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Aging, Neuropsychology, and Cognition

A Journal on Normal and Dysfunctional Development

ISSN: 1382-5585 (Print) 1744-4128 (Online) Journal homepage: https://www.tandfonline.com/loi/nanc20

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To cite this article: Holly J. Bowen, Cheryl L. Grady & Julia Spaniol (2019) Age differences in the neural response to negative feedback, Aging, Neuropsychology, and Cognition, 26:3, 463-485, DOI: 10.1080/13825585.2018.1475003

To link to this article: https://doi.org/10.1080/13825585.2018.1475003

AGING, NEUROPSYCHOLOGY, AND COGNITION
2019, VOL. 26, NO. 3, 463–485
https://doi.org/10.1080/13825585.2018.1475003

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Age differences in the neural response to negative feedback

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ABSTRACT

Affective processing is one domain that remains relatively intact in healthy aging. Investigations into the neural responses associated with reward anticipation have revealed that older and younger adults recruit the same midbrain reward regions, but other evidence suggests this recruitment may differ depending on the valence (gain, loss) of the incentive cue. The goal of the current study was to examine functional covariance during gain and loss feedback in younger and healthy older adults. A group of 15 older adults (mean age = 68.5) and 16 younger adults (mean age = 25.4) completed a revised Monetary Incentive Delay task (rMID; Knutson, Westdorp, Kaiser, & Hommer, 2000) while in the fMRI scanner. The rMID is a reaction time task where successful performance, either gaining a reward or avoiding a loss, is defined by hitting a button during the brief presentation of a visual target. Participants receive gain and loss anticipation cues before each trial and feedback after each trial with four possible outcomes: +$5.00, +0.00, -$5.00, and -$0.00. Using seed-voxel partial least squares analyses, with seed voxels in the caudate and ventromedial prefrontal cortex, whole-brain functional covariance revealed that younger and older adults engage the same network of regions to support general feedback processing. However, older adults engaged two additional networks to support processing of negative feedback, gain_miss (+0), loss_miss (-$5), and loss_hit (–0), specifically. These findings are in line with theories of a positivity effect in aging and may have implications for reward-stimulus learning and decision making following performance-contingent negative feedback.

ARTICLE HISTORY
Received 3 December 2017
Accepted 3 May 2018

KEYWORDS
Aging; reward; functional covariance; PLS; positivity effect

Even when pathology is not present, aging is often associated with cognitive decline (Harada, Natelson Love, & Triebel, 2013). Other domains such as affective processing show less impairment or even improvement in healthy aging (see Mather, 2016, for a review) and research on age differences in processing of gains and losses has been the focus of much recent empirical work (see Samanez-Larkin & Knutson, 2015, for a review). On the one hand, there is evidence of age-related decline in the dopaminergic system (Bäckman, Lindenberger, Li, & Nyberg, 2010; Li & Rieckmann, 2014), which plays a key role in incentive processing (Schultz, 1998), and has been implicated in age-related

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Supplementary data can be accessed here.

deficits in the acquisition of stimulus-reward pairings (Bäckman et al., 2010; Eppinger, Hammerer, & Shu-Chen, 2011; Eppinger, Schuck, Nystrom, & Cohen, 2013). On the other hand, reward-based modulation of episodic memory (Castel, 2007; Castel, Benjamin, Craik, & Watkins, 2002; Mather & Schoeke, 2011; Spaniol, Schain, & Bowen, 2013) remains intact in aging, as does activation in the reward network in response to incentive cues (Spaniol, Bowen, Wegier, & Grady, 2015), at least for cues signaling the opportunity to gain (Samanez-Larkin et al., 2007). Much of the prior work examining incentive processing in older adults has used univariate analyses of blood-oxygen-level dependent (BOLD) activation measures obtained at the anticipation stage. The current study focuses on brain response to incentive feedback and uses a multivariate analysis approach that characterizes network-level co-activation or functional covariance.

Neuroimaging studies in animals (Haber & Knutson, 2010) and humans (Liu, Hairston, Schrier, & Fan, 2011; Schultz, 2000) have shown that dopaminergic regions (e.g., dorsal striatum [caudate, putamen], and ventral striatum [ventral tegmental area and substantia nigra; VTA/SN]) are active and functionally connected during incentive processing (Camara, Rodriguez-Fornells, Ye, & Münte, 2010). The monetary incentive delay (MID) task (Knutson, Westdorp, Kaiser, & Hommer, 2000) – a speeded reaction time task in which participants can earn or avoid losing money for responding to a visual target – is often used to induce gain and loss motivation and to observe anticipation and feedback-related brain activity. Recently, we analyzed younger and older adult brain responses during gain and loss anticipation in the MID task (Spaniol et al., 2015).[1] In line with prior work (Rademacher et al., 2010; Samanez-Larkin et al., 2007), our findings indicated that both groups engaged the dopaminergic reward network including VTA/SN as well as caudate, thalamus, medial frontal gyrus, and bilateral insula. Additionally, older adults engaged lateral parietal and default mode network regions during anticipation of high and low incentive cues. Further, greater engagement of these additional regions was correlated with faster reaction time on the MID task for older adults only. The findings did not vary according to the valence (i.e., gain or loss) of the incentive cue. A previous study demonstrated striatal activation differences between older and younger adults as a function of cue valence despite no behavioral differences (Samanez-Larkin et al., 2007), with older adults showing similar levels of activation as younger adults in striatum and insula in response to gain cues, but reduced activation in response to loss cues. These findings were in line with the socioemotional selectivity theory (Carstensen, 1995; Mather & Carstensen, 2005) which posits that due to the acknowledgement of a limited lifespan, older adults exhibit a motivational shift which can manifest as a positivity bias: choosing to focus more on positive and less on negative stimuli. The divergent findings of Samanez-Larkin et al. (2007) and Spaniol et al. (2015) regarding the age x valence interaction may be due to different demands on learning and memory in the two studies (e.g., learning the incentive value of abstract symbols versus literal incentive cues), as well as differences in the analytic approach of the fMRI data (univariate versus multivariate, respectively).

Much of the literature has focused on age differences at the anticipation stage of incentive processing, but feedback also guides behavior and cognition (Gable & Harmon-Jones, 2010; Rademacher et al., 2010). For example, Mather and Schoeke (2011) found that memory for stimuli presented up to 20 s after positive reward feedback was enhanced for both younger and older adults, providing behavioral evidence of

intact processing of feedback cues in older age. Examining activation levels in response to varying valence, trial outcome, and monetary magnitude during feedback of the MID task, two studies found no age-related differences (Samanez-Larkin et al., 2007; Samanez-Larkin, Worthy, Mata, McClure, & Knutson, 2014). Using a different paradigm, involving gains and losses during a card-guessing task, Cox, Aizenstein, and Fiez (2008) reported an age-related reduction in the magnitude and spatial extent of striatal activation, as well as a trend toward a more pronounced effect in response to loss compared to gain feedback in older adults. Others have reported an age-related increase in activation of ventral and dorsal striatum during reward feedback (Schott et al., 2007), but this study examined responses to gain feedback only, and thus was not informative about potential age differences in valence effects (gain vs. loss) at the feedback stage.

In addition to regions in the striatum, the medial frontal cortex is also involved in feedback processing. Ventral medial prefrontal cortex (vmPFC) is thought to play a key role in coding the subjective value of a reward, monitoring the outcome of current choices (Delgado et al., 2016; Fellows, 2007; Haber & Knutson, 2010; Levy & Glimcher, 2012; Liu et al., 2011), and there is some suggestion that it may be particularly involved in learning from negative feedback (Wheeler & Fellows, 2008). The frontal lobe undergoes changes even during healthy aging which may compromise connections between frontal lobe and midbrain reward structures which develop during adolescence (Vink et al., 2014). Executive functions such as working memory (Salthouse, 2010), as well as gray matter volume in prefrontal cortex (Fjell et al., 2009; Raz et al., 1997) and white matter tracts (Salat et al., 2005) that connect the frontal lobe to other parts of the brain, begin to show degeneration. Interestingly, the vmPFC remains relatively intact with less volumetric deterioration than other parts of frontal cortex (Fjell et al., 2009). This is in line with evidence that vmPFC activation during incentive feedback is similar for younger and older adults (Cox et al., 2008; Samanez-Larkin et al., 2007, 2014; Schott et al., 2007; Vink, Kleerekooper, van den Wildenberg, & Kahn, 2015). These findings make the vmPFC a region of particular interest in the context of incentive feedback processing and aging.

