

## ORIGINAL ARTICLE

# Frontopolar Cortex Response to Positive Feedback Relates to Nonincentivized Task Persistence

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## Abstract

When individuals make decisions whether to persist at a task, their decision-making is informed by whether success is pending or accomplished. If pending, the brain facilitates behavioral persistence; if the goal is accomplished or no longer desired, the brain enables switching away from the current task. Feedback, which is known to differentially engage reward neurocircuitry, may modulate goal-directed behavior such as task persistence. However, prior studies are confounded by offering external incentives for persistence. This study tested whether neural response to feedback differed as a function of nonincentivized task persistence in 99 human participants ages 13–30 (60 females). Individuals who persisted engaged the frontopolar cortex (FPC) to a greater extent during receipt of task-relevant positive feedback compared with negative feedback. For individuals who quit, task-irrelevant monetary reward engaged the FPC to a greater extent compared with positive feedback. FPC activation in response to positive feedback is identified as a key contributor to task persistence.

**Key words:** adolescence, fMRI, frontopolar cortex, persistence, reward

## Introduction

Task persistence is a complex goal-directed behavior that is revered as an essential element of success (Bandura et al. 1999). However, little is known about the neural systems that contribute to persistence. Most existing neural investigations either correlate self-report measures with resting state fluctuations (e.g., Wang et al. 2018), offer external incentives to motivate continued engagement (i.e., points, money) (e.g., Kolling et al. 2018), or provide opportunities to repeatedly reengage with a goal (e.g., Bhanji and Delgado 2014). These approaches introduce confounds that prevent the identification of neural systems that underpin naturally occurring differences in persistence. In the real world, external incentives for persistence are typically distal in time or abstract in value (i.e., obtaining a degree), and as such likely lack immediate relevance at the time of decision-making. Persistence decisions are also often unaccompanied by opportunities to immediately reengage (i.e., dropping a course). The current study incorporates these real-world components of persistence in a new paradigm to test how neural response

to feedback relates to one-shot persistence decisions in the absence of external incentives.

Persistence is associated with numerous positive benefits both in terms of psychological well-being and objective measures of success. For example, individuals who persist at life goals report higher subjective well-being and are more resilient under stress (Bandura 1997; Carver and Scheier 2000). Greater persistence in adolescence is linked to higher educational attainment, income, and occupation level in adulthood (Andersson and Bergman 2011). Other work identifies associations between persistence and psychological well-being in adults (Steger et al. 2008). For example, individuals who report more persistence have been found to maintain positive emotions and expectations toward difficult tasks even when encountering failure (Lucas et al. 2015), and to report higher optimism (Lovering et al. 2015) and life satisfaction (Duckworth et al. 2009). The potential benefits of persistence beg the question: what facilitates persistence?

Models of goal-directed behavior typically consider reward optimization as the motivator of persistence. Reward is linked to

robust engagement of the striatum to positive feedback and better learning (Hiebert et al. 2014; Peters and Crone 2017; Cox and Witten 2019). However, persistence may be better conceptualized as an internal goal associated with consistent effort (Duckworth et al. 2007; Jachimowicz et al. 2018). Mastering a new or difficult task requires continued exploitation even if reward is not immediately attained (Porter et al. 2020). A distributed network of medial frontal cortices regulates executive control of goal-directed behavior to optimize exploitation and minimize costs (Frank et al. 2009; Mansouri et al. 2017). Feedback can inform whether to continue expending effort by signaling whether task success is likely, unlikely, or already accomplished. If task success is unlikely, performance-based costs can be interpreted as negative and the goal may be updated to explore alternatives. However, if task success is possible with continued effort, performance-costs may be seen as beneficial and exploitation will be prioritized (Wigfield and Eccles 2000). Estimations about whether one will succeed at a given task influence motivation and interact with enlistment of cognitive effort (Meyniel et al. 2013). As such, the extent to which continued behavior is needed because success is pending has particular relevance for persistence. It is important to disentangle neural contributors to persistence from differences in basal functioning of the reward system because of the involvement of reward and cost systems in motivating persistence. In the current study, responsivity of mesolimbic circuitry to task-relevant (nonmonetary positive feedback) and task-irrelevant (money) reward was examined. Perceived agency in achieving a reward increases activation of the striatum compared with passive receipt of reward (Tricomi et al. 2004). Thus, it was hypothesized that those who persisted would show greater responsivity to task-relevant reward (i.e., nonmonetary positive feedback) compared with those who quit and compared with responsivity to task-irrelevant monetary reward. The current task did not offer external incentives for persistence to reduce confounds between task persistence to achieve success and task persistence as a form of incentivized reward seeking.

Beyond the reward system, the frontopolar cortex (FPC) may subserve persistence. The FPC is thought to track the relative advantage of exploiting a current behavior versus disengaging during self-directed decision-making (Boorman et al. 2009), and transcranial stimulation studies have identified a causal role of the human FPC in arbitrating between exploration and exploitation (Raja Beharelle et al. 2015). Despite the unique expansion of the FPC in the human brain, the FPC also plays a role in evaluating self-generated decisions during feedback in nonhuman primates (Tsujiimoto et al. 2010). Monkeys with FPC lesions are unable to disengage from a course of action when the current goal is deemed to be no longer optimal (Mansouri et al. 2015). The ability to track evidence in favor of or against continuing with a course of action is necessary for the hallmark of persistence. When external incentives are offered, the FPC tracks the value of unselected targets to promote advantageous exploration (Boorman et al. 2009) and facilitates motivation for effort-based reward seeking (Soutschek et al. 2018). However, the FPC may also guide persistence by directing effort toward high-cost, high-benefit behavior through evaluation and rejection of choice alternatives, including quitting (Hosoda et al. 2020). The current study tests whether the FPC is relevant for persistence decisions in the absence of external incentives for persistence.

Persistence does not unilaterally lead to positive outcomes. Costly persistence has been identified as the inability to disengage from costly pursuits (Lucas et al. 2015), which is associated

with poorer physical health and subjective well-being (Wrosch et al. 2007). Although there may be contexts in which persistence is harmful, these contexts are generally conceptualized as those in which long-term goals are unable to be realized. Little work has characterized costly persistence using tasks, opting to focus on self-report that better captures long-term behavior (Wrosch et al. 2003). This is an important distinction from contexts in which a challenge is encountered but the likelihood of goal attainment is unclear. Prior to clear signals of impossibility, strategic directed exploration facilitates goal success (Somerville et al. 2017) and is linked to FPC activation (Zajkowski et al. 2017). Directed, as opposed to random, exploration is guided by the value of information that would be gained from making a particular decision. In the current study, feedback indicated at least 40% failure rate during the task. Thus, persisting would give participants additional opportunity to gain information about the likelihood of task success.

Developmental differences were examined given adolescence is a time of increased exposure to unfamiliar obstacles (Crone and Dahl 2012) and persistence is tied to achievement in adulthood (Andersson and Bergman 2011). Directed exploration also emerges during adolescence (Somerville et al. 2017), which may support persistence prior to goal fulfillment. Although persistence decisions are absent from the developmental cognitive neuroscience literature, prevailing understanding of neurobiological maturation informed hypotheses that persistence would increase from adolescence to adulthood. For example, neural development during adolescence contributes to the cognitive control necessary to modify behavior in response to feedback (DePasque and Galván 2017; Insel et al. 2017). Greater reliance on the frontoparietal network during feedback processing from adolescence to adulthood (Peters et al. 2016) was hypothesized to contribute to age-related improvements in persistence.

## Materials and Methods

### Data Availability

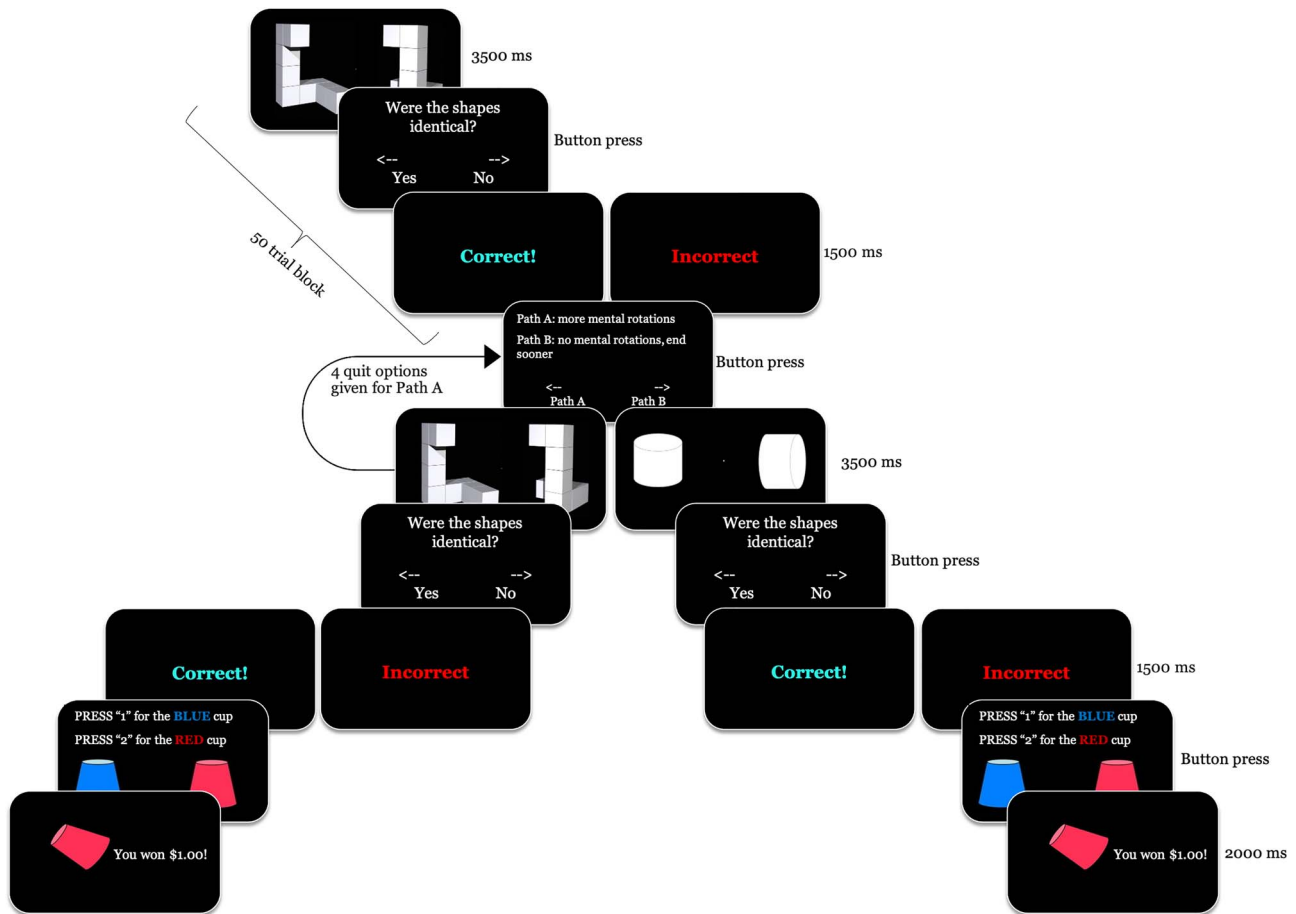
Task code and data generated during this study are available at Open Science Framework <https://osf.io/h69bu/>.

