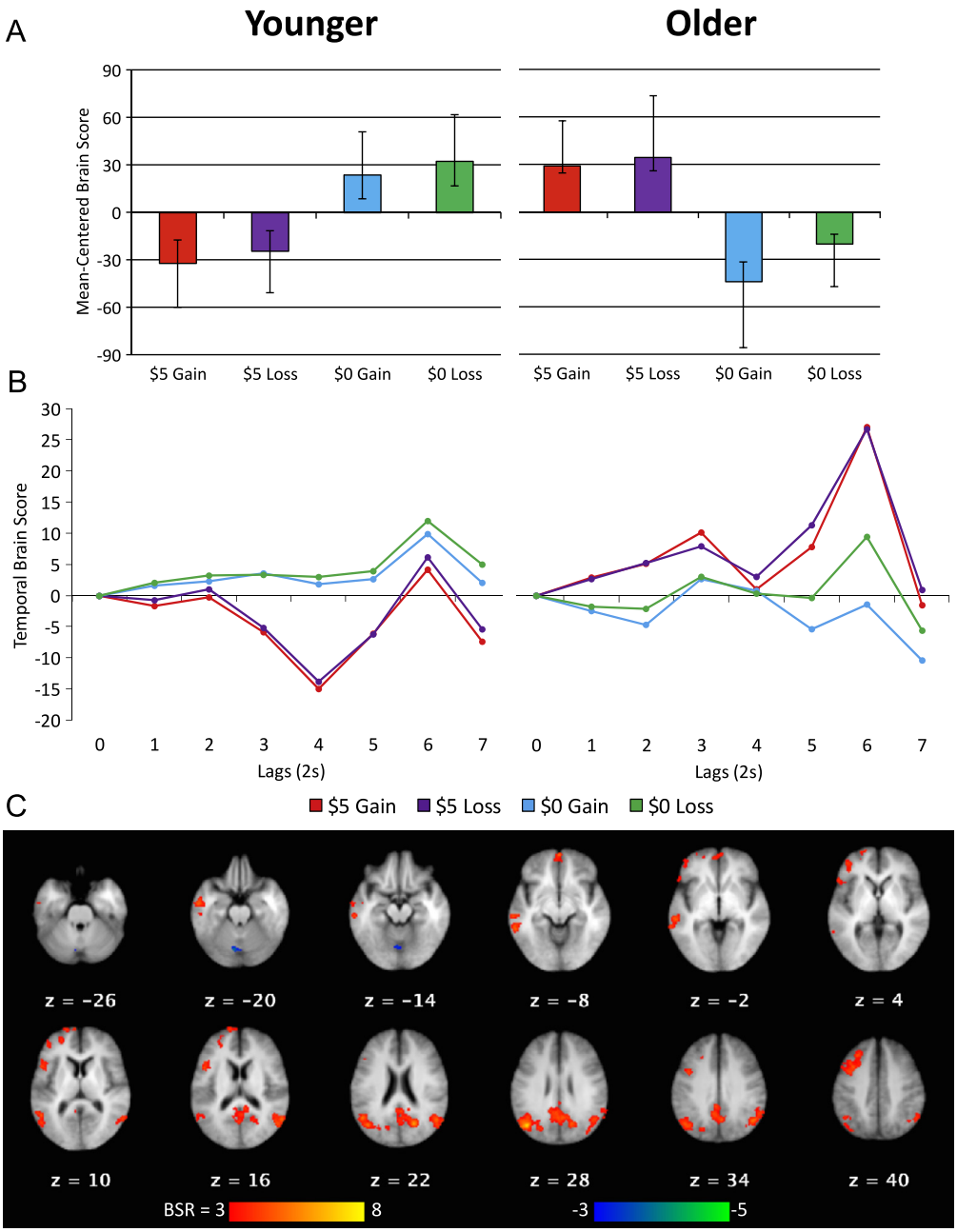

Fig. 4 – Latent Variable 2. (A) Mean-centered brain scores (averaged over all time points) for each age group and condition. Error bars are the 95% confidence interval around each mean. (B) Temporal brain scores for each group and condition. (C) Brain areas showing differences in activity as a function of reward magnitude ($5 vs. $0) and age (younger vs. older), for Lag 5 (10 s after cue onset). Significant clusters contained at least 80 voxels exceeding a bootstrap ratio of 3 ($p < .003$). Warm-colored areas had positive bootstrap ratios, indicating less activity following $5 cues compared with $0 cues in younger adults and the reverse in older adults. Cool-colored areas had negative bootstrap ratios, indicating more activity after $5 cues compared with $0 cues in younger adults and the reverse in older adults. The left hemisphere is shown on the left side. z-coordinates are in MNI space. The activation map is superimposed on the average anatomical scan for all 31 participants.