All the prior work in the area of incentive feedback processing and aging has used univariate BOLD activation analyses. It is well established that cognitive and affective processes emerge from activity within, and the interactions between, large-scale networks comprised of distributed brain regions. Such network activity is not captured in assessments of voxel-level mean activity, which form the focus of univariate fMRI analysis methods (Friston, 1994; McIntosh, 1999; Mesulam, 1990). In the current study, we employ partial least squares (PLS), a multivariate analysis approach, to examine neural interactions between seed voxels of interest and all other voxels in the brain (Burianova, McIntosh, & Grady, 2010; McIntosh, 1999; McIntosh & Gonzalez-Lima, 1994; McIntosh & Lobaugh, 2004). This technique allows for the identification of unbiased data-driven seed voxels of interest and has the advantage of providing a measure of co-varying activity or functional covariance among brain regions across experimental conditions which can occur even when there are no significant changes in mean activity level (Grady et al., 1998; McIntosh & Gonzalez-Lima, 1994). Examining functional covariance in the context of aging is important to understanding whether age affects how information in the brain is transferred and integrated (Sala-Llonch, Bartrés-Faz, & Junqué, 2015) particularly in light of recent evidence that aging leads to less distinction between networks, and weakened connectivity between nodes within a network that support

higher order cognitive functions (Chan, Park, Savalia, Petersen, & Wig, 2014; Geerligs, Renken, Saliasi, Maurits, & Lorist, 2015). We are not aware of any studies that have employed this method to examine whole-brain functional covariance during feedback processing in older adults.

The goal of the current study is to examine age-related differences in functional covariance during performance-contingent feedback processing. We specifically address whether any age-related covariance changes interact with trial valence (i.e., gain, loss) as well as trial outcome (i.e., successful, unsuccessful). This is an important question given research indicating that incentive feedback does have effects on subsequent behavior and cognition in both younger (Gable & Harmon-Jones, 2011) and older adults (Mather & Schoeke, 2011; Rademacher et al., 2010). Theoretically supported data-derived seeds from a preliminary analysis were selected, including one in the dorsal striatum (part of the canonical reward network (Schultz, 1998)), and a region in the ventromedial prefrontal cortex. Activity from these seeds was correlated with all other voxels in the brain to examine whole-brain functional covariance. Based on the prior work examining age-related changes in anticipation processing (Spaniol et al., 2015), we hypothesized that older adults would maintain reward network integrity during feedback processing. Given the mixed findings of age x valence interactions at the anticipation stage (Samanez-Larkin et al., 2007; Spaniol et al., 2015), and prior reports of no age x valence interactions at the feedback stage (Samanez-Larkin et al., 2007), it was an open question whether connectivity would differ depending on valence and outcome of the feedback.

Method

Participants

All procedures were approved by the ethics board at both Baycrest Hospital and Ryerson University. Younger adults were recruited from Ryerson University and the Toronto area via community websites (Craigslist.ca and Kijiji.ca) and older adults were recruited from both the Ryerson and Baycrest older adult participant pools. Before being scheduled to participate, study eligibility was determined with an extensive medical screening questionnaire to assess past and current conditions (e.g., psychiatric illness, depression, concussion, stroke, etc.) and medications that may affect cognition (e.g., sleep aids, prescription pain medication, etc.). Participants also completed an MRI safety questionnaire to ensure no contraindications to the MRI procedure (e.g., metal implants). Sixteen young adults (9 females) and 17 older adults (9 females) participated in exchange for $80 compensation in addition to performance-contingent rewards. Two older adult males were excluded from analysis, one due to an incidental MRI finding and another for failing to follow instructions in the scanner. The final sample thus included 15 older adults.

On average, older adults were 68.47 (*SD* = 5.38, range = 60–78) and younger adults 25.44 (*SD* = 3.79, range = 20–33) years old. The two groups did not differ on years of education (M_{older} = 16.47, *SD* = 1.96; $M_{younger}$ = 16.69, *SD* = 2.85), nor on any subscales of the revised 60-item NEO Five-Factor Inventory (Costa & McCrae, 1989). All participants scored 27 or higher on the Mini Mental State Exam (Folstein, Folstein, & McHugh, 1975), with the exception of one older adult with a score of 26. This individual was not excluded from the analyses since no other measures showed evidence of impairment,

and excluding the participant did not change the pattern of results. Older adults scored higher than younger adults on the positive mood scale (M_{older} = 33.07, *SD* = 7.08; $M_{younger}$ = 28.25, *SD* = 5.75) of the Positive and Negative Affect Schedule (PANAS; Watson, Clark, & Tellegen, 1988), $t(29) = 2.09$, $p = .046$, $\eta^2 = .13$, and on the Mill-Hill vocabulary scale, $t(28) = 3.50$, $p = .002$, $\eta^2 = .30$ (M_{older} = 23.00, *SD* = 4.02; $M_{younger}$ = 18.38, *SD* = 3.22).

Paradigm

While in the MRI scanner, participants completed a revised version of the Monetary Incentive Delay task (rMID; Knutson et al., 2000; see Figure 1). The rMID is a simple reaction time task in which each trial begins with a visual cue (Win $5.00, Win $0.00, Lose $5.00, and Lose $0.00) that indicates the outcome associated with successful performance on that trial. Successful performance is defined as hitting a button during the brief presentation of a visual target. "Win" cues indicate how much money will be won if the response is successful, whereas "Lose" cues indicate how much money the participant will avoid losing if the response is successful. After an interstimulus interval of varying duration, the cue was followed by the presentation of the visual target ("star"), during which the participant had to make a button press response. Task difficulty adjusted to each participant's speed, so each participant achieved a 66% hit rate overall (Knutson et al., 2000; Samanez-Larkin et al., 2007). At the end of each trial, participants received feedback regarding the trial outcome with the word "Hit" for successful trials and "Miss" for unsuccessful trials. The feedback also indicated the monetary results of that trial with four possible outcomes. The current study focuses on trials with $5 anticipation cues only to answer questions about age x valence interactions during feedback while participants are in a motivational state. We analyze the four feedback possibilities associated with $5 trials: +$5.00 (Gain_Hit), +0.00 (Gain_Miss), -$5.00 (Loss_Miss), and -$0.00 (Loss_Hit). OptSeq (Greve, 2002) was used to generate optimized jittered trial sequences for efficient estimation of the hemodynamic signal. Optseq created a randomized schedule oftrial between interstimulus interval lengths of 2000, 4000, 6000, and 8000 ms based on the study parameters (e.g., number of time points, repetition time).

Procedure

FMRI behavioral procedures

Participants spent the first 30 min of their session reading instructions and practicing the task in the MRI simulator. This ensured that participants were comfortable in the MRI environment, that they understood instructions, and had practice with the button presses necessary for responses. Participants then entered the MRI scanner and were instructed that the experiment was about to begin. After the anatomical scan, participants read over the instructions for the task one more time before staring the rMID task. This was an event-related design and participants completed three runs of thirty trials, each run was 6 min and 40 s. At the end of the session, participants were paid the full amount they had earned on the task in addition to $80 for participation.