### Participants

One-hundred adolescents and young adults age 13–30 (61 females;  $M_{\text{age}} = 18.330$ ,  $SD = 3.213$ ) completed the study. Ninety-nine participants completed the Persistence Task while undergoing fMRI (60 females;  $M_{\text{age}} = 18.353$ ,  $SD = 3.22$ ). One participant (female, age = 16) was unable to complete the task during the scan session due to a technical error. Analyses were conducted for the 99 participants for whom fMRI data were obtained.

All participants were right-handed and free of metal. Additional exclusionary criteria included previous diagnosis of a psychiatric, neurological, or developmental disorder and use of psychotropic medications.

Participants were recruited via flyers and prior participation in laboratory studies. After receiving approval from the Institutional Review Board, participant eligibility was determined by email (adults) or a phone screening with a parent (adolescents). Adult participants provided informed written consent. Adolescent participants provided informed written assent and their



**Figure 1.** Persistence Task. Initial mental rotation block received a mix of performance-based and manipulated feedback. After the block, path decisions resulted in two divergent tasks. For Path A, participants received additional mental rotation trials in blocks of five with an option to quit after each block. Quit options were presented four times. For Path B, participants received a set of simple shape rotation trials presented as a single block (participants were unaware of shape presentation prior to path selection). All feedback post path decisions were performance based. All participants, regardless of path choice, completed the cup game for monetary reward. Participants chose to overturn either the blue or red cup and received money varying in amounts.

parent or guardian provided informed written consent. Participants were treated in accordance with the ethical standards of American Psychological Association.

### Behavioral Task

Participants completed the Persistence Task, a new task created to assess nonincentivized decisions to persist on a challenging task, in a 3 T Siemens Magnetom Prisma MRI scanner (Fig. 1). Participants received spoken instructions and completed one example trial outside of the scanner before beginning the experimental session.

Participants were told that they were going to complete a series of mental rotations and that after a practice set, they could choose a path for the rest of the experiment. No encouragement or incentive was provided for persistence decisions. The task began with a series of 50 mental rotation trials using stimuli created by Ganis and Kievit (2015) (Fig. 1). All shapes were white presented on a black background for 3500 ms. Duration of presentation was based on average reaction time (RT) for the most difficult shape rotation (150°) identified in prior work with adults (3191 ms) (Ganis and Kievit 2015) to ensure all participants could successfully respond to a sufficient number

of trials, which was confirmed during piloting. Additional time was added (309 ms rounding up to 3500-ms presentation) to eliminate developmental differences in successful completion. When the shapes offset, participants saw a response screen during which they were instructed to make a button press to indicate whether or not they thought the shapes were identical. A separate decision screen was provided to discourage inattentive responding during mental rotation presentation. Mental rotation was chosen as the challenge task rather than a more familiar task (e.g., math) to reduce pretask differences in ability beliefs, which have been shown to influence performance (Wigfield and Eccles 2000). Additionally, spatial reasoning skills have been linked to success in science, technology, engineering, and mathematics domains improving ecological validity (STEM; Wai et al. 2009).

Participants received feedback for 1500 ms indicating that their responses were either correct (positive feedback) or incorrect (negative feedback). Feedback was quasi-manipulated such that 40% of trials received negative feedback regardless of performance to ensure a minimum number of negative feedback trials without increasing task difficulty. The focus of this study was on how feedback relates to persistence decisions rather than how ability relates to persistence, thus trial difficulty was kept

consistent across participants. Perceived and actual task difficulty have been previously identified as relevant for feedback-related performance (DePasque and Tricomi 2014). Sixty percent of trials received performance-based feedback. Manipulated negative feedback was randomly interspersed between performance-based feedback trials, and manipulated feedback was not given for the easiest trial type to reduce suspicion that feedback was controlled. A high percentage of negative feedback served two purposes: providing a sufficient number of trials for comparison with positive feedback and indicating to participants that task success had not yet been achieved. Early work on persistence suggests that a certain amount of failure is necessary to evoke persistence (Maehr and Videbeck 1968)—intertrial intervals (ITIs) of 1000 ms onset after the feedback screen and before the next mental rotation presentation.

Upon completing the set of mental rotations, participants made decisions as to whether they would continue on a path requiring more mental rotations (Path A, persist) or quit (Path B, quit) (Fig. 1). Path designations as “persist” or “quit” were not disclosed to participant; however, participants were aware that “Path A” included additional mental rotation trials, whereas “Path B” included no mental rotations and would end sooner. Participants were told that Path B would end sooner to reduce the likelihood that participants chose Path B out of curiosity to attempt a new task (i.e., exploration) and rather as a decision to “quit” (i.e., reduce effort). In everyday contexts, the decision to quit a challenge is often accompanied by a break in effortful expenditure. Additionally, lesion work in monkeys supports the notion that advantageous exploration may rely on the FPC (Mansouri et al. 2017) and we sought to isolate persistence from incentivized reward optimization. If participants chose to quit (Path B), they were shown 15 trials of simple rotated shapes. Simple rotation was included for participants who quit to approximate the amount of time on the task and additional receipt of feedback given to participants who persisted prior to the reward game (see below, Fig. 1). If participants chose to persist (Path A), they completed an additional five mental rotations (100° and 150° rotations only) and were given accurate performance-based feedback. Path A participants were then given a decision screen to continue on Path A or switch to Path B (Fig. 1). There were four total options to switch paths after the initial persistence choice.

Last, all participants completed a simple monetary reward game similar to a coin flip, but without an observable reward probability (Fig. 1). Participants were not informed of the monetary reward game prior to starting the Persistence Task in order to reduce the likelihood that participants chose to persist because of a belief, they would win more money. During the monetary reward game, participants overturned colored cups to earn money and received a percentage of their earnings as bonus payment. Location of the red and blue cups was counterbalanced. Rewards randomly varied in amount from \$0.40 to \$2.00 and were presented for 2000 ms.

### Task Questionnaire

Outside of the scanner after the Persistence Task, participants completed a questionnaire consisting of 13 questions regarding their choices and feelings about the Persistence Task. Three binary choice questions were analyzed for associations with decisions: path selection rationale, mental rotation enjoyment,

and comparative task enjoyment. Several free-response questions were also asked and a sampling of participant answers by path is reported in Table 1. Ninety-eight participants completed the Task Questionnaire. One participant who chose to quit did not complete the questionnaire. Of the 98 participants who completed the questionnaire, 59 chose to quit and 40 chose to persist.

### Analytic Plan

Behavioral data analyses were performed using R statistical software (version 4.0.3). Linear models were tested using the `lm()` function and logistic models were tested using `glm()`. Analyses predicting persistence were conducted using logistic regression (0 = quit, 1 = persist). Effect sizes are reported as 95% confidence intervals. Significance was determined using *P*-values <0.05.

### fMRI Data Acquisition

The scan was conducted on a 3 T Siemens Magnetom Prisma MRI scanner. Parameters for acquisition were as follows: voxel size = 3.0 × 3.0 × 4.0 mm, slices = 34, slice thickness = 4.0 mm, repetition time (TR) = 2000 ms, echo time (TE) = 30.0 ms, flip angle = 90°, interleaved slice geometry, and field of view (FoV) = 192 mm. A magnetization-prepared rapid-acquisition gradient echo (MPRAGE) scan was acquired for registration purposes (TR = 1900 ms, TE = 2.26 ms, FoV = 250 mm, slice thickness = 1 mm, 176 slices per slab). AutoAlign was used for automated positioning and alignment of anatomy-related slices using alignment perpendicular to the midsagittal plane and tilted along the corpus callosum contour. Images were slice aligned along the anterior/posterior commissure line to allow for interrogation of whole-brain effects.

Stimuli were projected onto a flat screen mounted in the scanner bore. Participants viewed the screen using a mirror mounted on a 32-channel head coil. Extensive head padding was used to minimize participant head motion and to enhance comfort. Participants made their responses with their right hand using a 4-finger-button response box.

