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Neural and behavioral substrates of intrinsically motivated perseverance in adolescents and adults

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Neural and behavioral substrates of intrinsically motivated perseverance in adolescents and adults

A dissertation submitted in partial satisfaction of the requirements for the degree of Doctor of Philosophy in Psychology

by

Sarah Marie Tashjian

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ABSTRACT OF THE DISSERTATION

Neural and behavioral substrates of intrinsically motivated perseverance in adolescents and adults

by

Sarah Marie Tashjian

Doctor of Philosophy in Psychology

University of California, Los Angeles, 2020

Professor Adriana Galván, Chair

Adolescence and early adulthood are marked by increased exposure to novel situations, frequently accompanied by failure and uncertainty about future success. Decision-making in these contexts is often motivated intrinsically, without explicit promise for future reward. However, little is known about the neural systems that support perseverance in the face of challenge when extrinsic reward is not offered. In this dissertation, a multi-method program of research was employed to investigate the neurobiological contributors to perseverance in a sample of 13- to 30-year-olds (*N*=99, 61 females). Findings indicate perseverance is associated with differential neural response to the motivational value of information and regulation of neural systems tracking affective signals associated with negative feedback. Of particular import were motivational and value systems located in the striatum and medial prefrontal cortex, salience regions including the insula, and connectivity between the executive control system and

fronto-insular regions. This research also identified age-related differences in perseverance decisions and neural functioning during a novel task assessing situational factors associated with motivation. Younger participants were less likely to persevere and demonstrated increased superior frontal gyrus activation to negative feedback, potentially reflecting less clear representation of the motivational value of negative feedback. A developmental shift toward increased valuation of positive feedback compared with monetary reward was also observed, consistent with extant understanding of reward sensitivity during adolescence. Finally, this research demonstrates individual differences in deliberative thinking and inflammation are associated both with perseverance behavior and neural response. Older participants reported more deliberative thinking, which was associated with perseverance and reduced activation in the salience network in response to negative feedback. Among adolescents, perseverance was associated with higher concentrations of the pro-inflammatory cytokine interleukin-6, which was in turn associated with reduced insula activation. These individual difference findings highlight the importance of neural and biological response to feedback as a contributor to perseverance. Intrinsically motivated perseverance is associated with numerous positive benefits and this dissertation makes a substantial contribution to explicating how situational factors contribute to engaging with challenge despite failure.

The dissertation of Sarah Marie Tashjian is approved.

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2020

This dissertation is dedicated in loving memory to my father, C. Wayne Newton, for his encouragement of education and enduring love.

To the love of my life Joel, all of this is possible because of you.

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Chapter 1

General introduction

Benefits of perseverance

For decades, perseverance has been revered as an essential element of success. Calvin Coolidge, the 30th president of the United States, famously remarked "*Nothing in this world can take the place of persistence. Talent will not; nothing is more common than unsuccessful people with talent. Genius will not; unrewarded genius is almost a proverb. Education will not; the world is full of educated derelicts. Persistence and determination alone are omnipotent.*" (Knowles, 1999). Perseverance 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 & Scheier, 2000; Seligman, 1975). The study of developmental consequences of perseverance has linked greater persistence in adolescence with higher educational attainment, income, and occupation level in adulthood (Andersson & Bergman, 2011). Other work identifies associations between perseverance and psychological well-being in adults (Steger et al., 2008). For example, grittier individuals who report more perseverance have been found to maintain positive emotions and expectations toward difficult tasks even when encountering failure (Lucas et al., 2015; note this perseverance may come with a cost, which is discussed further below), and to report higher optimism (Lovering et al., 2015) and life satisfaction (Duckworth et al., 2009). The potential benefits of perseverance beg the question: what facilitates perseverance?

Perseverance as intrinsically motivated behavior

This dissertation draws on foundational psychological theory characterizing perseverance as motivated behavior. Feather (1962) argued that motivational representations of persistence[1], in

[1] Persistence is described by Feather (1962) as: "The general paradigm of the persistence situation is that in which a person is confronted with a very difficult or insoluble task and is unrestricted in either the time or number of