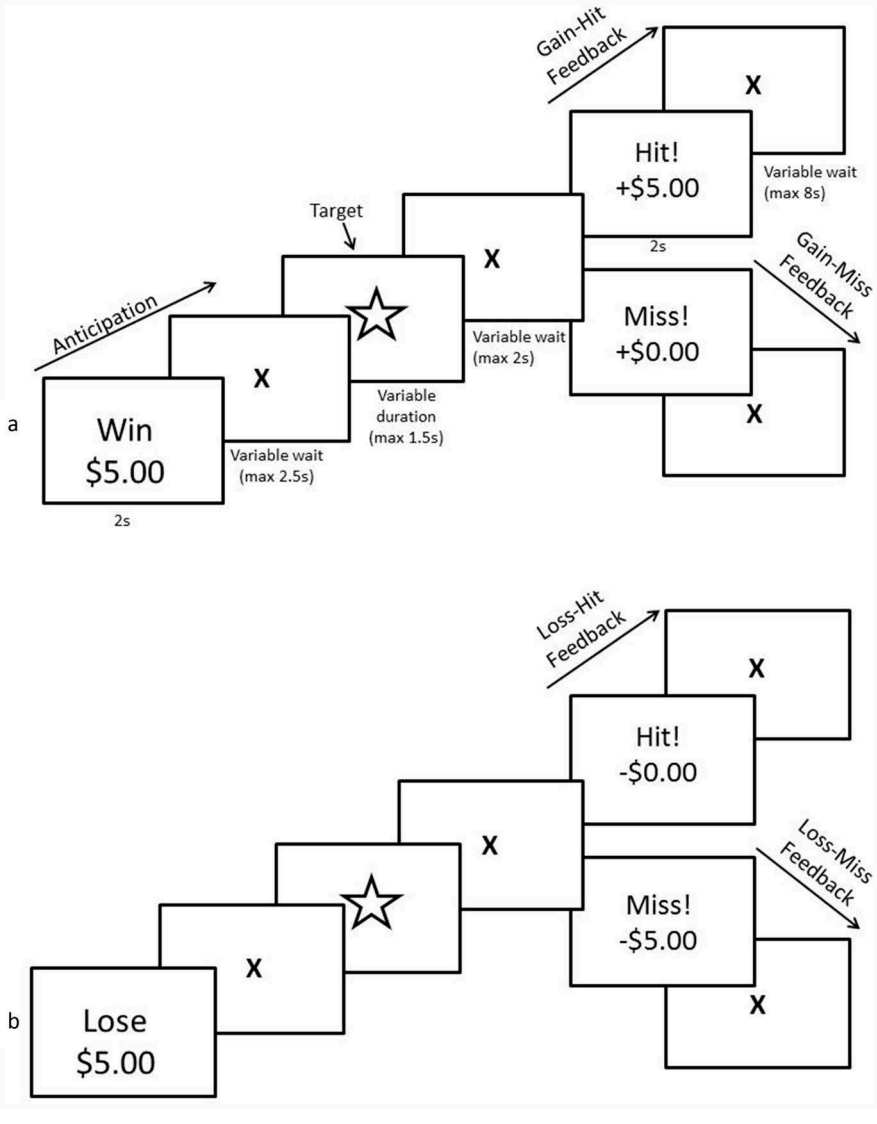

Figure 1. Schematic of the revised MID task. Panel A depicts a reward trial with a $5 cue and the two possible outcomes. Gain_hit feedback indicates the participant successfully made a button press to the target and won $5, and gain_miss feedback indicates the participant did not successfully make the button press and won $0. The timing of the trial is also indicated in Panel A (s = seconds). Panel B depicts a loss trial with a $5 cue and two possible outcomes. Loss_hit feedback indicates the participant made a successful button press and lost $0. Loss_miss feedback indicates the participant did not make the button press successfully and lost $5.

FMRI data acquisition

MRI scanning was conducted on a Siemens Trio 3.0T whole-body scanner using a 32-channel "matrix" head coil. Anatomical imaging protocol included three dimensional T1-weighted imaging (MPRAGE, FOV = 25.6 cm, 1x1x1mm voxels, TI/TE/TR = 1100/2.63/2000ms, flip angle = 9 deg, averages = 2, 160 slices, scan time = 5:44) and fluid attenuated inversion

recovery imaging (interleaved axial multislice FLAIR, FOV = 22.4cm, 0.9x0.9x5mm voxels, bandwidth = 315Hz/Px, TI/TE/TR = 2200/96/9000ms, averages = 1, concatenations = 3, 32 slices, 5 mm thickness, scan time = 3:38). Functional runs were acquired using an interleaved multislice EPI sequence (oblique axial orientation intercallosal line, 200 volumes; FOV = 19.2 cm, 64 × 64 acquisition matrix, 40 slices 3 × 3 mm^2 in-plane resolution, bandwidth = 2604 Hz/Px, TE/TR = 27/2000, flip angle = 70 deg). Stimulus presentation and image acquisition were synchronized with a trigger pulse sent by the scanner at the beginning of each experimental run. Using an LCD projector (NEC Model MTI065) with a 2.75–5 zoom lens (Navitar, Inc.), visual stimuli were projected on a screen at the back of the magnet bore and viewed by the participant through a mirror attached to the head coil. Responses to the stimuli were made via a Fiber-Optic Response Pad System (Current Designs Inc.; 4 buttons available per hand). fMRI-compatible prescription glasses were available to correct for visual acuity (SafeVision LLC., −6 to +6 diopters available in 0.5 increments). To reduce movement, foam sponges were used to restrain the participant's head and physiological data (heart rate, respiration, pulse) were also collected.

FMRI data analysis

Pre-processing of fmri data

Using Analysis of Functional Neuroimages software (AFNI; Cox, 1996), pre-processing steps included correction for head motion, physiological motion using cardiac and respiratory measures collected during data acquisition, and slice timing, as well as coregistration of image volumes to a standard MNI-space template, resampling to 2 mm^3 voxels (EPI.nii) and spatial smoothing with a 6-mm Gaussian kernel.

Multivariate analysis using partial least squares (PLS)

PLS is a multivariate technique that identifies spatiotemporal whole-brain patterns of activity related to a task, behavior, or correlated activity in specified brain area(s) to assess functional covariance (Grady, Grigg, & Ng, 2012). PLS operates on the covariance between brain voxels and the experimental design to identify orthogonal variables – latent variables (LVs) – that optimally relate the two sets of measurements (Grady et al., 2012). Each LV consists of a singular profile, singular image, and singular value (Habib, McIntosh, Wheeler, & Tulving, 2003). The singular profile, depicted as a bar graph, identifies the correlational relationship between activity in the seed voxel and activity in the rest of brain as function of the experimental conditions. The singular image includes the pattern of brain regions whose activity covaries with conditions and seed activity across each timepoint (i.e., lag). Within the singular image, each voxel is assigned a salience value characterizing how strongly that voxel represents the experimental effect expressed in the singular profile. A positive salience (warm colors in the image) indicates that the voxel expresses the effect and correlates with positive-going bars in the singular profiles, whereas a negative salience (cool colors in the image) indicates that the voxel expresses the reverse effect and negatively correlates with positive-going bars but positively correlates with negative-going bars in the singular image (Habib et al., 2003). The LV's singular value indicates the proportion of covariance accounted for by the pattern in the singular profile. To determine whether an LV is statistically

significant, the singular value is submitted to a permutation test (McIntosh, Bookstein, Haxby, & Grady, 1996; McIntosh & Lobaugh, 2004).

The permutation test procedure yields exact probabilities for all LVs and thus provides an objective method for determining the number of LVs to be retained at a given significance level (e.g., $p < .05$; Grady et al., 2012). To determine which voxels robustly contributed to the brain pattern identified by each LV, the saliences (i.e., brain weights) from each voxel are submitted to a bootstrap estimation of the standard errors which protects against the effects of outliers (Habib et al., 2003). All seed-PLS analyses were conducted with 1000 permutations and 1000 bootstraps. All voxels where the bootstrap ratio (BSR) exceeded ±3.0 are considered to contribute reliably to the pattern. The BSRs are analogous to z scores, so a BSR of ±3 is equivalent to $p < .005$ (Grady et al., 2012; Grigg & Grady, 2010). Finally, only foci that exceeded a cluster threshold of 80 voxels are reported in the results section and used as a cut-off in the mask which removed small clusters from the images of brain activation.

Bootstrap estimates are also used to derive 95% confidence intervals calculated around the LV correlation profiles to provide a measure of the reliability of the correlation pattern (McIntosh & Lobaugh, 2004). Overlapping confidence intervals indicate that seed correlations across conditions do not significantly differ from each other. Confidence intervals that overlap with zero indicate that the correlation for a given condition/seed is not significantly different from zero, and does not reliably contribute to the pattern of results (Grady et al., 2012; Grigg & Grady, 2010).