Unlike LV1, LV2 ($p = .016$, accounting for 13.49% of the covariance) revealed an age-variant pattern of activation (Fig. 4A). The pattern involved an interaction of age and incentive magnitude, with no modulation by cue valence (gain vs. loss). Inspection of the temporal brain scores (Fig. 4B) in both age groups and of the bootstrap values of peak activations at each lag indicated that LV2 was expressed most strongly at Lag 5 (i.e., 10 s after cue onset). The majority of activation clusters that contributed significantly at Lag 5 (Table 2, Fig. 4C) had positive saliences (i.e., positive voxel weights on LV2). Following $5 cues, these regions showed greater activity in older adults than in younger adults. The majority of these regions were *deactivated* in younger adults and showed either reduced deactivation or activation in older

Table 2 – Latent Variable 2: Peak coordinates of clusters sensitive to the cue value × age interaction.

Region	BA	X	Y	Z	BSR	Cluster size
L middle temporal gyrus	39	−44	−66	28	7.62	1239
R precuneus	31	20	−64	22	6.18	1296
R medial frontal gyrus	10	2	58	−6	5.63	126
L middle frontal gyrus	6	−34	14	44	5.57	747
R superior temporal gyrus	39	50	−58	36	5.43	908
L middle temporal gyrus	21	−56	−10	−18	5.37	148
L superior frontal gyrus	9	−12	64	18	5.12	176
L middle temporal gyrus	20	−58	−44	−8	5.1	332
L inferior frontal gyrus	45	−54	24	2	4.88	250
L middle frontal gyrus	10	−42	44	8	4.58	257
L cerebellum		−14	−30	−38	−4.71	121
L cerebellum		−6	−70	−22	−4.11	91

Key: BA, Brodmann area; BSR, bootstrap ratio; L, left; R, right. Peak MNI coordinates are listed in descending order of bootstrap ratio. Results from Lag 5 (i.e., 10 s after cue onset) are shown. For italicized regions, percent signal change is shown in Fig. 3.

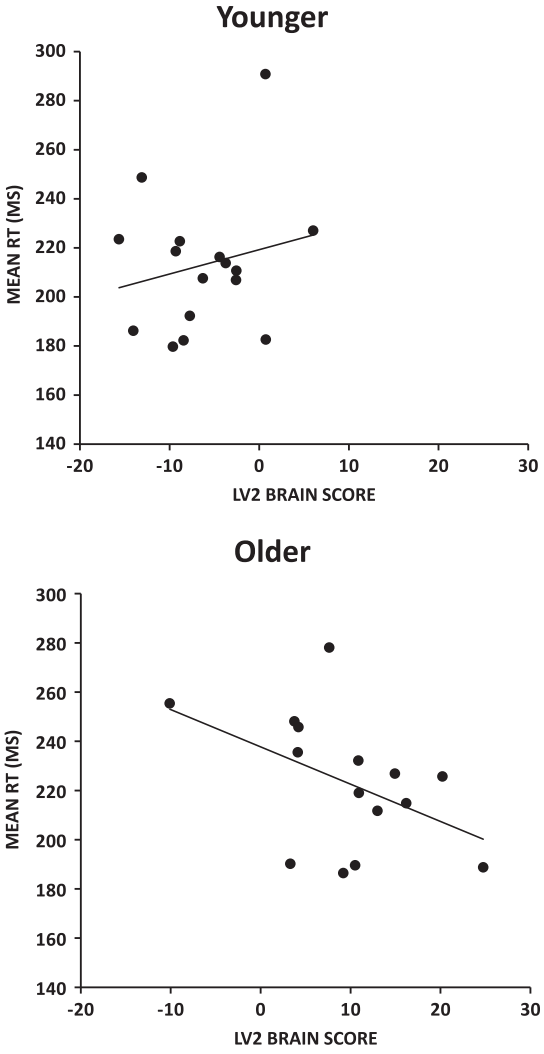

Fig. 5 – Brain-behavior correlations. RT: mean individual reaction time. LV2 brain score: mean individual brain score on Latent Variable 2, across $5 gain and loss conditions.