### fMRI Preprocessing

Preprocessing was conducted using FMRI Expert Analysis Tool version 6.00, part of FSL version 6.0.1 (FMRIB Software Library, [www.fmrib.ox.ac.uk/fsl](http://www.fmrib.ox.ac.uk/fsl); RRID:SCR\_002823). Preprocessing consisted of nonbrain removal using BET (Brain Extraction Tool for FSL), high-pass filtering (100-s cutoff), and spatial smoothing using a Gaussian kernel of FWHM 5 mm. The first three volumes were discarded to allow for image stabilization. Motion correction was performed with MCFLIRT (intramodal motion correction tool) using 24 standard and extended regressors as well as additional individual spike regressors created using `fsl_motion_outliers` (frame displacement threshold = 75th percentile plus 1.5 times the interquartile range). Two participants exceeded 2.0-mm maximum displacement (1 adolescent 2.778 mm and 1 adult 3.986 mm). Analyses were replicated removing these participants and results remained the same. Each participant's functional data was registered to their MPRAGE using boundary-based registration (Greve and Fischl 2009) and then to Montreal Neurological Institute (MNI) 2.0 × 2.0 × 2.0 mm stereotaxic space with 12° of freedom using FSL's registration method via FLIRT (FMRIB's Linear Image

Table 1 Sample free-response answers to the Task Questionnaire

Question	Persist responses	Quit responses
Why did you choose [the path you chose]?	<p>"Because I'd been getting a lot of 'incorrect' responses that confused me, and I wanted to challenge the game"</p> <p>"I wanted to try to do better"</p> <p>"Because I was getting incorrect answers when I first played it and I wanted to get it right and prove to myself I could"</p> <p>"I wanted to understand what I was doing wrong. I wanted to understand what I didn't see before"</p> <p>"I felt as though I needed to try to get all of them right before giving up"</p> <p>"Feeling good that I was able to get the mental rotations correct"</p> <p>"Realizing I could hold the image and rotate it in my head"</p> <p>"Mental rotations was like a fun exercise for the brain"</p> <p>"It was a challenge and the farther I went along, the more I improved. This was a satisfying feeling"</p> <p>"probably getting the hard problems right"</p>	<p>"It was easier and because I wanted to finish earlier"</p> <p>"The mental rotation questions were frustrating me"</p> <p>"I wasn't very good at the mental rotations, and got a lot wrong"</p> <p>"Because it seemed like the easier path"</p> <p>"The mental rotations were difficult for me to figure out, I kept getting many wrong"</p>
What was the most enjoyable part of the mental rotation and cups [monetary reward] tasks?	<p>"getting so many incorrect and feeling frustrated"</p> <p>"Getting the answer wrong"</p> <p>"Not showing me why I was wrong"</p> <p>"Getting the rotation wrong"</p> <p>"There was no skill or effort required in the cups task so it felt like a waste of time"</p>	<p>"The cups required little effort and earned money"</p> <p>"It was fun earning money with the cups, I didn't really like the mental rotation"</p> <p>"The most enjoyable part were the ones I got right"</p> <p>"Wouldn't call it enjoyable. I guess it was better if I got it right"</p>
What was the least enjoyable part of the mental rotation and cups [monetary reward] tasks?	<p>"I felt good, smart"</p> <p>"Good, validated"</p> <p>"I felt excited and wanted to do more"</p> <p>"I felt as though I am smart, in order to get them right"</p> <p>"Proud because I kept getting more wrong in the beginning"</p>	<p>"Earning money with the cups task"</p> <p>"Some of the mental rotations were fairly difficult and made me question my intelligence"</p> <p>"When I got a lesser amount of money"</p> <p>"The least enjoyable part were the ones I did not get right and the more difficult ones"</p> <p>"The least enjoyable part was getting it wrong and everything about the cups was enjoyable"</p> <p>"Challenging mental rotations"</p> <p>"smart and excited"</p> <p>"Validated"</p> <p>"Less stressed"</p> <p>"I felt pretty good and I felt that it showed that I was smart"</p>
How did you feel when you got a mental rotation answer correct?	<p>"Ready for the next one"</p> <p>"A little bit of frustration but made me more engaged for the next one"</p> <p>"Same as when I got it right"</p> <p>"I felt a little discouraged at first, but it got me excited to get the next one right"</p> <p>"Like I was somehow failing"</p>	<p>"I felt really great. I like being right"</p> <p>"I felt frustrated with the answers I got wrong"</p> <p>"sad, disappointed"</p> <p>"I felt like giving up because I would get them incorrect frequently"</p> <p>"I felt terrible"</p> <p>"I felt ashamed I felt like I was dumb for getting it wrong"</p>

(Continued)

Table 1 Continued

Question	Persist responses	Quit responses
How did you feel earning money during the cups [monetary reward] game?	<p>"Made me happy, relieved"</p> <p>"Excited"</p> <p>"I really didn't feel anything particularly strong, but it was nice to put in minimal effort and earn money"</p> <p>"Unexpectedly and pleasantly surprised"</p> <p>"I didn't feel anything. I knew the game was based on luck, so it didn't matter if I earned or not."</p> <p>"I felt I was going the right way to challenge myself again"</p> <p>"Confident in choosing an answer typical of myself (staying true to myself)"</p> <p>"Determined"</p> <p>"I felt motivated to challenge myself"</p> <p>"Determined. I wanted to keep doing mental rotations to see if I could get more correct ones than incorrect"</p> <p>"I was pleased with myself because it was a chance to show I could improve upon my skills"</p> <p>"I was happy with myself that I was willing to do the more challenging/longer trial"</p>	<p>"Good, not stressed"</p> <p>"Very little effort. I was ok with it"</p> <p>"I felt good. I like earning money"</p> <p>"I felt excited and tried aiming for more money"</p> <p>"Good, I like games like that"</p>
How did you feel when you selected your path?	<p>"Conflicted"</p> <p>"I felt relieved because it was much easier and made me feel more self-confident and it reaffirmed my intelligence despite its simplicity"</p> <p>"A little lousy. I feel I should have taken the harder choice"</p> <p>"Almost regretful"</p> <p>"Good because it said it was faster"</p> <p>"I just chose the one that didn't have any more mental rotations so it would be easier I guess I felt lazy"</p> <p>"I kind of regretted it because it's always good to challenge yourself but I felt it was right choice in the moment"</p> <p>NA</p>	<p>"Conflicted"</p> <p>"I felt relieved because it was much easier and made me feel more self-confident and it reaffirmed my intelligence despite its simplicity"</p> <p>"A little lousy. I feel I should have taken the harder choice"</p> <p>"Almost regretful"</p> <p>"Good because it said it was faster"</p> <p>"I just chose the one that didn't have any more mental rotations so it would be easier I guess I felt lazy"</p> <p>"I kind of regretted it because it's always good to challenge yourself but I felt it was right choice in the moment"</p> <p>NA</p>
Why did you switch paths? (Path A only)	<p>"I felt that I got them correct and if I were to do something like that in the future I would be able to get them right"</p> <p>"I did well on Path A so I didn't want to ruin the hot hand. Also I wanted to try something new"</p> <p>"I was getting bored of choosing Path A so many times"</p> <p>"I was tired of being incorrect"</p>	<p>NA</p>

All answers reproduced verbatim.

Registration Tool). Alignment was visually confirmed for all participants.

One general linear model (GLM) (Friston et al. 1994) was defined for each individual including regressors for each event: mental rotation stimuli, mental rotation decisions, positive feedback presentation, negative feedback presentation, instruction screens, postdecision mental rotation stimuli, postdecision mental rotation decision, postdecision positive feedback, postdecision negative feedback, monetary reward gamble, and monetary reward receipt. Events were modeled with a canonical (double-gamma) hemodynamic response function for a duration from stimulus onset to stimulus offset. Temporal derivatives were included as covariates of no interest for all regressors, allowing a better fit for the whole model and reducing unexplained noise. Motion parameters were included as covariates of no interest. ITIs were not explicitly modeled and served as an implicit baseline.

### Whole-Brain Analyses

For group-level analyses, FMRIB's Improved Linear Model prewhitening was performed to estimate voxelwise autocorrelation and improve estimation efficiency. Group-level analyses were performed using the FMRIB Local Analysis of Mixed Effects (FLAME-1) module in FSL (Beckmann et al. 2003),  $Z > 3.1$ , FWE-corrected  $P < 0.05$ . Outliers were deweighted in the multisubject statistics using mixture modeling (Woolrich 2008). All results are reported in MNI space.

First, whole-brain analyses were conducted to assess differences in activation by task state across all participants. Next, whole-brain effects by persistence decision (Path A choosers vs. Path B choosers) were tested for each task contrast. Figures and results focus on decision contrasts of persist > quit, but the nature of whole-brain GLM contrasts indicates that the inverse association is also true for the opposite contrast (e.g., a region activated to a greater extent for persist > quit for positive > negative feedback is activated to a greater extent for quit > persist for negative feedback > positive feedback). Last, a single-group average with additional covariate design was used with age as a demeaned regressor (mean centered across all participants) to examine associations between age and neural activation at a whole-brain level.

### Parametric Modulation Analyses

Over the course of goal-pursuit, relevance of positive versus negative feedback shifts. Positive feedback acts to instill goal commitment early on and negative feedback provides signals for increase effort after goal commitment is established (Fishbach et al. 2010). Parametric modulation analyses were conducted to determine whether there were differences in response to positive and negative feedback accumulation over the course of the task. In two separate individual-level models, one for positive and one for negative feedback, linear modulation regressors were added to test trial-by-trial fluctuations in neural activation modulated by the amount of prior feedback received. Modulation regressors were orthogonalized with respect to the lower order regressor representing average activation of positive and negative feedback trials (Mumford et al. 2015).