Two different PLS analyses were used. The first was a mean-centered analysis, the results of which were used to identify seed voxels and extract the mean BOLD activity for each condition. These BOLD values were then entered into the seed-voxel analysis to measure functional covariance across the whole brain.

Mean-centered PLS

Mean-centered PLS is a data-driven analysis that is helpful for exploring the data without pre-specified contrasts. It offers an estimate of how brain activity varies across experimental conditions without a priori hypotheses. The results of the mean-centered analysis can be used to identify regions of interest or "seed regions" to be used in subsequent analyses of functional covariance (Habib et al., 2003).

Seed-voxel PLS

Functional covariance can be assessed using "seed-voxel PLS" (McIntosh et al., 1996). This technique probes correlations between mean signal brain activity in a specified seed region and brain activity across the whole brain (across subjects and time points) as a function of experimental condition (Della-Maggiore et al., 2000; Habib et al., 2003; McIntosh, 1999; McIntosh, Nyberg, Bookstein, & Tulving, 1997). Seed voxel selection can be data-driven (e.g., based on other analyses) or hypothesis-driven, or both (Habib et al., 2003). In the current study, we use the data-driven approach to identify seed voxels from regions that were considered of theoretical importance. LVs are produced with singular value decomposition using the correlation maps of each condition. LVs indicate the pattern of correlation or connectivity that characterizes each condition across subjects and lags (Grady et al., 2012; McIntosh, 1999).

Results

Behavioral data

The behavioral data were analyzed using SPSS (Statistical Package for Social Sciences 18.0. SPSS Inc., Chicago, USA). On average, younger adults earned more performance-based rewards (M = $56.56, *SD* = $11.06) than older adults (M = $44.33, *SD* = $15.10), t (29) = 2.58, $p = .015$, $\eta^2 = .19$.

Hit rate

A 2 (age group: young, older) x 2 (cue magnitude: $5, $0) x 2 (valence: gain, loss) mixed ANOVA on the hit rate yielded a main effect of cue magnitude, $F(1, 29) = 47.65$, $MSE = .92$, $p < .001$, $\eta^2_p = .62$, which was qualified by a significant Magnitude x Group interaction $F(1, 29) = 6.33$, $MSE = .12$, $p < .02$. This interaction was followed up with separate ANOVAs for younger and older adults. In younger adults, hit rates were higher following $5 cues ($M = .77$, $SD = .05$) compared to $0 cues ($M = .53$, $SD = .06$), $F(1, 15) = 87.41$, $MSE = .44$ $p < .001$, $\eta^2_p = .85$. This same pattern was also present for older adults who had higher hit rates after $5 cues ($M = .71$, $SD = .07$) compared to $0 cues ($M = .60$, $SD = .11$), $F(1, 14) = 6.18$, $MSE = .09$, $p < .03$, $\eta^2_p = .31$. The overall hit rate on the MID task did not differ between the two groups, ($M_{young} = .65$, $SD = .02$; $M_{older} = .65$, $SD = .03$), suggesting the calibration to hold hit rate at about 66% overall was successful.

Reaction time (RT)

The same 2 (age group: young and older) x 2 (cue magnitude: $5, $0) x 2 (valence: gain, loss) mixed ANOVA was run on median reaction times. This yielded a main effect of cue magnitude, $F(1, 29) = 22.22$, $MSE = 8512.84$, $p < .001$, $\eta^2_p = .43$, which was qualified by a significant Magnitude x Group interaction $F(1, 29) = 12.68$, $MSE = 4856.53$, $p = .001$, $\eta^2_p = .30$. This interaction was followed up with separate ANOVAs for younger and older adults. This revealed that younger adults had significantly shorter RTs following $5 cues (M = 198 ms, *SD* = 23 ms) compared to $0 cues (M = 228 ms, *SD* = 36 ms), $F(1, 15) = 28.76$, $MSE = 8512.84$, $p = .001$, $\eta^2_p = .66$. The effect of magnitude on RT was not significant for older adults $F(1, 14) = .86$, $MSE = 246.88$, $p = .37$, $\eta^2_p = .06$, and on average RTs were similar following $5 cues (M = 221 ms, *SD* = 30 ms) and $0 cues (M = 225 ms, *SD* = 27 ms). No effects involving valence were significant.

FMRI results

The analyses focused on feedback processing on $5 trials. We examined the effects of valence (gain, loss) and trial outcome (hit, miss), resulting in four task conditions: gain_hit (+$5), gain_miss (+$0), loss_hit (-$0), and loss_miss (-$5).

Identification of seed voxels

Given prior work outlined in the introduction, we decided a priori to select one seed region from the reward network and one from the prefrontal cortex. To identify seed regions, mean-centered PLS analysis was used, which identified spatiotemporal fMRI signal patterns associated with variation in feedback-related activity. The results of this

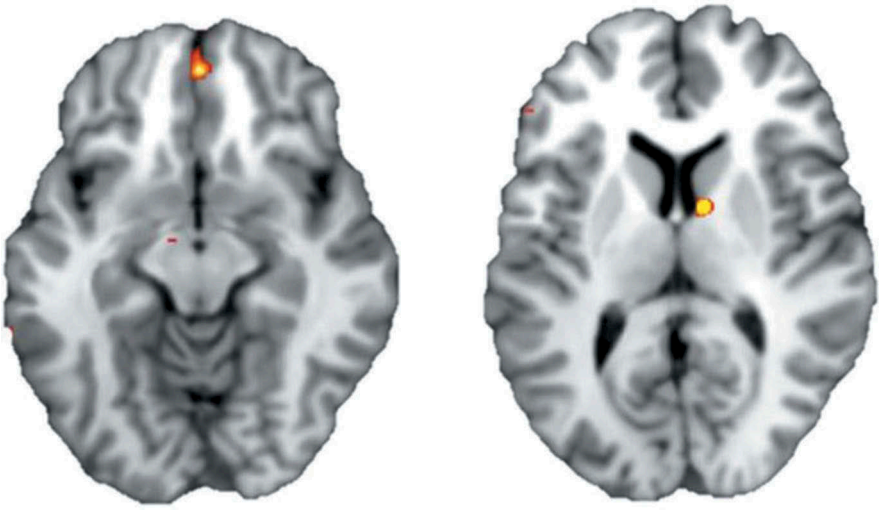

Figure 2. Location of the two regions that were identified from LV2 of the mean-centered analysis. The medial prefrontal cortex seed (MNI: x = 0, y = 48, z = − 8) shown on the left at z = − 8, and the right caudate (MNI: x = 10, y = 0, z = 10) seed shown on the right at z = 10. The two seeds were entered into a subsequent seed-voxel analysis.

analysis are reported in the supplementary material. From this analysis, the two seeds were chosen: the vmPFC and the right caudate (see Figure 2).

Seed-voxel PLS

The BOLD data for both seeds were extracted from the mean-centered analysis and then entered simultaneously into the seed-voxel PLS analysis to examine effects of age, valence and trial outcomes on functional covariance during feedback processing. In the singular profile bar graphs[2] representing each LV pattern, the left bar represents the caudate seed, and the right bar represents the vmPFC seed within each condition. Overlapping confidence intervals (CIs) in the singular profile indicate that conditions are not significantly different from each other. Only those conditions with CIs not containing zero are considered to be reliably and significantly contributing to the pattern.