adults. This was the case for default-network areas including bilateral posterior cortices (lateral temporal gyrus extending into inferior parietal lobule), medial posterior cortex (precuneus extending into posterior cingulate), and ventromedial prefrontal cortex. A representative example of this pattern is shown in Fig. 3C. There were also left lateral prefrontal clusters, in locations typically associated with cognitive control such as the inferior frontal gyrus and dorsolateral prefrontal cortex, that showed decreased activity in younger adults and increased activity in older adults (Fig. 3D).

To examine the functional significance of the age-related activation increases reflected in LV2, we calculated Pearson's correlations between LV2 brain scores ($5 gain and loss conditions, Lag 5) with average RT, separately for younger and older adult groups. For younger adults, the correlation was positive and failed to reach significance, $r=.21$, $p=.44$. In contrast, for older adults, the correlation was negative and marginally significant, $r=-.46$, $p=.09$. A stronger expression of LV2 thus tended to be associated with faster responding in older adults (Fig. 5).

3. Discussion

We used fMRI to investigate neural responses to incentive cues in younger and older adults. Similar to previous studies (Rademacher et al., 2014; Samanez-Larkin et al., 2007, 2014), we employed a learning-free variant of the MID task. Unlike previous studies, we employed a multivariate functional neuroimaging analysis approach optimal for detecting whole-brain networks sensitive to monetary incentives. Analyses of behavioral and brain data compared four incentive conditions defined by the combinations of incentive magnitude ($0 or $5) and valence (gain vs. loss). Despite an age-related reduction in the behavioral response to variation in incentive cues, the fMRI data revealed similar reward-network activation in younger and older adults, consistent with prior findings of preserved motivational functioning in old age. A novel finding in the context of the literature on aging and motivation, however, was that older adults overrecruited default-network and cognitive-control regions in response to incentive cues, compared with younger adults. Lastly, cue valence had no effect on behavioral or brain responses in either age group. Each of these findings will be discussed in turn.

$5 cues gave rise to a higher hit rate than $0 cues, in both age groups, confirming that incentives successfully modulated task effort. However, this modulation was more pronounced for younger adults, whose responses were also significantly faster on $5 trials than on $0 trials. Older adults, in contrast, showed no significant modulation of RT as a function of reward magnitude. While these results may not tell the full story (e.g., RTs were not recorded for the 34% of trials in which a response was made outside the variable response window), it is clear that older adults' behavior was less responsive to fluctuating incentives than younger adults. This may reflect a reduced willingness to engage in cognitive effort to earn money (or other extrinsic rewards) in older adults (e.g., Hess et al., 2012); indeed, average earnings in the present study were higher for younger adults. Alternatively, the behavioral pattern may be due to an age-related increase in the difficulty of trial-by-trial *adjustments* in task effort, as would be expected based on well-documented findings of age-related decline in executive functions such as task switching (e.g., Kray and Lindenberger, 2000). Although neither explanation can be ruled out, the latter appears more likely in view of older adults' intact neural response to incentives, discussed next.

The analyses of the fMRI data identified two coherent activation patterns. The first pattern was expressed similarly by younger and older adults, and included a network of regions that were more active in response to $5 cues than to $0 cues. Critically, this network included the reward circuit (midbrain, ventral and dorsal striatum) and the insula, regions typically implicated in reward anticipation in the MID task (for a review, see Knutson and Greer, 2008). Their engagement is thought to reflect motivational processes as well as emotional arousal in the face of uncertain gains and losses. The finding of age-invariant midbrain and striatal responses during learning-free incentive delay tasks is consistent with previous reports in the literature (Cox et al., 2008; Rademacher et al., 2014; Samanez-Larkin et al., 2007, 2014). The current study thus provides further evidence that aging is associated with preserved sensitivity to incentive signals. Additional regions implicated in the age-invariant pattern included dorsomedial and dorsolateral PFC and inferior parietal lobule, regions associated with a range of attentional and executive-control processes (e.g., Corbetta and Shulman, 2002; Vincent et al., 2008). Finally, the involvement of cerebellum and visual cortex likely reflects the demands of the MID task, in which rewards are contingent on speeded motor responses to visual targets following the presentation of reward cues.