## Results

### Persistence Decisions

Forty participants (40.40%, 20 females  $M_{\text{age}} = 19.28$ ,  $SD = 3.82$ , range = 14–30 years) chose to persist (Path A). Fifty-nine participants (59.60%, 40 females  $M_{\text{age}} = 17.73$ ,  $SD = 2.60$ , range = 13–26 years) chose to quit (Path B).

Of the 40 participants who persisted, 12 chose Path A throughout the entire course of the task and 28 chose to quit at some point after the initial decision. Average accuracy on the postpath mental rotation trials was 84.70%,  $SD = 16.2\%$ , which did not differ among those who persisted throughout versus those who eventually quit,  $t(38) = -0.65$ ,  $P = 0.520$ . Of those who eventually quit, only 4 cited frustration or task performance as a reason for quitting, whereas the remainder cited a desire for novelty, a feeling of competency, or some other strategy (Table 1). Of the 59 participants who quit initially (Path B), 25% reported reflecting on their decisions with negative appraisal (i.e., regret).

### Persistence Was Associated with Age but Not Accuracy nor Amount of Manipulated Negative Feedback

On average, participants were accurate on 39.6 (79.37%) of the first 50 mental rotation trials, range = 23–50,  $SD = 5.94$ . Of those correct trials, 15.72 (39.60%) received manipulated negative feedback, range = 8–20,  $SD = 2.61$ . Accuracy and amount of manipulated negative feedback received were not significantly associated with persistence, accuracy Estimate = 0.063,  $SE = 0.077$ ,  $z = 0.816$ ,  $P = 0.415$ , 95%CI [-0.087, 0.219]; feedback Estimate = 0.050,  $SE = 0.173$ ,  $z = 0.290$ ,  $P = 0.772$ , 95%CI [-0.288, 0.399]. Those who chose to persist answered on average 2.67 more questions correct than those who chose to quit. Those who chose to persist received manipulated negative feedback for 1.10 additional mental rotation trials compared with those who quit.

Age was significantly positively associated with persistence, Estimate = 0.156,  $SE = 0.069$ ,  $z = 2.270$ ,  $P = 0.023$ , 95%CI [0.026, 0.299]. This association held controlling for accuracy, Estimate = 0.164,  $SE = 0.069$ ,  $z = 2.375$ ,  $P = 0.018$ , 95%CI [0.032, 0.305]. Age was not significantly associated with mental rotation accuracy or amount of manipulated negative feedback received, accuracy Estimate = -0.029,  $SE = 0.187$ ,  $t = -0.152$ ,  $P = 0.879$ , 95%CI [-0.400, 0.343]; feedback Estimate = 0.001,  $SE = 0.082$ ,  $z = 0.011$ ,  $P = 0.991$ , 95%CI [-0.162, 0.164]. There were no significant sex differences in mental rotation accuracy or amount of manipulated negative feedback received, accuracy  $t(98) = 0.847$ ,  $P = 0.399$ , 95%CI [-1.320, 3.284]; feedback  $t(98) = 0.656$ ,  $P = 0.514$ , 95%CI [-0.689, 1.369].

### Persistence Was Motivated by Self-Reported Challenge Seeking

#### Path Selection Rationale

Seventy-eight percent of participants who chose to persist ( $n = 31$  out of 40) reported that they chose Path A because it was more difficult, whereas 100% of participants who chose to quit ( $n = 57$  out of 57) reported that they chose Path B because it was less difficult (one participant who chose to quit reported “neither” as the decision reason and was excluded from this analysis). This group difference in path rationale was significant,  $X^2(1, N = 97) = 61.409$ ,  $P < 0.001$ . Age was not significantly associated with path rationale, Estimate = 0.059,  $SE = 0.067$ ,  $z = 0.871$ ,  $P = 0.384$ , 95%CI [-0.075, 0.193].

### Mental Rotation Enjoyment

Sixty-three percent of participants who chose to persist ( $n=25$  out of 40) reported enjoying the mental rotation trials they got correct more than those that were challenging and 78% ( $n=45$  out of 58) of participants who chose to quit reported the same, which did not significantly differ by group  $X^2(1, N=98)=1.953$ ,  $P=0.162$ . Age was significantly associated with enjoying mental rotation trials that received positive feedback versus those that were challenging, Estimate = 0.180, SE = 0.073,  $z=2.450$ ,  $P=0.014$ , 95%CI [0.041, 0.332], such that more older participants reported liking challenging trials compared with younger participants. The association between age and mental rotation enjoyment held controlling for persistence decisions, age Estimate = 0.162, SE = 0.075,  $z=2.158$ ,  $P=0.031$ , 95%CI [0.020, 0.317].

### Comparative Task Enjoyment

Eighty-two percent of participants who chose to quit ( $n=48$  out of 58) reported that they enjoyed the monetary reward game more than the mental rotations, whereas only 43% of participants who chose to persist reported enjoying the monetary reward game more ( $n=17$  out of 40). This group difference was significant,  $X^2(1, N=98)=15.424$ ,  $P<0.001$ . Comparative task enjoyment was significantly associated with age, Estimate = 0.239, SE = 0.077,  $z=3.088$ ,  $P=0.002$ , 95%CI [0.096, 0.402], such that older participants reported liking mental rotation trials more than monetary reward trials. The association between age and task enjoyment held controlling for persistence decisions, age Estimate = 0.201, SE = 0.083,  $z=2.474$ ,  $P=0.012$ , 95%CI [0.051, 0.380].

### RT Reflected Individual Differences

On average, participants made mental rotation decisions in 994.394 ms after receiving positive feedback and in 1032.996 ms after receiving negative feedback. RT after positive and after negative feedback were strongly correlated,  $r(99)=0.822$ ,  $P<0.001$ , 95%CI [0.745, 0.877], indexing an individual difference in RT. RT after negative feedback was not significantly related to persistence decisions, Estimate = -0.399, SE = 0.543,  $z=-0.735$ ,  $P=0.463$ , 95%CI [-1.515, 0.642] nor was RT after positive feedback, Estimate = -0.820, SE = 0.611,  $z=-1.341$ ,  $P=0.180$ , 95%CI [-2.070, 0.348]. Average RT after negative feedback was quadratically associated with task accuracy such that those with respectively fast RT and respectively slow RT after receiving negative feedback had highest accuracy, Estimate<sub>quadratic</sub> = 17.630, SE<sub>quadratic</sub> = 5.571,  $t_{quadratic}=3.164$ ,  $P_{quadratic}=0.002$ , 95%CI [6.571, 28.689]. This association held controlling for persistence decision and average RT across the full task, Estimate<sub>quadratic</sub> = 14.023, SE<sub>quadratic</sub> = 5.532,  $t_{quadratic}=2.535$ ,  $P_{quadratic}=0.013$ , 95%CI [3.038, 25.007]. Average RT after positive feedback was linearly associated with accuracy, Estimate = -6.253, SE = 1.588,  $t=-3.937$ ,  $P<0.001$ , 95%CI [-9.405, -3.100]. This association held controlling for persistence decision and average RT across the full task, Estimate = -12.729, SE = 4.999,  $t=-2.546$ ,  $P=0.013$ , 95%CI [-22.654, -2.804]. Persistence did not significantly moderate either RT—accuracy association, negative feedback RT: Estimate<sub>interaction</sub> = 0.649, SE<sub>interaction</sub> = 3.013,  $t_{interaction}=0.215$ ,  $P_{interaction}=0.830$ , 95% CI [-5.334, 6.631]; positive feedback RT: Estimate<sub>interaction</sub> = 4.571, SE<sub>interaction</sub> = 3.458,  $t_{interaction}=1.322$ ,  $P_{interaction}=0.189$ , 95% CI [-2.295, 11.436].

### Persistence Was Associated with Increased Frontopolar Response to Positive Feedback

Across participants, whole-brain analyses revealed negative versus positive feedback elicited activation in salience network hubs, whereas positive versus negative feedback elicited activation in the ventral striatum and FPC (Fig. 2a and Table 2). Participants who persisted demonstrated heightened activation in the FPC and occipital cortex to positive versus negative feedback, whereas participants who quit demonstrated comparatively blunted occipital cortex activation and increased activation in the FPC to negative versus positive feedback (Fig. 2b and Table 2).

#### Age

Feedback elicited differential activation associated with age such that older participants exhibited greater activation in the right posterior superior frontal gyrus (SFG) and juxtapositional lobule cortex (formerly supplementary motor cortex, SMA) to positive versus negative feedback (Fig. 2c and Table 2). Activation in the SFG/SMA was significantly associated with persistence, Estimate = 0.007, SE = 0.003,  $z=2.223$ ,  $P=0.026$ , 95%CI [0.001, 0.014], such that those who persisted had increased activation to positive versus negative feedback.

#### Habituation and Sensitization to Feedback

Parametric modulation analyses revealed participants showed habituation (decreased response) to linear accumulation of negative feedback in the FPC, thalamus, anterior cingulate gyrus, bilateral anterior insula, and occipital cortex (Table 2, Fig. 3a). Sensitization (increased response) to the accumulation of negative feedback was observed in the precentral gyrus, posterior cingulate gyrus, precuneus, and bilateral posterior insula (Table 2, Fig. 3b). No regions showed sensitization to the accumulation of positive feedback, but habituation to positive feedback was observed in the bilateral striatum, anterior cingulate gyrus, FPC, bilateral angular gyrus, bilateral dorsolateral PFC (dlPFC), and occipital cortex (Table 2, Fig. 3c). No differential activation by persistence at the whole-brain level was associated with the accumulation of either negative or positive feedback. No significant differential activation by age at the whole-brain level was associated with linear accumulation of either negative or positive feedback.