LV1

The first LV accounted for 54.46% of the covariance, $p < .001$, and identified a general network of covariance that characterized both the groups, all conditions and both seeds, with the exception of the vmPFC seed for younger adults during gain_miss and loss_hit. The correlations for these conditions had CIs that overlapped with zero and did not significantly contribute to the pattern. The singular profile for LV1 is shown as a bar graph in Figure 3a. The network of brain regions associated with the LV is depicted in singular image Figure 3b. Figure 3b shows the regions from Lag 3 (4–6 s post feedback onset), and coordinates of these regions are reported in Table 1 (see Supplementary Material Table 1 for a full list of regions at each lag correlated with this LV). Feedback processing across conditions and groups

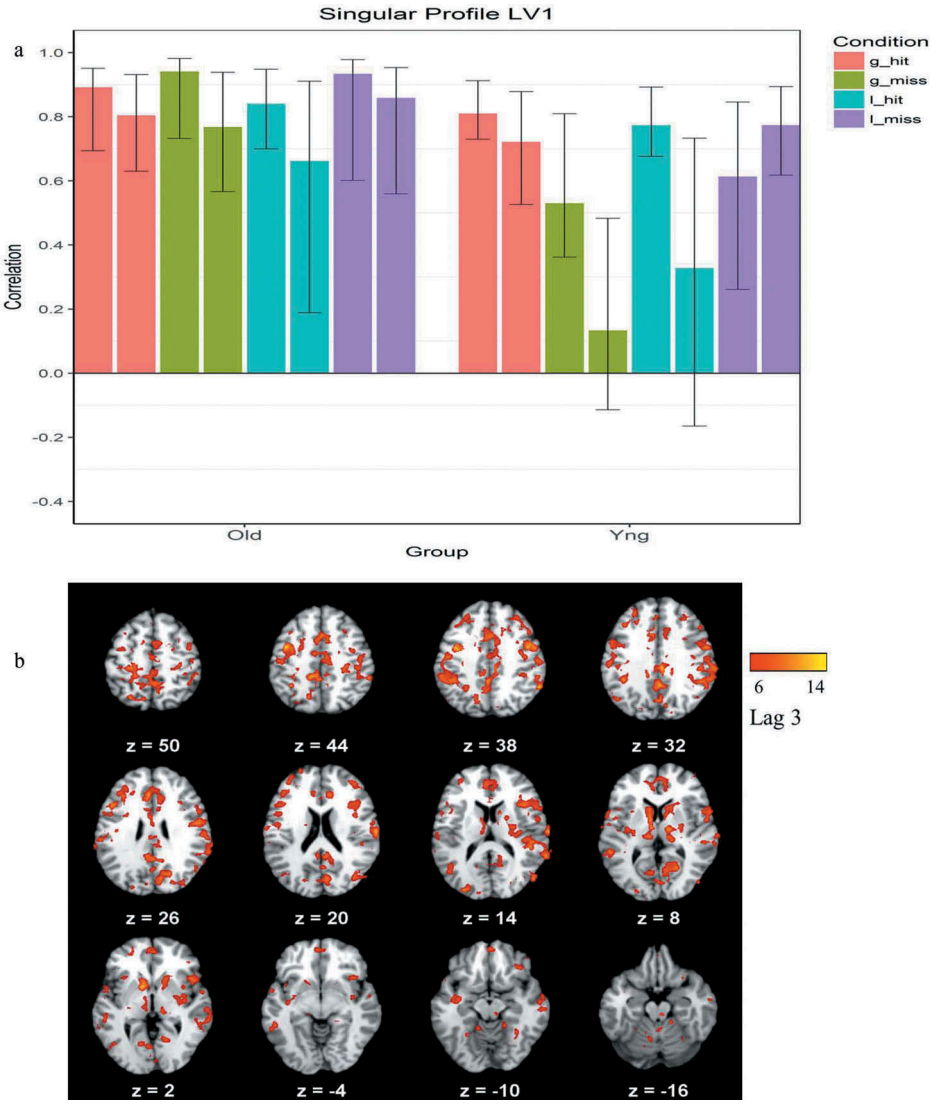

Figure 3. Pattern associated with LV1. (a) Singular profile depicting the LV pattern is shown as a bar graph. The left bar of each color represents the caudate seed, and the right bar represents the vmPFC seed within each condition. Older adult (old) brain correlations are shown on the left and young adults (yng) on the right. Confidence intervals (95%) calculated around the LV correlation profiles were derived from 1000 bootstrap estimates. The feedback conditions depicted in the graph are as follows: g_hit = gain_hit (+$5), g_miss = gain_miss (+$0), l_hit = loss_hit (-$0) and l_miss (-$5). (b) An image illustrating the network of regions from Lag 3 (4 – 6 s post feedback onset) supporting the pattern in the singular profile with bootstrap ratios ranging from 6 to 14. Numbers below each slice indicate z coordinate. The full list of regions and coordinates associated with this pattern are in Table 1.

was supported by covariance between the two seed regions and the midbrain reward network including dorsal and ventral striatum (e.g., caudate, SN/VTA), as well as a diffuse set of regions including the thalamus, cingulate extending into pre- and post-central gyrus, middle and superior temporal gyrus.

Table 1. LV1 correlations with seed activity during Lag 3.

Hem	Lobe	Region	BA	BSR	Talairach Coordinate			cluster
					x	y	z	
L	Frontal	Precentral Gyrus extending into Middle Frontal Gyrus and Postcentral Gyrus	6	14.7261	−37	−4	41	44,339
L	Temporal	Superior Temporal Gyrus	22	6.4206	−48	13	−3	102
L	Occipital	Middle Temporal Gyrus	19	8.3221	−43	−59	13	332
L	Other	Claustrum	NA	8.3693	−35	−10	−5	246

Lag: TR (2 s); Hem: hemisphere; L: left; R: right; BA: Brodmann's area; NA: no Brodmann area; BSR: bootstrap ratio; x: x coordinate in Talairach space; y: y coordinate in Talairach space; z: z coordinate in Talairach space; cluster: size of cluster in voxels; BSR thresholded to ±4.5 and cluster extent of at least 100 voxels.

LV2

The second LV depicted in Figure 4a accounted for 9.17% of the covariance, $p = .006$, and characterized a different pattern of covariance for younger and older adults. For younger adults, the pattern captured all conditions and both seeds, but for older adults, the CIs for most conditions and seeds overlapped with zero. Exceptions were the caudate seed for loss_hit feedback (left blue bar), and the vmPFC seed for loss_miss feedback (right purple bar). This suggests a different pattern of covariance for loss feedback processing in older adults depending on the outcome (hit versus miss). The pattern for older adults' loss_miss feedback emerged early at Lag 1 (0–2 s post feedback onset), and included covariance between the vmPFC and inferior frontal as well as midbrain reward regions, depicted in cool colors in Figure 4b. The pattern shown by younger adults across all conditions, and by older adults during loss_hit feedback, peaked later, in Lag 4 (6 – 8 s after feedback onset). It is depicted in warm colors in Figure 4c. This network included covariance between the seeds and several cortical areas, including bilateral frontal and temporal gyri, as well as anterior cingulate. Coordinates of the regions shown in these images are reported in Table 2 (see Supplementary Material Table 2 for a full list of regions at each lag correlated with this LV).

LV3

Finally, a third pattern identified an LV that accounted for 8.19% of the covariance, $p = .02$ (see Figure 5a). Again, for younger adults, this pattern of covariance characterized all conditions and both seeds with the exception of the vmPFC seed during loss_miss feedback. For older adults, in contrast, a different pattern of covariance emerged for the two types of miss feedback. The pattern for older adults' gain_miss feedback started early in Lag 1 and included strong covariance between the seeds and medial and lateral frontal regions, depicted in warm colors in Figure 5b. A different pattern of covariance emerged for older adults for loss_miss feedback, and for younger adults across conditions. This pattern peaked in Lag 3 (4–6 s post feedback onset) and is shown in cool colors in Figure 5c. Here the seeds covaried with more posterior regions, including posterior cingulate and precuneus. Coordinates of the regions depicted in these images are reported in Table 3 (see Supplementary Material Table 3 for a full list of regions at each lag correlated with this LV).