The second spatiotemporal pattern to emerge from the analyses included regions showing an interaction of age and incentive magnitude. The pattern peaked late (~10 s after cue onset) and may thus capture activity related to both cue and target. As targets were perceptually identical across trials, however, any modulation of activity had to be driven by variation in the incentive cues. Closer inspection of the pattern revealed that it was driven by opposing responses to $5 cues in younger and older adults. In younger adults, regions associated with the default network (Raichle et al., 2001) were more deactivated following $5 cues than following $0 cues. Because deactivation of these regions has been associated with externally-directed attention (for a review, see Buckner et al., 2008), our finding suggests that the prospect of gaining (or not losing) money may have caused younger adults to shift the focus of their attention to the buttonpress task. Older adults, puzzlingly, showed the opposite pattern, of greater deactivation of default-network regions after $0 cues than after $5 cues. This pattern cannot be attributed to a *general* age-related reduction of default-network deactivation (e.g., Andrews-Hanna et al., 2007; Campbell et al., 2013; Grady et al., 2010; Lustig et al., 2003) because it was dependent on reward magnitude. One interpretation is that older adults were not motivationally engaged by the prospect of monetary reward, and thus shifted the focus of their attention away from the task after seeing a $5 cue. However, this would be hard to reconcile with the age-equivalent response to incentives in neural regions associated with motivation and arousal, discussed above. An alternative possibility is that the lack of default-network deactivation was a consequence of increased incentive-related activation of left ventrolateral and dorsolateral PFC in older adults. These regions are known to form part of cognitive-control circuits (e.g., Braver, 2012) whose activity correlates with activity in the default network during goal-directed cognitive tasks, such as planning for the future (Spreng et al., 2010).

If older adults' recruitment of lateral PFC in the face of incentives reflects the use of cognitive control, it should be associated with enhanced task performance. Indeed, an analysis of brain-behavior correlations (Fig. 5) revealed a marginally significant negative correlation with reaction time in older but not younger adults. This pattern is consistent with the view that age-related cortical over-recruitment serves a compensatory function (e.g., Grady, 2012). Given that the MID task makes only minimal demands on cognitive control, future research should examine how incentive-driven upregulation of lateral PFC activity would affect older adults' performance in tasks that require higher levels of cognitive control (e.g., attention, working memory, episodic memory, and decision making).

The lack of an age × valence interaction in both behavioral and fMRI data in the current study is inconsistent with the prior report of a selective age-related reduction in the response to loss cues (Samanez-Larkin et al., 2007), and fails to support the prediction of lifespan theories postulating an age-related positivity shift (Mather and Knight, 2005; Carstensen, 2006), as well as theories postulating a shift towards loss avoidance in aging (Baltes, 1997; Ebner et al., 2006).[1] While any null result must be interpreted with caution, it should be noted that other studies have also found no age × valence interactions in learning-free incentive delay tasks (Cox et al., 2008; Samanez-Larkin et al., 2007, outcome

[1]To examine more closely whether the null finding of an age × valence interaction in the primary analyses held up for the specific regions of interest reported by Samanez-Larkin et al. (2007), we performed a supplementary mixed ANOVA of age group, valence, and magnitude on % signal change, relative to Lag 0, for voxels in the left medial caudate (Talairach coordinates: −9, 13, 9) and right anterior insula (39, 19, 7; Samanez-Larkin et al., 2007). Similar to the primary analyses, the supplementary analysis yielded no age × valence interactions.

analyses; Samanez-Larkin et al., 2014). This suggests that valence-based asymmetries between younger and older adults may not be a reliable phenomenon, at least in contexts that minimize demands on learning and memory. As others have noted (e.g., Eppinger et al., 2011; Mata et al., 2011; Samanez-Larkin et al., 2014), reward-based learning tasks more often show age-related decline than learning-free incentive delay tasks, and age × valence interactions have also been more commonly reported in the reward-based learning literature. Interestingly, many (though not all) of these studies have found evidence for an age-related increase in the relative sensitivity to *negative* outcomes, contrary to the idea of an age-related positivity effect (for a review, see Eppinger et al., 2011; see also Eppinger et al., 2013).