contrast to trait conceptualizations, account for both person- and situation-level factors and, thus, are able to provide a better explanation of perseverance. Support for a motivational account of perseverance is provided by prior work that indicates perseverance is malleable and can be boosted (Destin et al., 2018; White et al., 2017). According to an expectancy-value model, goal persistence is a multiplicative function of goal value and the expectancy of goal attainment (Atkinson, 1957; Eccles et al., 1983; Feather, 1962; Lewin et al., 1944). Subjective task value is comprised of several value components including intrinsic value (also referred to as interest-enjoyment value), attainment value, utility value, and relative cost (Eccles et al., 1983). Values and expectancies are influenced by numerous person-level factors (e.g., avoidance tendencies, competency beliefs) and situational factors (e.g., performance feedback), and are thereby continuously updated (Eccles, 2009). Importantly, these person-level and situational factors are influenced by the individual's interpretations and perceptions (e.g., affective response to prior achievement experiences; perceptions of task demands) (Eccles & Wigfield, 2002; Eccles, 2009). Thus, choices motivated by expectancy-value calculations are not strictly the result of a conscious logical process, but rather inclusive of other, less-rational, contextual and affective components that influence motivation (Eccles & Wigfield, 2002). Values and expectancies in turn influence the motivation to achieve success at a task (approach motivation) and the motivation to avoid failure at a task (avoidance motivation). Whether an individual perseveres depends on the balance between approach and avoidance motivations (Atkinson, 1957). This motivational balance is updated and may change as the individual receives additional information informing value and expectancy calculations (i.e., feedback indicating increased/reduced likelihood of achieving success at the task).

attempts he can work at it. He is unsuccessful at each of these attempts at the task, but can turn to an alternative activity whenever he wishes."

Perseverance is a eudaimonic behavior that may or may not result in subsequent reward. As such, models of intrinsic motivation provide a relevant framework for studying behavioral perseverance. Intrinsic motivation generally refers to one's tendency to perform an act because doing so is inherently interesting or enjoyable, rather than because a separable consequence is connected to performance (Ryan & Deci, 2000; see also intrinsic value as a component of the expectancy-value model proposed by Eccles et al., 1983). Intrinsic motivation was observed in rhesus monkeys as early as 1950 when Harlow coined the term to describe persistent playing with puzzles in the absence of external rewards. Meta-analyses suggest intrinsic motivation can result in quality learning and creativity in the school environment (Froiland & Worrell, 2016; Taylor et al., 2014), and thus educators are interested in understanding what factors can support or undermine intrinsic motivation. Prevailing views are that intrinsically motivated exploration is not driven by a desire to reduce anxiety (Deci & Ryan, 1985), but rather to discover and seek to solve novel problems (Harlow, 1953; White, 1959; Deci & Ryan, 1985). The act of discovery is naturally accompanied with potential failure. Thus, intrinsically motivated behavior likely results from an outweighing of the motivation to achieve success (in this case, gain new knowledge or skill) compared with motivation to avoid failure (Figure 1.1). Although correlations between intrinsic motivation and persistence have been identified (Boyd, 2002; Vallerand & Bissonnette, 1992), it has yet to be determined whether perseverance involves a motivational tradeoff between the desire to achieve success and desire to avoid failure. In the present study, positive and negative feedback are used to elicit individual differences in calibration of this motivational balance.

In contrast to intrinsic motivation, extrinsic motivation occurs when one engages in a behavior to obtain a consequence distinct from the inherent nature of the behavior itself, most

frequently to obtain an external reward or avoid a punishment. In some cases, offering a performance-based extrinsic reward can undermine intrinsic motivation (Deci et al., 1999). It is worth noting that the intrinsic / extrinsic motivation distinction has garnered debate as to whether intrinsically motivated behaviors are actually motivated by anticipated future benefits or intermittent reward (Cameron & Pierce, 1994). Here, it is acknowledged that intrinsically motivated behaviors may be related to anticipation of future reward, but critically the reward is defined and attached by the actor (e.g., internal locus of causality; Deci & Ryan, 2000) rather than an external force. Although perseverance may result in rewards objectively valued as positive (e.g., achievement, skill acquisition) as opposed to rewards objectively valued as negative (e.g., pleasure from drug use), the receipt of positive rewards is not certain, in contrast to extrinsically motivated behavior.

Significance of this work

The conceptualization of perseverance as a behavioral manifestation of intrinsic motivation distinguishes it from personality constructs of grit and conscientiousness. Trait studies of perseverance as a facet of grit and conscientiousness assume stable characteristics of a person that transcend situational factors to determine consistency in behavior. A motivational account of perseverance behavior acknowledges both person and situation parameters, having the potential to account for variations in perseverance within person from situation to situation as well as differences between persons. Recent psychophysiological investigation of perseverance add further support for a motivational model. Individuals reporting higher perseverance (as measured by the self-reported grit scale) showed greater sympathetic and parasympathetic activity during an active coping task, a result that the authors interpreted as high perseverance individuals demonstrating greater motivational engagement on the task (Silvia et al., 2013).

While these findings support a motivational framework, the authors use grit as a personality facet and theorize that grit influences motivational engagement by making goals more or less important. Thus, these findings do not speak to how responsivity to situational factors (i.e., performance feedback) influence motivational determinants of perseverance and are limited in uncovering mechanistic explanations of individual differences in perseverance. The present program of work considers the relation between persistence at a task and motivation by asking: how do individual differences in response to success versus failure relate to subsequent perseverance?