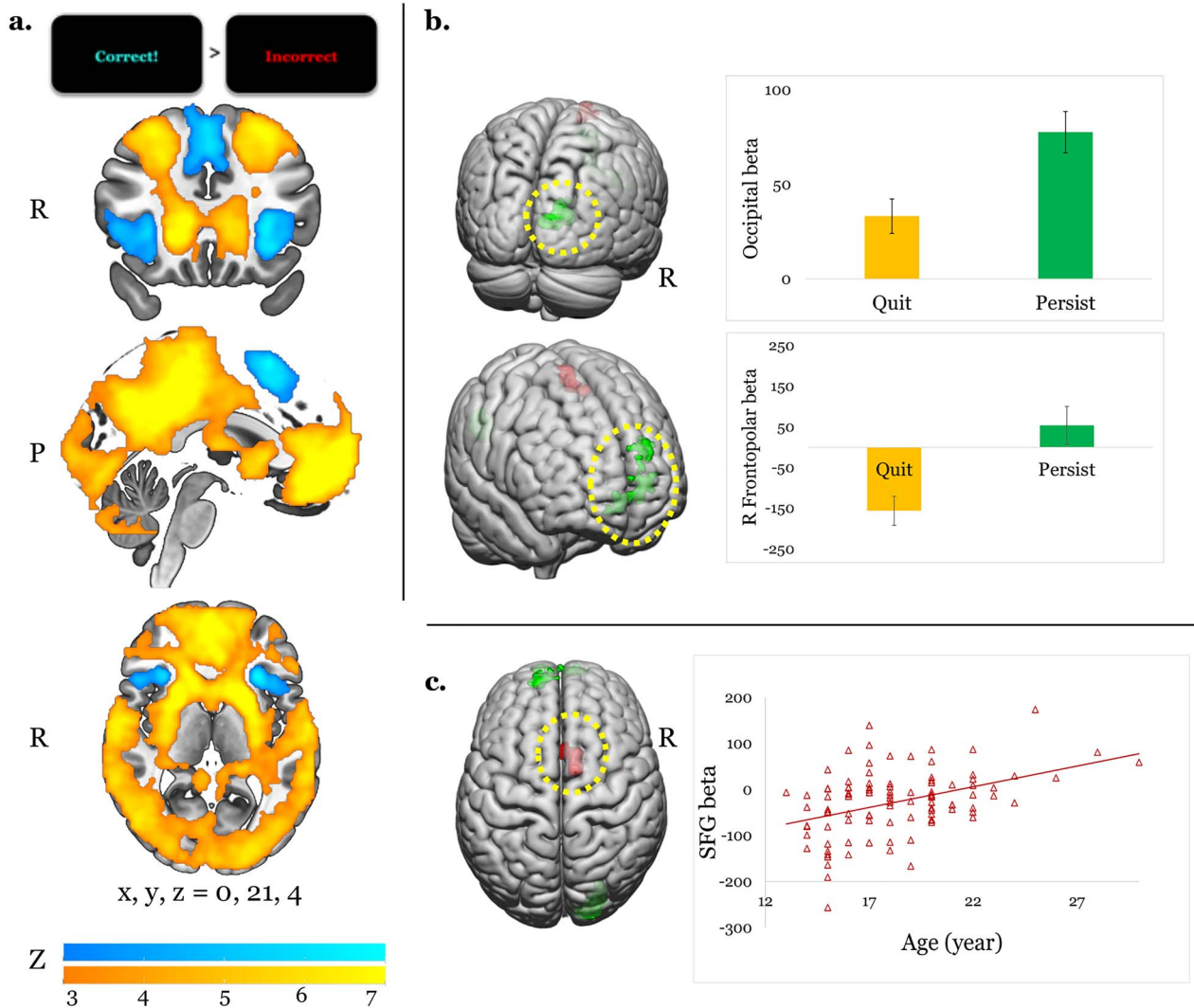
#### Manipulated Feedback

On manipulated negative feedback trials, there was no differential activation on trials for which participants received negative feedback for correct responses versus those for which participants received negative feedback for incorrect responses. Age was not significantly associated with activation on manipulated feedback trials. Rate of negative feedback received was not associated with activation for the contrasts of positive feedback versus negative feedback, mental rotations after positive versus after negative feedback, or positive feedback versus monetary reward.

### Persistence Was Associated with Greater Parietal Operculum Engagement Following Negative Feedback

During mental rotation trials following negative feedback compared those following positive feedback, greater activation was elicited in the mPFC, posterior cingulate gyrus, and striatum (Fig. 4a and Table 3). These regions are associated with encoding outcomes necessary for altering goal-directed behavior





**Figure 2.** Visualization of significant activation for the contrast of (a) positive feedback > negative feedback (hot) and negative feedback > positive feedback (cool), all participants; (b) positive feedback > negative feedback for participants who persisted > participants who quit with visualization by persistence decision at right, error bars represent standard error; (c) positive age association for the contrast of positive feedback > negative feedback. All analyses, whole-brain Flame1,  $Z > 3.1$ , FWE-corrected  $P < 0.05$ , outliers deweighted. Color bar indicates Z intensity values. Coordinates are in MNI space. R = right hemisphere, P = posterior.  $N = 99$ .

(Pearson et al. 2011). Compared with individuals who quit, individuals who persisted demonstrated heightened activation in the parietal operculum cortex, a region evoked by cognitive tasks, including mental rotation (Hugdahl et al. 2015) (Fig. 4b and Table 3). No regions were activated to a greater extent during mental rotation trials following positive feedback compared with mental rotation trials following negative feedback. Age was not significantly associated with differential response on trials following negative feedback compared those following positive feedback.

Across all trials, mental rotation decisions evoked activation in anterior salience network hubs, including the anterior cingulate and bilateral insula, as well as regions of the visuospatial network involved in visuospatial attention (Table 3). No differential activation by group was significant for mental rotation decisions versus baseline. Age was not significantly associated with mental rotation decisions versus baseline.

### Quitting Was Related to Greater Corticolimbic Activation to Monetary Reward

Across all participants, monetary reward receipt versus baseline elicited activation in distributed reward regions including the striatum, lateral orbitofrontal cortex, bilateral insula, and middle and superior frontal gyri (Table 4). Participants who quit compared with those who persisted activated the lateral orbitofrontal cortex, bilateral insula, thalamus, and middle and superior frontal gyri to a greater extent for monetary reward receipt versus baseline (Table 4). Activation to monetary reward receipt versus baseline was not significantly associated with age.

### Persistence Was Associated with Greater FPC Activation to Task-Relevant Positive Stimuli

When compared with positive feedback, monetary reward evoked greater activation in the striatum, paracingulate gyrus,

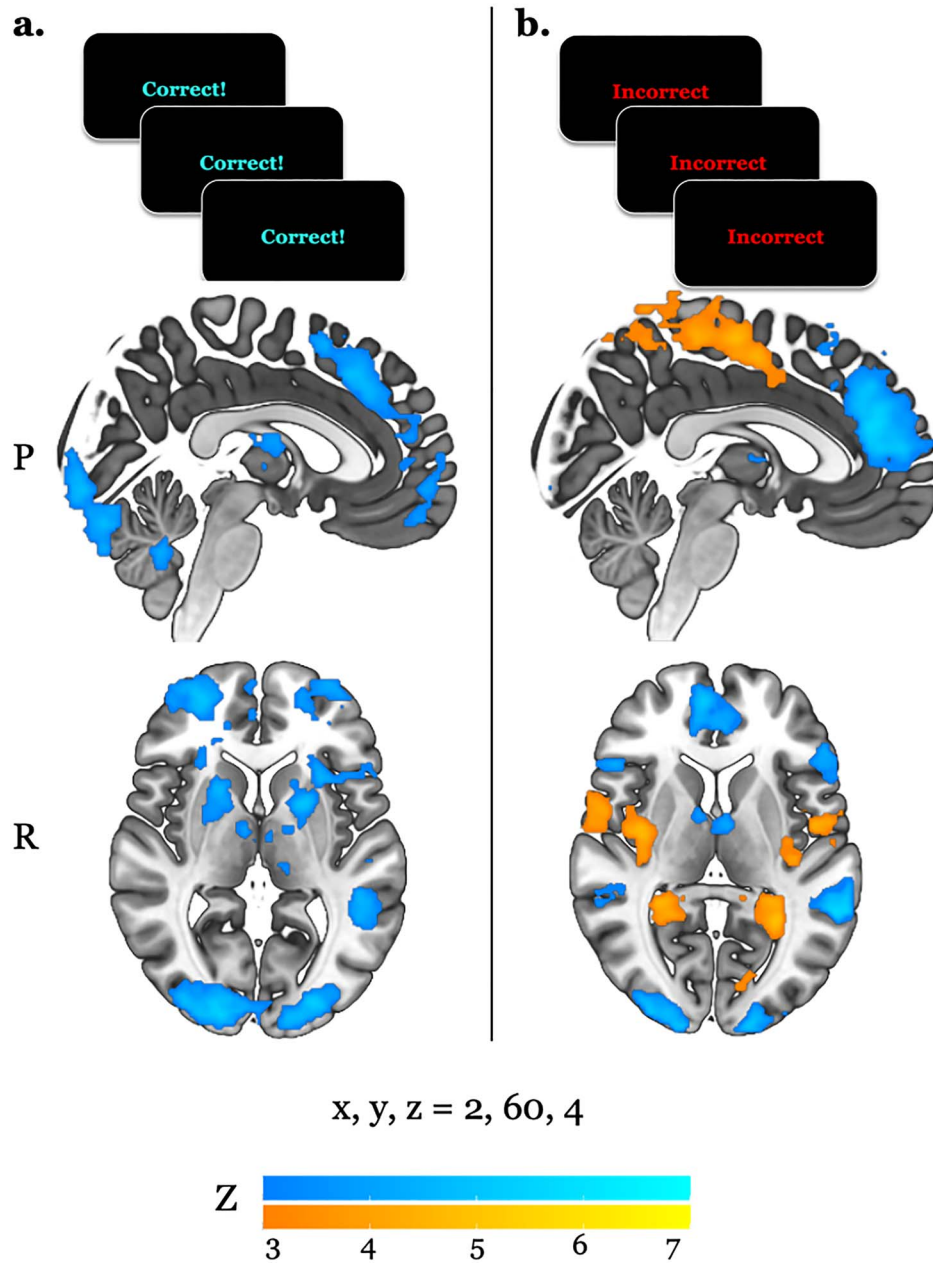
**Table 2** Significant clusters from group level whole-brain analyses for feedback contrasts