A limitation of the current study is the fact that only two levels of incentive magnitude were used ($0 and $5). Parametric manipulations of this factor would give finer-grained information about how brain activity scales to incentive magnitude in younger and older adults (Cox et al., 2008; Rademacher et al., 2014; Samanez-Larkin et al., 2007, 2014). Another limitation is the lack of affective ratings for gain and loss cues (e.g., Samanez-Larkin et al., 2007). Such ratings would have allowed us to examine whether the patterns seen in behavioral and brain responses converged with participants' subjective experience of their motivational states. Finally, a general issue in studies using monetary incentives is the question of whether valuation of these incentives may differ among age groups (e.g., Rademacher et al., 2014). Unlike some other researchers (Samanez-Larkin et al., 2007) we did not assess socioeconomic variables on which younger and older samples may have differed, and which – together with other age-related differences – may have contributed to the effect of age on the response to experimental incentives. Even though the fMRI data (in particular, the age-invariant pattern captured by LV1) showed striking similarities in younger and older adults' neural responses to incentives, it cannot be ruled out that socioeconomic factors may have influenced these findings.

In conclusion, this research supports the hypothesis that motivational signaling in the reward network is relatively intact in old age. A novel finding in the current study is that younger and older adults differ with respect to how incentive cues modulate activity in the default-network and in prefrontal cognitive-control regions. While younger adults deactivated default regions during the anticipation of gains and losses (compared with non-gains and non-losses), older adults showed the opposite pattern. At the same time, older adults (but not younger adults) activated lateral prefrontal regions associated with cognitive control when anticipating gains and losses. We interpret these differences in terms of an age-related shift in the incentive-based modulation of correlated cortical networks. How incentive-based prefrontal recruitment affects older adults' performance in high-level cognitive domains, such as memory and decision making, is an important question for future research.

4. Experimental procedure

4.1. *Participants*

All study procedures were approved by the Research Ethics Boards at Ryerson University and Baycrest Hospital, and all participants gave informed consent for their participation. Sixteen right-handed young adults (9 females) and 17 right-handed older adults (9 females) participated in the study. Data from one older male participant were excluded due to an incidental MRI finding, and data from another older male participant were excluded due to failure to complete the experimental tasks during the MRI scan. Only the remaining 15 older adults (9 females) will be described in this report. Younger participants were recruited with flyers posted on the Ryerson campus and with advertisements on online community billboards (Craigslist.ca and Kijiji.ca). Older adults were recruited from the Ryerson Senior Participant Pool. All participants received $80 for their participation in addition to performance-contingent rewards. Participants had normal or corrected-to-normal vision and hearing and were screened for conditions that may affect neurocognitive function,

Table 3 – Participant characteristics.

	Younger adults (N=16)	Older adults (N=15)
Number of females	9	9
Age (years)	25.44 (3.79)	68.47 (5.38)
Age (range)	20–33	60–78
Education (years)	16.69 (2.85)	16.47 (1.96)
Vocabulary	18.38 (3.22)[a]	23.00 (4.02)
MMSE	29.31 (1.08)	28.87 (1.30)
Neuroticism	19.00 (7.62)	16.57 (6.96)
Extraversion	27.56 (7.23)	28.93 (5.88)
Openness	33.44 (5.79)	34.07 (5.31)
Agreeableness	32.88 (9.34)	33.43 (6.01)
Conscientiousness	31.94 (7.33)	34.00 (6.84)
Positive mood	28.25 (5.75)[a]	33.07 (7.08)
Negative mood	11.56 (1.55)	11.47 (2.10)

Note: Vocabulary is the raw score (maximum of 33) on the Mill Hill Vocabulary scale. Neuroticism, extraversion, openness, agreeableness, and conscientiousness are from the revised NEO Five-Factor Inventory. Positive mood and negative mood are Positive and Negative Affect Schedule scores. Standard deviations are in parentheses. MMSE=Mini-Mental State Examination.