Perseverance is commonly defined as the act of doing something despite difficulty or delay in achieving success. Applying this definition to the present work, perseverance entails persisting at a task despite prior failure. Scholarly interest in perseverance is not new (Ryans, 1939), but surprisingly little contemporary research has examined contributors to individual differences in intrinsically motivated perseverance. Additionally, although Feather (1962) called for the consideration of perseverance as a motivational construct over 50 years ago, more recent, popularized conceptualizations of perseverance have characterized the behavior as a personality trait (Duckworth et al., 2007). As such, little research has sought to uncover mechanisms, including differences in engagement of neurobiological systems, that might promote or interfere with perseverance. Instead, the primary method of investigating perseverance over the past decade has been self-report and has focused on determining whether perseverance correlates with objective success (e.g., Duckworth et al., 2007; Credé et al., 2017). This dissertation combines a novel behavioral task (the "Perseverance Task"), functional magnetic resonance imaging (fMRI), self-report questionnaires, and inflammatory assays in adults and adolescents to elucidate neural correlates, developmental differences, and individual variability relating to perseverance.

Although the present work uses one task as an initial attempt to behaviorally measure perseverance, the paradigm provides a foundation for future expansion. The paradigm developed for the present work shares some features with unfixed tasks[2] that measure effort as a function of the importance of success as parameterized by Motivational Intensity Theory[3] (Brehm & Self, 1989; Wright et al., 2008). For both tasks, participants have some control over the amount of effort they expend to achieve success on the task. One difference is the explicit decision to continue expending effort on the Perseverance Task used in the present work compared with more implicit measures of effort like reaction time (RT), number of problems solved, or physiological response used in unfixed tasks (for a review, Richter et al., 2016). By directly measuring perseverance decisions, a better understanding of mechanistic antecedents of perseverance can be identified.

The current research

Taking a motivational approach, Figure 1.1 depicts a proposed model of the iterative process by which perseverance decisions are made in the context of the Perseverance Task created for the present work. In the Perseverance Task, participants were exposed to positive and negative performance feedback as a situation-level factor likely to influence motivation. Negative feedback can strengthen the relative contribution of success motivation by signaling a discrepancy between goals and performance (Carver & Scheier, 1990), thereby reinforcing goal value and indicating a need for increased effort to reach goal attainment. Negative feedback can alternatively strengthen failure avoidance motivation by signaling a likelihood of future failure

[2] Also known as "do your best" or piece-rate tasks that lack a fixed level of difficulty because people can work as quickly or slowly as they choose. Outcome measures are number of problems solved or reaction time. Effort is interpreted as a function of task value to the individual.

[3] Motivational intensity theory predicts that effort is a function of success importance: the higher the success importance (analogous to value), the more effort one will expend.

(Soman & Cheema, 2004), thereby reducing expectancy. Negative feedback can also reduce task value by increasing the perceived cost of engaging in an activity (Eccles, 2009). Cost is influenced, like other expectancy and value calculations, by many person-level factors like fear of failure and anxiety. The utility of negative feedback for perseverance is likely related to an individual's ability to regulate their response to failure, with more regulated reactions being more likely to result in perseverance (Zimmerman, 2000). Positive feedback may also reinforce goal value (Eccles & Wigfield, 2002; expectancies and values are positively related), but according to a discrepancy model of self-regulation (Carver & Scheier, 1990), positive feedback can weaken success motivation by signaling that effort can be reduced because goal attainment has been or will easily be achieved. Additionally, positive expectations of success are necessary but not sufficient predictors of choice behavior (Eccles et al., 1999). Person-level factors such as impulsivity are also examined as potential contributors to perseverance motivation. Perseverance behavior is the quantifiable manifestation of the motivational balance to achieve success and avoid failure. To examine perseverance as an intrinsically motivated behavior, this task does not offer any extrinsic reward for perseverance.