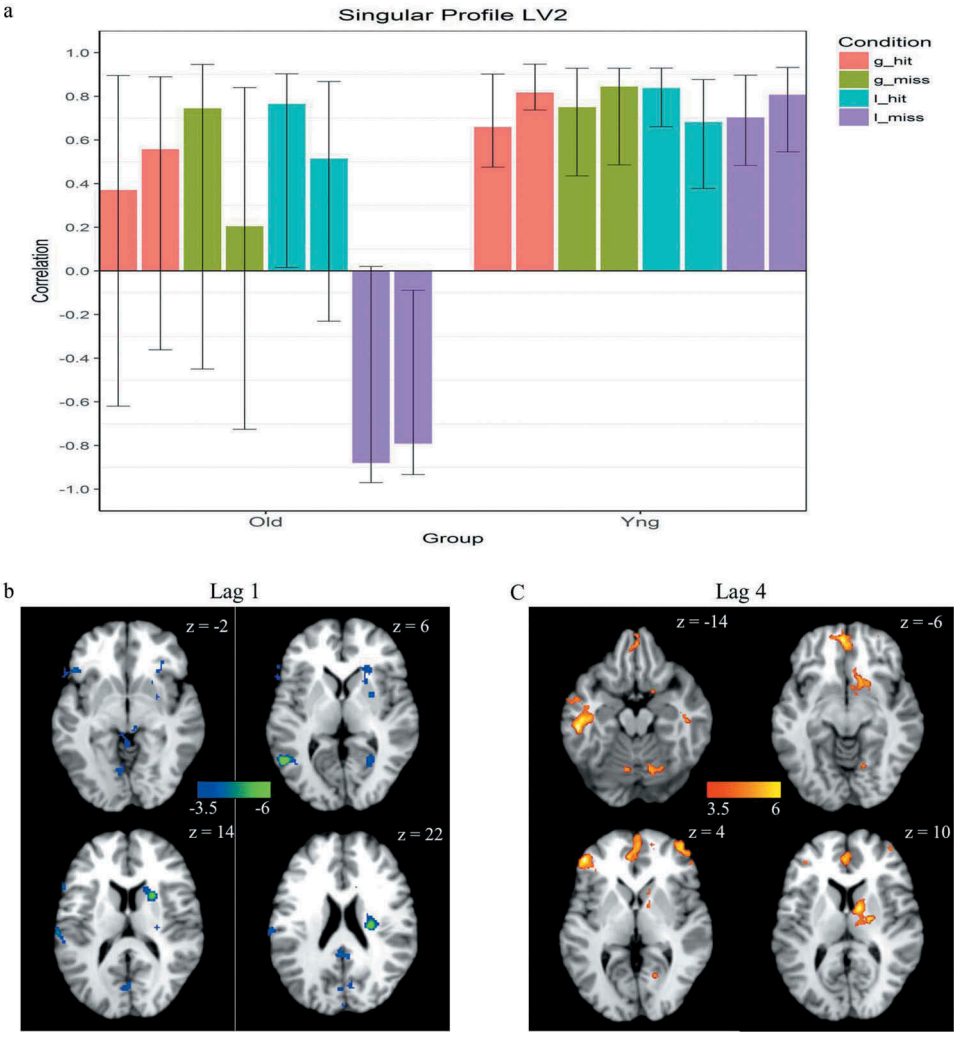

Figure 4. Pattern associated with LV2. (a) Singular profile depicting the LV pattern is shown as a bar graph. The left bar of each color represents the caudate seed, and the right bar represents the vmPFC seed within each condition. Older adult (old) brain correlations are shown on the left and young adults (yng) on the right. Confidence intervals (95%) calculated around the LV correlation profiles were derived from 1000 bootstrap estimates. The feedback conditions depicted in the graph are as follows: g_hit = gain_hit (+$5), g_miss = gain_miss (+$0), l_hit = loss_hit (-$0) and loss_miss (-$5).(b) A pattern of correlated activity at Lag 1 (0 – 2 s post feedback onset). Negative values in the singular image positively correlated with regions in cool colors (bootstrap ratios from −3.5 to −6 are shown). (c) A pattern of correlated activity at Lag 4 (6 – 8 s post feedback onset). Positive values in the singular image positively correlate with regions in warm colors (bootstrap ratios from 3.5 to 6 are shown). Z-coordinates are indicated at each slice.

Discussion

Using fMRI, we examined functional covariance between two theoretically supported, data-driven seed voxels, and voxels in the rest of the brain during performance contingent gain and loss feedback. Specifically, we tested for interactions between age (young, old), valence (gain, loss), and outcome (hit, miss) feedback on whole-brain

Table 2. LV2 correlations with seed activity during Lags 1 and 4.

						Talairach Coordinates			
Lag	Hem	Lobe	Region	BA	BSR	x	y	z	cluster
Negative Saliences									
1	L	Frontal	Inferior Frontal Gyrus	47	−5.6277	−44	22	1	164
	L		Precentral Gyrus	6	−6.1086	−17	−15	60	269
	L	Limbic	Posterior Cingulate	29	−5.1957	−3	−43	22	89
	R			30	−4.9089	21	−53	9	114
	L	Temporal	Middle Temporal Gyrus	37	−7.7130	−50	−56	4	118
	L		Superior Temporal Gyrus	42	−5.0682	−59	−25	16	116
	L	Occipital	Cuneus	18	−5.0300	−3	−70	14	136
	L			19	−4.8475	−2	−79	32	101
	L	Cerebellum	Extending into Lingual Gyrus	NA	−6.6391	−12	−61	−8	122
	L	Cerebellum		NA	−4.4463	1	−35	−6	80
	R	Other	Caudate	NA	−6.3377	19	7	19	358
	R		Thalamus	NA	−6.5152	25	−16	21	146
Positive Saliences									
4	L	Frontal	Inferior Frontal Gyrus	46	7.5964	−44	38	8	174
	L		Superior Frontal Gyrus	8	6.4542	−14	49	40	195
	R			9	5.9582	12	55	32	109
	L	Limbic	Anterior Cingulate extending into Medial Frontal Gyrus	32	7.6082	−3	46	6	488
	R		Anterior Cingulate	32	5.7381	14	45	8	232
	L	Temporal	Inferior Temporal Gyrus extending into Middle Temporal Gyrus and Parahippocampus	20	7.8949	−50	−24	−13	447
	L	Parietal	Superior Parietal Lobule	7	6.0611	−30	−64	49	98
	L	Cerebellum		NA	8.4472	−23	−39	−27	2707
	R			NA	5.5425	18	−65	−27	282
	R			NA	5.4418	14	−59	−4	113
	L			NA	5.5959	−36	−45	−36	161
	L			NA	6.8397	−14	−73	−27	173
	R	Other	Putamen extending into Caudate and Globus Pallidus	NA	5.9299	16	10	−2	225
	R		Caudate extending into Thalamus	NA	6.1806	10	−2	13	183

Lag: TR (2 s); Hem: hemisphere; L: left; R: right; BA: Brodmann's area; NA: no Brodmann area; BSR: bootstrap ratio; x: x coordinate in Talairach space; y = y coordinate in Talairach space; z: z coordinate in Talairach space; cluster: size of cluster in voxels; BSR thresholded to ±3.5 and cluster extent of at least 80 voxels.

functional covariance using seeds in the dorsal striatum (i.e., caudate) and vmPFC. The analysis revealed three significant LV patterns in the data. The first, a general neural pattern that characterized both age groups and all conditions, was comprised of a large network of regions including the midbrain reward network. The second LV was sensitive to the type of loss feedback (i.e., loss_miss [-$5] vs. loss_hit [-$0]), but only for older adults. Finally, a third pattern characterized different networks for miss feedback in older adults, differentiating gain_miss (+$0) versus loss_miss (-$5) conditions. Younger adults did not show network-level modulation based on either valence or outcome, but did significantly contribute to the patterns in LV2 and LV3.