Cluster peak region	Voxels	P-value	Max Z value	R/L	Peak MNI coordinates		
					X	Y	Z
<b>Positive &gt; negative feedback</b>							
Cingulate gyrus; Precuneus	96558	<0.001	10.10	M	0	-36	42
Putamen	LM		10.10	R	20	8	-4
Accumbens	LM		9.88	R	10	6	-8
Cingulate gyrus; Precuneus	LM		9.79	R	10	-42	36
Putamen	LM		9.78	L	-20	6	-10
Occipital cortex	LM		9.77	L	-42	-66	38
<b>Negative &gt; positive feedback</b>							
Superior frontal gyrus	1640	<0.001	7.26	M	0	18	58
Insular cortex	692	<0.001	7.23	L	-30	24	2
Insular cortex	579	<0.001	6.11	R	32	24	4
<b>Positive &gt; negative feedback, Persist &gt; quit</b>							
Occipital pole	392	<0.001	4.55	R	22	-98	20
Frontal pole	313	<0.001	4.83	L	-14	60	32
<b>Negative feedback habituation&gt; baseline</b>							
Paracingulate gyrus; Cingulate gyrus	3819	<0.001	5.88	M	0	42	20
Superior temporal gyrus; Middle temporal gyrus	1829	<0.001	7.18	L	-58	-30	0
Occipital pole	1704	<0.001	6.54	L	-32	-94	-4
Insular cortex	1466	<0.001	5.66	R	32	22	-6
Frontal orbital cortex; Frontal operculum cortex	1448	<0.001	6.33	L	-48	24	-6
Occipital pole	1187	<0.001	6.19	R	28	-94	-4
Middle temporal gyrus; Superior temporal gyrus	1040	<0.001	5.73	R	56	-20	-8
Angular gyrus	803	<0.001	5.82	L	-56	-58	32
Middle frontal gyrus	574	<0.001	5.23	L	-42	6	46
Thalamus	155	0.009	4.56	L	-6	-2	2
<b>Negative feedback sensitization &gt; baseline</b>							
Superior parietal lobule	9942	<0.001	5.97	R	16	-48	68
Insular cortex	2166	<0.001	5.51	R	38	0	-6
Lingual gyrus	1992	<0.001	5.75	L	-28	-50	2
Occipital pole	428	<0.001	4.51	L	-12	-88	28
Lingual gyrus	218	0.001	4.07	L	-16	-70	0
<b>Positive feedback habituation&gt; baseline</b>							
Occipital fusiform gyrus	15556	<0.001	6.93	R	20	-86	-8
Precentral gyrus; Middle frontal gyrus	5167	<0.001	5.95	L	-46	2	38
Middle frontal gyrus	3070	<0.001	5.96	R	40	4	54
Frontal pole	2120	<0.001	5.67	R	26	56	8
Paracingulate gyrus	1915	<0.001	5.72	R	6	32	32
Lateral occipital cortex	1835	<0.001	6.13	R	38	-58	48
Frontal pole	1669	<0.001	5.21	L	-24	54	-6
Cerebellum	223	<0.001	4.58	M	0	-56	-34
Frontal pole; Frontal medial cortex	223	<0.001	4.30	R	4	56	-6
<b>Positive &gt; negative feedback, positive association with age</b>							
Superior frontal gyrus; Supplementary motor cortex	183	0.005	4.02	R	8	4	70

Note: N=99. Z > 3.1, FWE-corrected P < 0.05, Flame1. R=Right hemisphere, L=Left hemisphere, M=medial. Local maxima not listed, except for positive feedback > negative feedback and local maxima are noted with LM in the voxel column. Cluster peak regions based on the Harvard-Oxford Structural Atlas.

bilateral anterior insula, and other lateral cortical regions including the middle frontal gyrus and occipital cortex (Fig. 5a and Table 4). Positive feedback versus monetary reward receipt evoked greater activation in several cortical regions, including the medial orbitofrontal cortex, anterior cingulate, bilateral posterior insula, and bilateral superior temporal gyrus, as well as the bilateral hippocampus and bilateral amygdala (Fig. 5a and Table 4).

Participants who persisted activated the medial and lateral FPC, anteromedial SFG, and right postcentral gyrus of the parietal lobe to a greater extent for positive feedback versus receipt of monetary reward, whereas those regions were activated to a greater extent for monetary reward versus positive feedback for those who quit (Fig. 5b and Table 4). Age was positively associated with neural response to positive feedback versus monetary reward receipt in the left occipital cortex such that



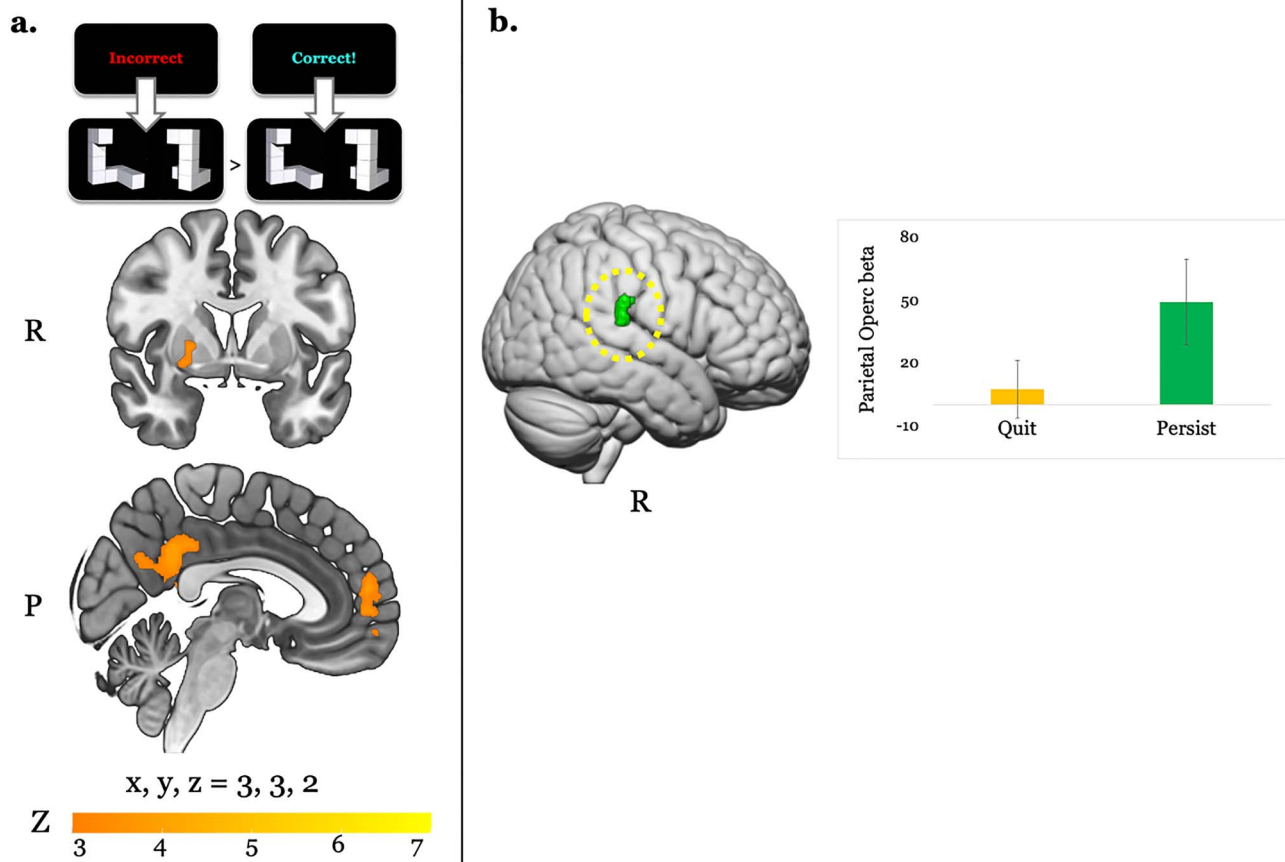
**Figure 3.** Visualization of significant activation for the contrast of (a) linear accumulation of positive feedback (habituation), all participants. No significant activation for sensitization to positive feedback; (b) linear accumulation of negative feedback (sensitization, hot; habituation, cool), all participants. Flame1,  $Z > 3.1$ , FWE-corrected  $P < 0.05$ , outliers deweighted. Color bar indicates Z intensity values. Coordinates are in MNI space. R=right hemisphere, P=posterior. N=99.

older participants evinced greater activation (Fig. 5c and Table 41). Age-related activation in the occipital cortex was not significantly associated with persistence, Estimate=0.001, SE=0.001,  $z = 1.035$ ,  $P = 0.301$ , 95%CI [-0.0005, 0.002].