[a] Significant age group difference ($p<0.05$).

including stroke, cardiovascular disease, neurological disorders, and psychiatric illness. Participants also underwent a safety screening to rule out MRI contra-indications, such as claustrophobia, neck or back pain, or metal implants. Each participant's structural MRIs were inspected to screen for abnormalities such as severe atrophy or white-matter alterations. All participants scored 27 or higher on the Mini Mental State Examination (Folstein et al., 1975), with the exception of one older participant with a score of 26. This participant performed normally on all other assessments. Excluding the participant did not affect any of the experimental results. The participant was therefore not excluded. Due to a researcher error, one older adult did not complete the revised 60-item NEO Five-Factor Inventory (Costa and McCrae, 1989) or the Mill-Hill Vocabulary Scale (Raven, 1982). Younger and older adults did not differ significantly on education or other measures (see Table 3), with two exceptions: older adults scored more highly than younger adults on the positive mood scale of the Positive and Negative Affect Schedule (PANAS; Watson et al., 1988), $t(29)=2.09$, $p=.046$, $\eta^2=.13$, and they had significantly higher scores on the Mill-Hill vocabulary scale, $t(28)=3.50$, $p=.002$, $\eta^2=.30$.

4.2. Tasks

Participants gave informed consent, completed the MRI safety screening, and spent 30 min reading instructions and practicing tasks in an MRI simulator. Participants then underwent 30 min of anatomical and fMRI scanning, during which they completed a memory encoding task not further described here. Next, participants completed an adapted version of the Monetary Incentive Delay task (MID; Knutson et al., 2000), similar to the version used in a previous study with younger and older adults (Samanez-Larkin et al., 2007). In the MID, participants made speeded button-press responses to a visual target of uncertain onset and duration. Responses made before target offset were hits, whereas responses made after target offset were misses. Each MID trial started with a 2000-ms visual cue indicating the consequence of a hit. "Win" cues indicated how much money the participant would *win* in the case of a hit, whereas "Lose" cues indicated how much money the participant would *avoid losing* in the case of a hit. The amount was either $5 or $0, yielding 4 possible cues: Win $5.00 (gain condition), Win $.00 (nongain condition), Lose $5.00 (loss condition), and Lose $.00 (nonloss condition). The cue was followed by a fixation screen of variable duration (2000–2,500 ms), after which the target (a white star) was presented centrally. The target duration was initially set to 400 ms. On each subsequent trial, the target duration increased or decreased by 20 ms relative to the previous trial, depending on whether the participant's current hit rate was below or above 66%. The target duration thus varied from trial to trial, with the constraint that it could not exceed 1500 ms. Each participant's final target duration from the pre-scan task practice was used as initial target duration in the scanner. A post-target fixation cross (duration: 2000 ms – target duration) was replaced by a 2000-ms feedback screen. The feedback included the word "Hit" or "Miss," along with the monetary outcome: +$5.00, +$.00, −$5.00, or −$.00. The feedback screen was replaced by a fixation screen that ended when the overall trial duration had reached 12, 14, 16, or 18 s. OptSeq software (http://surfer.nmr.mgh.harvard.edu/optseq/) was used to generate optimally jittered sequences of trial durations. Stimulus presentation, synchronization with the scanner, and response collection were handled by E-Prime 1.0 software (Schneider et al., 2002). All text was presented in white 24-point Calibri font, centered on the screen, against a black background. Participants completed three runs of the MID task, with 28 trials/run, for a total of 84 trials (21/cue type). Each run lasted 6 min 46 s. After the session, participants received the amount they had earned during the MID task, in addition to their compensation for participating. Measures of mood, personality, vocabulary, and cognitive status were administered in a separate session 1 day post-scan.

4.3. Image acquisition and preprocessing

MRI scanning was conducted on a 3.0 T Siemens Trio scanner using a 32-channel matrix head coil. Anatomical scans were acquired with a 3D MP-RAGE sequence (160 slices of 1 mm thickness, field of view [FOV]=25.6 cm^2, TI/TE/TR=1100/2.63/2000 ms, flip angle=9°, 2 averages) and an interleaved axial multislice FLAIR sequence (32 slices of 5 mm thickness, FOV=25.6 cm^2, bandwidth=315 Hz/Px, TI/TE/TR=2200/96/9000 ms, 1 average, 3 concatenations). Functional volumes were acquired with an interleaved multislice EPI sequence (oblique axial orientation; 200 volumes; FOV=19.2 cm^2, 64×64 acquisition matrix, 40 slices of 3×3 mm^2 in-plane resolution, 3.5 mm thick, no gap, bandwidth=2604 Hz/Px, TE/TR=27/2000, flip angle=70°).