In line with the hypotheses, LV1 characterized a general pattern of covariance expressed similarly for younger and older adults. The pattern strongly suggests that there is a common set of regions, particularly in the reward network, that jointly support feedback processing regardless of valence or trial outcome. This network remains intact in healthy aging. Of particular interest was how the two seed regions would correlate with other regions in the network. Both the caudate and vmPFC correlated strongly with this network supporting our rationale for using these seeds regions as both regions are

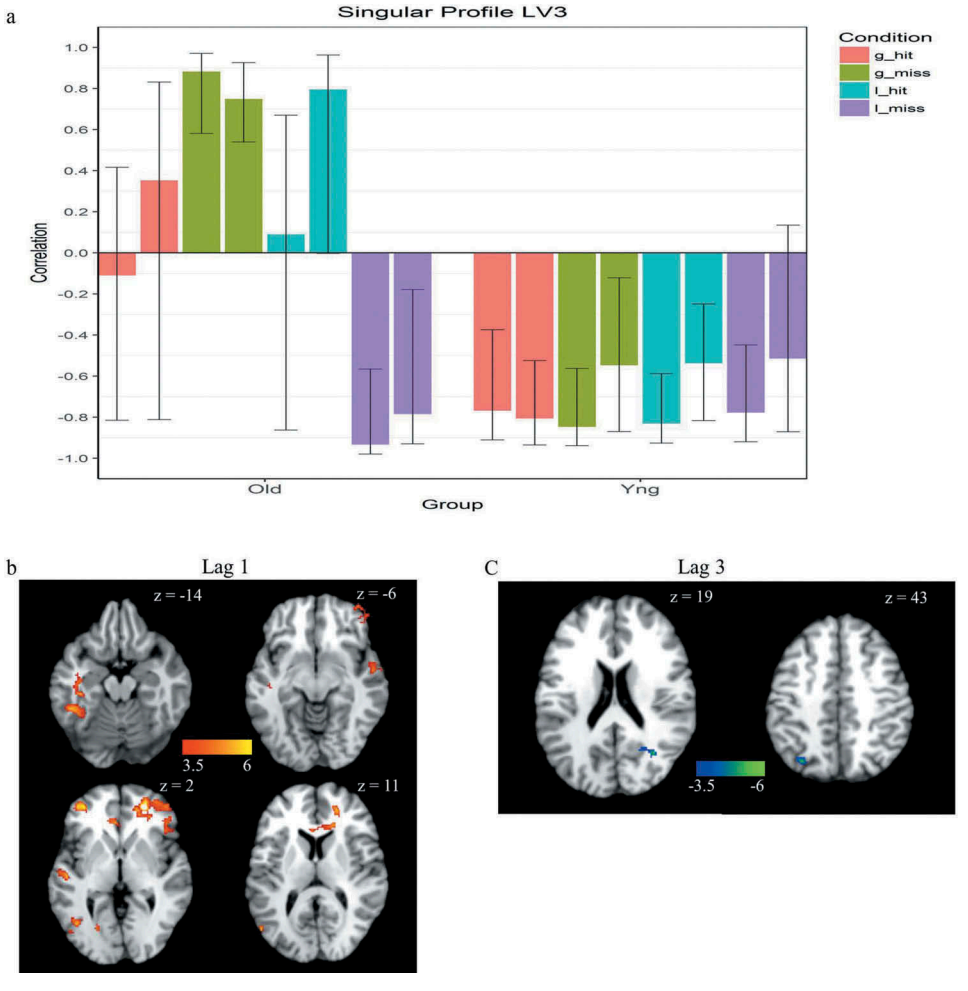

Figure 5. Pattern associated with LV3. (a) Singular profile depicting the LV pattern is shown as a bar graph. The left bar of each color represents the caudate seed, and the right bar represents the vmPFC seed for each condition. Older adult (old) brain correlations are shown on the left and young adults (yng) on the right. Confidence intervals (95%) calculated around the LV correlation profiles were derived from 1000 bootstrap estimates. The feedback conditions depicted in the graph are as follows: g_hit = gain_hit (+$5), g_miss = gain_miss (+$0), l_hit = loss_hit (-$0) and loss_miss (-$5). (b) A pattern of correlated activity at Lag 1 (0 – 2 s post feedback onset). Positive values in the singular image positively correlate with regions in warm colors (bootstrap ratios from 3.5 to 6 are shown). (c) A pattern of correlated activity at Lag 3 (4 – 6 s post feedback onset). Negative values in the singular image positively correlated with regions in cool colors (bootstrap ratios from −3.5 to −6 are shown). Z-coordinates are indicated at each slice.

integral in supporting incentive feedback processing for both younger and older adults, as has been shown previously with activation analyses (Haber, 2011; Haber & Knutson, 2010; Samanez-Larkin et al., 2014; Schott et al., 2008; Vink et al., 2015).

Like LV1, in both LV2 and LV3, younger adults engaged a network of regions common across the experimental conditions. The networks engaged to support incentive feedback in younger adults are not modulated by the valence or outcome of that feedback.

Table 3. LV3 correlations with seed activity in Lags 1 and 3.

						Talairach Coordinates			
Lag	Hem	Lobe	Region	BA	BSR	x	y	z	cluster
Negative Saliences									
3	L	Parietal	Precuneus	19	−7.0217	−30	−65	42	90
	R			31	−5.7967	27	−60	19	249
Positive Saliences									
1	R	Frontal	Medial Frontal Gyrus	9	8.4866	20	41	11	809
	L		Middle Frontal Gyrus	10	6.3074	−38	44	7	80
	R	Temporal	Superior Temporal Gyrus	22	5.3137	55	3	−4	111
	L			22	5.621	−48	−18	2	253
	L		Middle Temporal Gyrus	37	5.7602	−41	−58	2	167
	L		Fusiform Gyrus	37	5.3032	−42	−40	−13	139
	R	Parietal	Postcentral Gyrus	3	5.7709	55	−19	35	291
	L		Precentral Gyrus	6	5.5907	−39	−7	33	81
	L	Occipital	Lingual Gyrus	19	4.8576	−20	−65	−5	80
	L	Cerebellum		NA	6.4694	−31	−40	−27	393
	R			NA	6.6816	9	−36	−39	208
	R			NA	5.9413	5	−64	−36	144
	L	Other	Caudate	NA	5.5296	−12	25	11	243

Lag: TR (2 s); Hem: hemisphere; L: left; R: right; BA: Brodmann's area; NA: no Brodmann area;BSR: bootstrap ratio; x: x coordinate in Talairach space; y: y coordinate in Talairach space; z: z coordinate in Talairach space; cluster: size of cluster in voxels; BSR thresholded to ±3.5 and cluster extent of at least 80 voxels.

In LV2 the pattern for younger adults peaked around 6–8 s post feedback. Both the vmPFC and caudate seeds strongly and positively correlated with this network which included other regions in the midbrain reward network as well as medial and lateral frontal cortex. In LV3, the pattern peaked about 4 – 6 s post feedback and included regions in posterior cortex. Work with adolescents has previously shown that striatal activity during feedback was reduced compared to anticipation suggesting that the striatum may be less involved in feedback processing as it is during anticipation (Vink et al., 2015). As discussed in the introduction, it is possible to find effects in functional covariance regardless of the direction – activation or deactivation relative to baseline – of BOLD activity (Grady et al., 1998; McIntosh & Gonzalez-Lima, 1994). From this functional covariance analysis, it is clear that the striatum still contributes to the networks supporting gain and loss feedback processing in younger adults potentially also indicating a developmental difference between adolescents and younger adults' reliance on striatal processing during feedback.

There were two age-variant neural patterns in the data associated with different experimental conditions. In addition to recruiting the general incentive feedback network (LV1) described above, older adults relied on additional networks to support negative feedback processing. Specifically, older adults relied on different networks during processing of the two types loss feedback (hit and miss) and different networks during processing of the two types of miss feedback (gain and loss). These two patterns will be discussed in turn.

The pattern in LV2 indicated that older adults recruited a network of regions in response to most negative type of feedback in the task, a loss of $5. The network included covariance between the vmPFC and subcortical structures in the reward network, as well as a small but diffuse set of regions in frontal, temporal, and posterior cortices. The covariance between the vmPFC and these other regions occurred very early, within two seconds post loss_miss feedback onset. This early pattern was specific

to older adults, but younger adults did significantly contribute to a later pattern that emerged 6–8 s post feedback onset that included covariance between the caudate seed and frontal and temporal regions. While this pattern was associated with younger adult feedback processing across all conditions, this network was recruited by older adults after successfully avoiding a loss (loss_hit). This was a positive outcome (-$0), but was still associated with a "negative" loss context.