#### Head Motion Was Not Associated with Age or Decisions

Age was positively associated with persistence, and, in general, younger participants tend to have greater in-scanner head motion, which can lead to spurious results. However, no significant age differences were observed in motion

parameters: average translation, Estimate=0.010, SE=0.011,  $t = 0.895$ ,  $P = 0.373$ , 95%CI [-0.012, 0.032]; average rotation, Estimate=0.0002, SE=0.0002,  $t = 1.003$ ,  $P = 0.318$ , 95%CI [-0.0002, 0.0005]; maximum translation, Estimate=0.018, SE=0.019,  $t = 0.933$ ,  $P = 0.353$ , 95%CI [-0.020, 0.055]; maximum rotation, Estimate=0.0006, SE=0.0004,  $t = 1.329$ ,  $P = 0.187$ , 95%CI [-0.0003, 0.001]. Persistence was also not significantly associated with motion: average translation, Estimate=-0.483, SE=0.639,  $z = -0.756$ ,  $P = 0.450$ , 95%CI [-1.937, 0.676]; average rotation, Estimate=-71.107, SE=48.837,  $z = -1.456$ ,  $P = 0.145$ , 95%CI [-181.119, 11.610]; maximum translation, Estimate=-0.276,



**Figure 4.** Visualization of significant activation for the contrast of (a) mental rotation decisions after negative feedback > mental rotation decisions after positive feedback, all participants. No significant activation for mental rotation decisions after positive feedback > mental rotation decisions after negative feedback; (b) mental rotation decisions after negative feedback > mental rotation decisions after positive feedback for participants who persisted > participants who quit with visualization by persistence decision at right, error bars represent standard error. Flame1,  $Z > 3.1$ , FWE-corrected  $P < 0.05$ , outliers deweighted. Color bar indicates Z intensity values. Coordinates are in MNI space. R = right hemisphere, P = posterior.  $N = 99$ .

**Table 3** Significant clusters from group level whole-brain analyses for mental rotation contrasts

Cluster peak region	Voxels	P-value	Max Z value	R/L hemisphere	Peak MNI coordinates		
					X	Y	Z
<b>Mental rotation decisions &gt; baseline</b>							
Cingulate gyrus; Paracingulate gyrus	2990	<0.001	6.66	R	6	26	30
Frontal operculum cortex; Insular cortex	1240	<0.001	6.95	R	32	20	10
Supramarginal gyrus; Superior parietal lobule	1004	<0.001	4.81	R	38	-40	46
Frontal pole	981	<0.001	5.60	R	34	54	26
Superior parietal lobule; Supramarginal gyrus	778	<0.001	5.66	L	-36	-44	44
Frontal operculum cortex	441	<0.001	6.39	L	-32	16	12
Frontal pole	216	0.002	5.02	L	-34	52	22
<b>Mental rotation decisions after negative feedback &gt; after positive feedback</b>							
Cingulate gyrus	717	<0.001	4.12	R	4	-44	32
Frontal pole	293	<0.001	4.19	R	2	56	14
Putamen	106	0.033	3.77	R	22	2	2
<b>Mental rotation decisions after negative feedback &gt; after positive feedback, Persist &gt; Quit</b>							
Parietal operculum cortex; Planum temporale	107	0.032	4.19	R	64	-26	18

Note:  $N = 99$ .  $Z > 3.1$ , FWE-corrected  $P < 0.05$ , Flame1. R = Right hemisphere, L = Left hemisphere. Local maxima not listed. Cluster peak regions based on the Harvard-Oxford Structural Atlas.

**Table 4** Significant clusters from group level whole-brain analyses for reward contrasts

Cluster peak region	Voxels	P-value	Max Z value	R/L hemisphere	Peak MNI coordinates		
					X	Y	Z
<b>Monetary reward receipt &gt; baseline</b>							
Frontal pole	46 587	<0.001	10.40	R	46	46	6
Occipital cortex	1250	<0.001	7.76	L	-44	-70	0
Cerebellum	1125	<0.001	6.67	L	-38	-72	-28
<b>Monetary reward receipt &gt; baseline, Quit &gt; Persist</b>							
Superior frontal gyrus	1092	<0.001	4.50	R	4	36	46
Frontal pole	646	<0.001	4.28	L	-28	64	4
Frontal pole	630	<0.001	5.30	R	44	60	16
Occipital fusiform gyrus	583	<0.001	5.33	L	-18	-80	-26
Middle frontal gyrus	396	<0.001	4.69	L	-54	14	40
Insular cortex	189	0.027	4.66	L	-32	20	-4
Frontal orbital cortex	171	0.040	4.90	R	30	20	-10
Thalamus	166	0.045	4.52	R	4	-24	10
Superior parietal lobule	162	0.049	4.41	R	42	-38	56
<b>Positive feedback &gt; monetary reward receipt</b>							
Cuneal cortex	12 633	<0.001	9.48	R	4	-80	26
Central opercular cortex	4472	<0.001	6.59	L	-36	2	14
Central opercular cortex; Insular cortex	1543	<0.001	7.25	R	36	8	10
Cingulate gyrus	1176	<0.001	5.96	R	2	36	8
Superior temporal gyrus	651	<0.001	6.05	R	48	-34	4
Inferior frontal gyrus; Frontal pole	338	<0.001	5.48	L	-54	32	4
Hippocampus	295	<0.001	5.16	R	32	-28	-8
Cingulate gyrus	154	0.025	4.76	L	-8	-12	42
<b>Monetary reward receipt &gt; positive feedback</b>							
Superior frontal gyrus	32 997	<0.001	8.51	R	26	2	64
Frontal pole	169	0.017	5.33	L	-30	52	20
<b>Positive feedback &gt; monetary reward receipt, Persist &gt; Quit</b>							
Superior frontal gyrus	1143	<0.001	4.67	L	-16	18	44
Frontal orbital cortex	222	0.004	4.24	L	-28	34	-6
Frontal pole	184	0.011	4.25	R	40	60	2
Paracingulate gyrus; Frontal pole	168	0.016	4.32	R	6	54	-2
Postcentral gyrus	147	0.029	4.31	R	22	-38	54
<b>Positive feedback &gt; monetary reward receipt, positive association with age</b>							
Occipital cortex; Occipital fusiform gyrus	441	<0.001	5.01	L	-42	-74	-12

Note:  $N = 99$ .  $Z > 3.1$ , FWE-corrected  $P < 0.05$ ,  $F_{\text{max}} = 1$ . R = Right hemisphere, L = Left hemisphere, M = medial. Local maxima not listed. Cluster peak regions based on the Harvard-Oxford Structural Atlas.

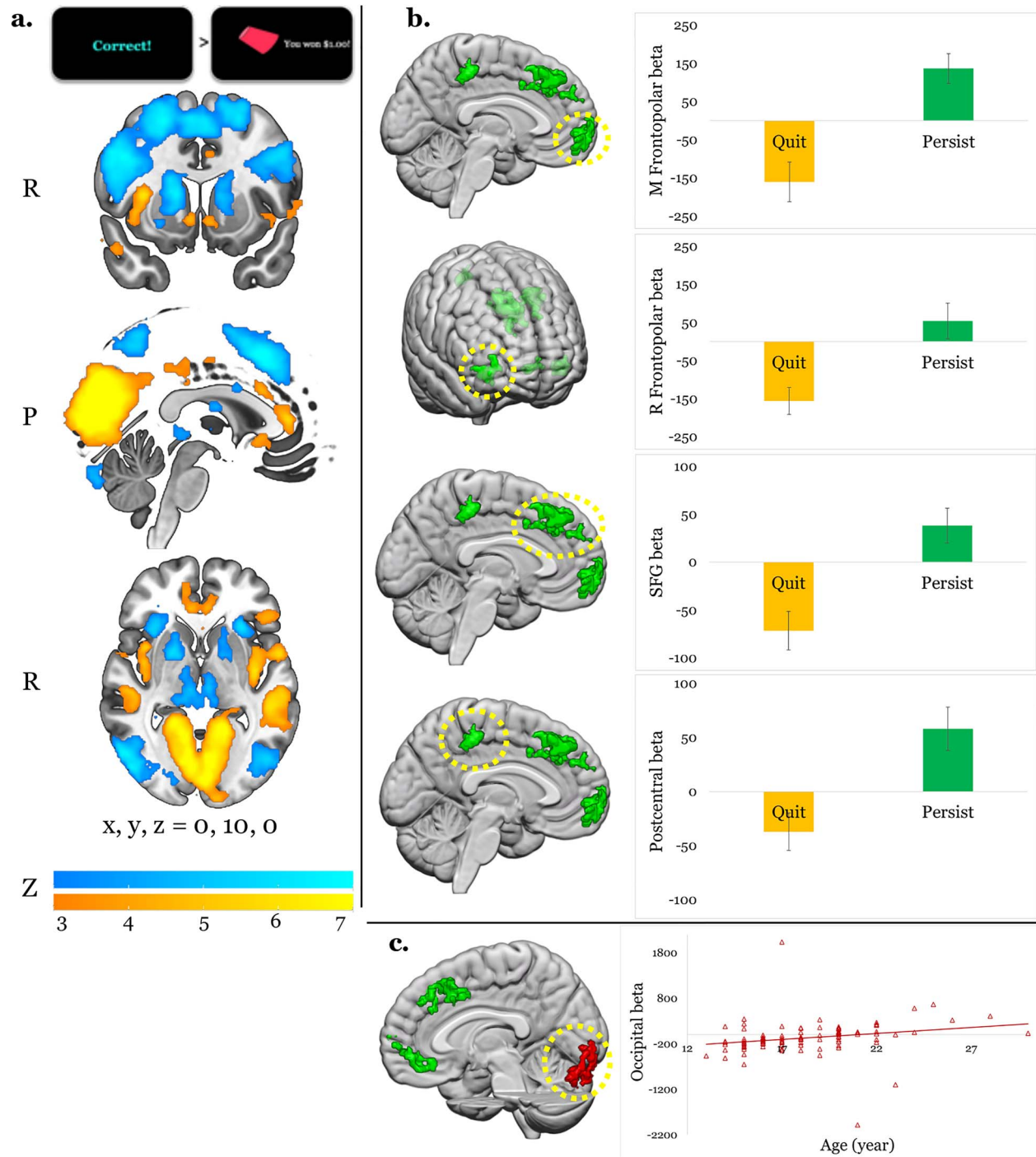
$SE = 0.374$ ,  $z = -0.738$ ,  $P = 0.461$ , 95%CI [-1.098, 0.414]; maximum rotation, Estimate = -30.994,  $SE = 21.674$ ,  $z = -1.430$ ,  $P = 0.153$ , 95%CI [-81.680, 4.491].