A trigger pulse sent by the scanner synchronized stimulus presentation and fMRI acquisition at the beginning of each scanning run. Visual stimuli were presented using an LCD projector (NEC Model MTI065) with a 2.75–5 zoom lens (Navitar, Inc.) and an fMRI-compatible display screen mounted within the magnet bore. Visual stimuli displayed on the screen were viewed through an angled mirror in the Matrix coil. If necessary, participants wore fMRI-compatible prescription glasses to correct for visual acuity (SafeVision LLC., −6 to +6 diopters available in .5 increments). The participant's head was restrained using foam sponges. Button press responses were recorded using a Fiber-Optic Response Pad System (Current Designs Inc.; 4 buttons available per hand). Physiological data (heart rate, respiration, pulse) were also collected.

The first 10 volumes of each run were discarded to allow for scanner stabilization. Preprocessing was performed with Analysis of Functional Neuroimages freeware (AFNI; Cox, 1996) and included correction for cardiac and respiratory parameters, differences in the timing of slice acquisition, rigid-body motion correction, spatial normalization to the MNI template, resampling to 2-mm isotropic voxels, and smoothing with a 6-mm Gaussian filter.

4.4. fMRI data analysis

We analyzed the preprocessed fMRI data with spatiotemporal partial least squares (PLS; McIntosh, 1999; McIntosh et al., 1996, 2004), using PLS software (http://research.baycrest.org/

pls_software) and MATLAB Version 2013A (The Mathworks Inc.). PLS is a multivariate technique for identifying whole-brain patterns of activity related to differences between groups or task conditions. In contrast to univariate analyses, PLS makes no assumptions about the shape of the hemodynamic response function, thereby enabling analysis of task-related activity at various time points along the length of an event. Instead of using a priori task contrasts, we used mean-centered PLS, a data-driven approach; note that group differences in the expression of activation patterns identified using this approach can be readily identified, even when not explicitly entered as contrasts. Mean-centered PLS operates on the cross-covariance between a design matrix (i.e., the experimental conditions) and the data matrix (i.e., the voxel values). Using singular value decomposition, a new set of orthogonal latent variables (LVs) is extracted from the cross-covariance matrix. LVs are extracted in the order of the amount of covariance explained, so that the LV accounting for the most covariance is extracted first. Each LV contains a linear contrast between experimental conditions, and an image identifying the brain regions that show the highest covariance with the contrast at each time point. We averaged across all trials for each of the four cue conditions ($5 gain, $0 gain, $5 loss, $0 loss). Because we were interested in neural responses to incentive cues, rather than in behavioral responses to the target, no trials were excluded on the basis of behavioral performance. As a result, all participants had 21 trials included for each condition, with the exception of one younger adult who, due to head motion, had only 17 trials in the $5 loss condition and 18 trials in the $0 loss condition.

We used a 14-s time window following the onset of each incentive cue (i.e., 7 lags). Activity at each time point was normalized to activity at the first time point of the trial. For each LV and each time point, every brain voxel had a weight ("salience") that was proportional to the covariance of brain activity and the task contrast. Each voxel's salience was multiplied by its BOLD signal value, and the resulting products were summed across all voxels. The result was a "brain score" specific to each participant, LV, and lag. The rise and fall in lag-specific brain scores for a given participant and LV is analogous to a hemodynamic response function.

The significance of each LV was established through a permutation test (McIntosh et al., 1996) with 500 permutations. As such, the smallest possible p value for each LV was $p<.002$. The reliability of the voxel saliences for each time point was tested with a bootstrap estimation of the standard errors (Efron and Tibshirani, 1986). The reliability of each voxel salience was determined from the ratio of the salience over the standard error for that voxel. A bootstrap ratio of at least 3.00 was used as a voxel-level significance threshold, corresponding to approximately $p<.003$ (Sampson et al., 1989). Furthermore, similar to prior studies using PLS with younger and older adults (e.g., Campbell et al., 2013; Grady, 2012), we employed a cluster threshold corresponding to a minimum cluster volume of.64 cm^3 (i.e., at least 80 contiguous voxels given a voxel size of 2 mm^3). The local maximum for each cluster was defined as the voxel with a bootstrap ratio higher than any other voxel in a 2-cm cube centered on that voxel. Locations of cluster maxima are reported in terms of MNI space coordinates. For each condition, 95% confidence intervals for the brain scores (mean-centered and collapsed across all 7 lags) were also calculated from the bootstrap. Differences between groups and experimental conditions were considered reliable if there was no overlap between the corresponding confidence intervals.

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