The pattern in LV3 revealed different interregional connectivity patterns during gain_miss feedback and loss_miss feedback for older adults. Again at an early lag, 0 – 2 s post gain_miss feedback onset, older adults recruited a neural pattern where both seeds correlated strongly with medial and lateral frontal regions. Like LV2, in this pattern, older adults recruited an additional network to process negative feedback, this time after not successfully attaining a reward. A second pattern associated with loss_miss feedback for older adults peaked later, 4–6 s post feedback onset, and the seeds correlated with regions in posterior, rather than frontal cortex. Younger adults also contributed to this later pattern, but again this was across all feedback types.

Taken together, in both LV2 and LV3, older adults show correlations with medial parietal regions and caudate in the conditions where they lose money (loss_miss), and correlations with lateral frontal and ventral temporal cortex in conditions where due to performance, no money is lost or gained (loss_hit, gain_miss). One additional difference in these patterns however is the timing. Older adults recruited neural patterns very early to support miss feedback, loss_miss compared to loss_hit in (LV2) and gain_miss compared to loss_miss in (LV3). Younger adults did not show this temporal modulation.

PLS is a spatiotemporal analysis technique that provides information not only about interregional connectivity, but also about the temporal dynamics of these networks and how the seed regions contribute to the overall pattern across time. LVs 2 and 3 indicate that not only do the regions that additionally support feedback processing vary by age group, but also vary by the time courses of these networks. Younger adult patterns consistently peaked between Lags 3 and 4, and never contributed to the patterns in the earlier lags. To process the two types of miss feedback, monetary loss, and unsuccessful gain, older adults recruited neural networks very early after feedback onset. This early neural engagement by older adults after an unsuccessful trial might reflect a negative reward prediction error (Hollerman & Schultz, 1998) indicative of age differences in detecting or sensitivity to this type of error. The hit rate in the task was calibrated and miss feedback was statistically less expected, only occurring on ~33% of trials, thus participants received miss feedback much less often. Older adults may pay more attention to performance-based errors as poor performance might confirm metacognitive knowledge of their age-related declines (see Barber & Mather, 2013 for related ideas on stereotype threat). This sensitivity to the performance-based miss feedback may have led to earlier patterns of covariance associated with this feedback compared to younger adults. Negative reward prediction has been shown to be associated with decreased activation in the dopaminergic midbrain (Hollerman & Schultz, 1998; Tremblay, Hollerman, & Schultz, 1998), but negative prediction error has not been assessed using functional covariance analyses. As noted, activation and functional covariance analyses can reveal different patterns of neural results. These early patterns displayed by older adults may reflect negative prediction error, which when analyzed in this way include recruitment of regions in the midbrain and vmPFC.

Unlike our prior work examining the anticipation stage of this task using PLS analyses (Spaniol et al., 2015), in the current study, we found that functional covariance patterns in older adults did differ by valence (gain, loss), and outcome (hit, miss). This is somewhat in line with other findings of valence effects at anticipation, such that older adults activated similar regions as younger adults during gain anticipation, but had reduced activation in striatum and insula during loss anticipation (Samanez-Larkin et al., 2007; Samanez-Larkin & Knutson, 2015), although analysis of the feedback stage of the task found no age differences in activation (Samanez-Larkin et al., 2007). Evidence from the current study that older adults did not show separate or additional patterns of connectivity related to gain feedback compared to younger adults could be interpreted as a positivity effect (Mather & Carstensen, 2005; Reed & Carstensen, 2012) associated with motivational shifts in line with socioemotional selectivity in later life (Carstensen, 1995). However, evidence from the current study also indicated that older adults recruited additional functional networks to support more "negative" feedback (i.e., feedback associated with the loss context and unsuccessful performance) which fit with a slightly different interpretation of the positivity effect. Specifically, the recruitment of additional networks to support negatively associated feedback could indicate that this type of processing is more cognitively demanding and requires compensatory mechanisms to make up for age-related cognitive losses or performance difficulties (Labouvie-Vief, Grühn, & Studer, 2010; Vallesi, McIntosh, & Stuss, 2011), but given older adults did not modulate behavioral RT performance based on the experimental condition, this is speculative.

Understanding feedback processing in older adults has implications for learning, memory and decision making. Behavioral work has already shown that both younger and older adults show feedback-based modulation of long-term memory (Mather & Schoeke, 2011). Our results suggest that this might be due to older and younger adults relying on the same functional network to support positive feedback. The affect-integration-motivation (AIM) model (Samanez-Larkin & Knutson, 2015) outlines possible affect and motivational brain circuits that may influence decision making. In particular, the authors posit that motivational processes are associated with dorsal striatal and insular glutamatergic neurons that project to the pre-supplementary motor area which may degrade, even in healthy aging. This degradation may result in diminished value integration and suboptimal choices. In support of this model, our findings suggest that these regions indeed form a functional network during negative feedback.

Limitations and future directions

Older adults did not, or perhaps could not, modulate their reaction times[3] based on the experimental condition in the same way as younger adults. It is possible that older adults were expending their maximum effort on all trials and could not modulate effort based on the incentive value or valence. Although older adults showed neural modulation without behavioral modulation, tasks where older and younger adults are matched on performance would be beneficial to ensure no behavioral differences can account for the differences in age-related brain responses.

Older adults recruited additional networks of regions to support processing of unsuccessful "miss" feedback. Due to the calibration of hit rate during the behavioral task, miss

feedback was also statistically less frequent or less expected feedback. It is possible that neural modulation correlated with unsuccessful feedback is not associated with the "negativity" of the feedback, but instead characterized by how unexpected or novel it is. This would not fit with current theories of healthy aging which predict a motivational shift in affective processing leading to a positivity bias (Carstensen, 1995; Mather & Carstensen, 2005; Samanez-Larkin & Knutson, 2015). Further, if it were related to novel outcomes per se, one might expect to see the seeds correlating with the salience network (Seeley et al., 2007), including the insula and dorsal anterior cingulate (Ferdinand & Opitz, 2014), but this was not the neural pattern associated with either LV2 or LV3.

PLS affords information about the temporal aspects of the functional covariance patterns. Interestingly, older adults showed a different time course than younger adults in two of the patterns. Future work using EEG, a technique with higher temporal resolution, could provide more fine-grained information about potential age-related differences in the temporal dynamics of feedback processing.

Finally, the study included a group of 16 younger adults and 15 older adults. Future research looking to replicate and extend this line of work would benefit from larger sample sizes.

Conclusions

In the current study, we examine functional covariance patterns supporting incentive feedback processing in younger and older adults. Using PLS, the results indicate that older and younger adults recruit the same network of regions to support general feedback processing. Older adults recruited two additional networks to support negative feedback, in line with the positivity bias in aging. Further, the two seed regions, right caudate and vmPFC, both contributed to the networks associated with feedback processing. Taken together, the results indicate that healthy older adults maintain the ability to process gain and loss feedback, but require additional networks to support performance contingent monetary loss and unsuccessful feedback. The results have real-world implications such that older adults may show differential stimulus-reward learning and suboptimal decision making following negative feedback in particular.

Notes

1. The dataset used to analyze the anticipation stage of the MID task reported in Spaniol et al. (2015), is the same dataset used in the current study, but here we examine neural responses to the feedback stage of the MID task.
2. Brain scores in the singular image are arbitrarily assigned to either negative or positive salience. Negative brain scores (i.e., negative-going bars in the singular profile) are positively correlated with brain regions in cool colors and negatively correlated with brain regions in warm colors in the singular image. Similarly, positive brain scores (i.e., positive-going bars in the singular image) are positively correlated with brain regions in warm colors and negatively correlated with brain regions in cool colors in the singular image.
3. In an analysis, not reported in the manuscript, reaction times across conditions and brain scores in LV2 and LV3 were correlated separately for younger and older adults. No significant correlations emerged suggesting that differences in reaction time likely cannot account for the differences in functional covariance between groups.

In another analysis (not reported in the manuscript), negative and positive mood scores from the PANAS and brain scores in LV2 and LV3 were correlated separately for younger and older adults and each of the four feedback conditions. No significant correlations emerged indicating that differences between younger and older adults on positive mood could not explain the differences in functional covariance between the groups.

Funding

This research was part of Holly J. Bowen's doctoral dissertation. This work was supported by the Canadian Institutes of Health Research grant IAP 107854 awarded to JS.

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