## Discussion

This work identifies neural systems associated with task persistence. Persistence was associated with increased activation in the FPC after positive feedback and enhanced recruitment of task-relevant resources in the parietal operculum following negative feedback. Individuals who persisted also demonstrated greater activation in attentional control regions (SFG, SMA) and the FPC to positive feedback compared with monetary reward. Theoretical models demonstrate flexible responsivity in the brain depending on motivational signals via external factors such as feedback and reward, as well as their interactions with goal expectancy (e.g., Kim 2013). The Persistence Task elucidates how motivationally relevant neural systems respond

to such factors and findings point to the importance of feedback evaluation and control processes for persistence.

The FPC responded to positive feedback to a greater extent than negative feedback for those who persisted compared with those who quit. Those who quit showed positive activation in the FPC to negative feedback compared with positive feedback, demonstrating differential tracking of disparately valenced evidence as a function of persistence decision. Compared with monetary reward, which is also positively valenced, task-relevant positive feedback elicited greater activation in the medial and lateral FPC, anteromedial SFG, and parietal lobe for participants who persisted compared with those who quit. These regions comprise a network involved in goal-pursuit (Mansouri et al. 2017). The importance of positive feedback for persistence is consistent with the motivational relevance of positive feedback in instilling goal commitment and the assertion that positive feedback increases goal attainment expectancies (Fishbach et al. 2010). The FPC in particular may



**Figure 5.** Visualization of significant activation for the contrast of (a) positive feedback > monetary reward receipt (hot) monetary reward receipt > positive feedback (cool), all participants; (b) positive feedback > monetary reward receipt for participants who persisted > participants who quit with visualization by persistence decision at right, error bars represent standard error; (c) positive age association for the contrast of positive feedback > monetary reward receipt. Flame1,  $Z > 3.1$ , FWE-corrected  $P < 0.05$ , outliers deweighted. Color bar indicates Z intensity values. Coordinates are in MNI space. R = right hemisphere, P = posterior, M = medial.  $N = 99$ .

support this goal commitment by removing alternative actions from the current choice space when success has not been attained but is perceived as achievable. This conclusion is supported by recent work showing upregulation of the FPC via transcranial direct current stimulation increases the willingness of humans to exert effort to achieve incentivized reward

(Soutschek et al. 2018). The current study extends upon this work to identify a role for the FPC in motivating nonincentivized persistence.

Although RT was not significantly related to persistence, RT after negative feedback was quadratically associated with improved accuracy. Negative feedback provides valuable

information that facilitates performance monitoring and strategy adaptation in order to improve subsequent performance (Holroyd and Coles 2002). The quadratic association is interpreted to reflect two strategies for improved accuracy after negative feedback: increased deliberation (slow RT) and increased attention or motivation (fast RT) (Tricomi et al. 2006). Neurally, those who persisted demonstrated recruitment of the parietal operculum on trials following negative feedback. The parietal operculum is involved in cognitive task performance, including mental rotation. Recruitment of this task-relevant region after negative feedback is interpreted to reflect strategy evaluation for participants who persisted (Fishbach et al. 2010). A linear association was present between slower RT after positive feedback and reduced accuracy. Slower RT after positive feedback thus likely does not reflect increased deliberation but rather reduced attention or motivation.

Individuals who persisted reported a challenge-oriented motivation: 78% of those who persisted reported that they chose to persist because it was more difficult, whereas 100% of those who quit reported that they chose to quit because it was easier. Persistence was also associated with enjoying mental rotation trials more than monetary reward trials, which coincided with greater FPC activation to positive feedback compared with reward for those who persisted. Importantly, persistence was not associated with the extent to which participants enjoyed getting mental rotation trials correct. Thus, it was not that participants who quit did not value doing well on the mental rotations but that those who persisted perceived the challenge of the task as more rewarding. Additionally, 25% of participants who quit reported reflecting on their decision with disappointment or another negative appraisal. It may be that reflection could facilitate persistence in individuals who experience aversive responses to negative feedback by illustrating that quitting is not always accompanied by relief. Offering “opt-in” options to reflect on regretful quit decisions would be a fruitful avenue for future investigation as would trial-by-trial changes in willingness to persist as positive feedback is encountered.

As hypothesized, older participants were more likely to persist than younger participants. However, the prefrontal cortex was not differentially activated as a function of age. Older participants demonstrated increased activation of the right posterior SFG/SMA in response to positive compared with negative feedback. This region shows linear increases in activity from pre-adolescence to early adulthood (Peters et al. 2016), and adolescents demonstrate a shift from reliance on the ACC to SMA during feedback learning (Johnson 2011). Increases in SFG/SMA activity are associated with better cognitive control and response inhibition (Hu et al. 2016), both of which are likely important contributors to persistence. Age was also positively associated with left occipital cortex activation to positive feedback versus monetary reward receipt. Reward-stimulus associations influence the representation of sensory information in the occipital cortex in order to guide subsequent behavior (Serences 2008; Anderson et al. 2014). That the FPC did not demonstrate age-related differences but did distinguish persistence behavior which is important to highlight. General trajectories of protracted prefrontal cortex development across adolescence have been well documented, but recent work also identifies substantial individual differences in brain maturation (Becht and Mills 2020; Mills et al. 2021). Similarly, individual differences in the development of delay of gratification abilities have been observed (Romer et al. 2010). Interestingly, the FPC has been shown to orchestrate precommitment, which relies on

delay of gratification and bears similarity to persistence in that it involves imposing costs for deviating from long-term goals (Crockett et al. 2013). It may be that individual differences in FPC maturation hamper persistence development for those with impaired delay of gratification skills. However, because experiential inputs lay the foundation for future neural responding (Spear 2013; Gabard-Durnam et al. 2016), working to improve delay of gratification may help adolescents promote the development of neural systems important for persistence. Altogether, these findings point to various neural systems beyond prefrontal circuitry that contribute to age-related differences in feedback processing and suggest individual differences in FPC engagement relate to persistence independent of age.

Interpretation of the current findings should be made in the context of study specifics. Causal conclusions cannot be made between behavioral persistence and neural activation. The Persistence Task was not designed to test all possible external factors that may influence persistence. For example, fatigue or cognitive load may play a role in the assessment of personal resources available for continued effort expenditure (Shenhav et al. 2017; Müller and Apps 2019). The task was not individualized to each participant's interests; thus, it is possible that some participants may not have been equally engaged or motivated by the task (Jachimowicz et al. 2018; Uusberg et al. 2019). However, there are several factors that point toward the ecological validity of a task that does not attempt to tap individualized interests. For example, in academic domains, adolescents and young adults are often required to pursue success without regard for task-level interest. Participants were not told about the monetary reward game in advance, thus eliminating potential confounds that those who persisted did so to increase monetary reward or that those who quit did so to expedite playing the monetary reward game. Participants were not told about the purpose of the study (i.e., that the study focused on task persistence) and therefore made their decisions to persist or quit independent of any experimenter encouragement or acquiescence bias, which has been shown to affect task performance (McCambridge et al. 2012). Although it is possible that manipulated negative feedback had differential effects based on underlying performance abilities, no differential neural activation was observed based on the amount of manipulated feedback received nor was persistence associated with the amount of manipulated feedback. Additionally, post-task surveys revealed that participants believed feedback was veridical.

Adolescents and young adults face a myriad of challenges every day. Persisting in the face of challenge can lay the foundation for future achievement by instantiating neural responses that help sustain engagement. Although mesolimbic circuitry is often highlighted in decision neuroscience, the striatum was not differentially activated by persistence decisions. Rather, persistence was associated with increased FPC response to positive feedback compared with negatively feedback as well as engagement of the FPC and other attentional resources to positive feedback compared with task-irrelevant monetary reward. This study supports the supposition that the FPC is involved in evaluating whether one should emphasize exploiting a current behavior rather than exploring alternative options if pending success is signaled. Behavior was elicited rather than evoked by promises of external incentives for persisting, improving the generalizability of findings to naturally occurring differences in persistence. Persistence did not hinge on the down-regulation of negative information but instead reflected increased neural

response to success signals. These findings indicate that persistence may be potentially enhanced by targeting perceived utility of positive feedback when balancing goal exploitation versus alternative task exploration.

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## Notes

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