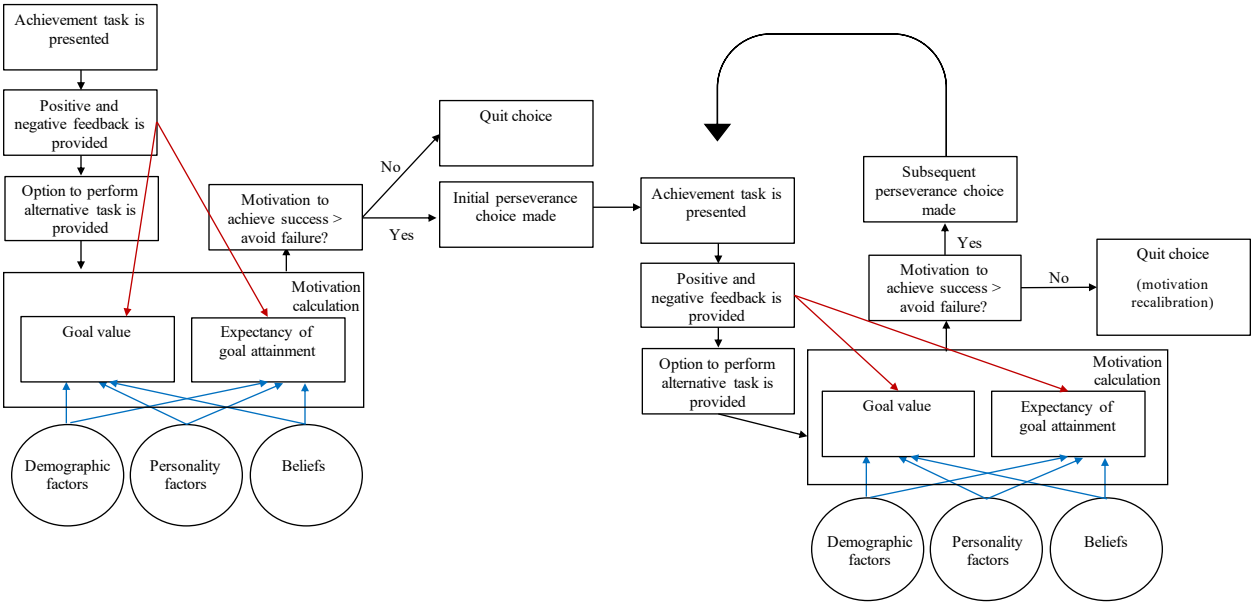


Figure 1.1. A proposed model of the iterative process by which perseverance decisions are made in the context of the Perseverance Task. Circles denote person level factors that are theorized to affect motivational calculations via influences on goal value and expectancy. Situational factors, in this case performance feedback, are also theorized to affect motivation. Black arrows denote temporal components of the Perseverance Task. Colored arrows denote pathways through which person factors (blue) and situation factors (red) influence motivation to persevere. Perseverance entails ongoing motivational calculations, which are not directly measured, but are observed as decisions.

The decision to continue engaging in an effortful task without immediate success does not occur in a vacuum. Response to environmental cues about one's performance may influence motivation to persist. Additionally, salience of potential reward for persevering and eventually achieving success may provide motivation that overrides negative feelings of failure or deterrence. The current dissertation aimed to identify potential underpinnings of differences in behavioral manifestations of the motivation to persevere by leveraging human neuroimaging techniques to examine differential neural response to feedback and anticipation of reward. Examining response to situational factors, rather than personality traits, provides a better opportunity to target perseverance behavior in individuals who may otherwise tend to avoid persistent effort in the face of failure (i.e., perseverance).

Development of perseverance was examined in adolescents for three reasons: (1) adolescence is a time when the ability to regulate one's behavior is still developing but the drive to seek novel and rewarding experiences peaks (Steinberg et al., 2018), (2) neural response to feedback is differentially evoked in children and adolescents compared to adults (van den Bos et al., 2009), and (3) adolescence is a developmental period during which autonomy increases and a

sense of autonomy can facilitate intrinsic motivation (Deci & Ryan, 1987). The conflicting psychological processes of self-control and the drive to seek gratification are thought to be mechanisms of perseverance (Duckworth & Steinberg, 2015). During adolescence, the relative differences in expression of self-control and reward-sensitivity have been linked to differential maturational trajectories of neural systems associated with each respective behavioral phenomenon (Casey et al., 2008; Steinberg, 2008; Shulman et al., 2016). Additionally, adolescents exhibit a unique response to learning from positive and negative feedback compared with children and adults (van der Schaaf et al., 2011). Adolescents exhibit an intermediate pattern of feedback learning with reward learning similar to children and punishment learning similar to adults, suggesting a shift in responding to negative rather than positive feedback with age (van den Bos et al., 2009; van der Schaaf et al., 2011). Combining these findings with motivational models that propose the weighting of potentially positive versus potentially negative outcomes as antecedents of perseverance (e.g., Atkinson, 1957; Feather, 1962), I propose that developmental differences in valuation of different kinds of feedback may explain developmental differences in the choice to persevere. Understanding whether positive versus negative feedback, or both, contribute to perseverance can inform theoretical models of motivational systems contributing to perseverance (i.e., approach toward reward or blunted sensitivity to negative information), which may have application for fostering perseverance in the classroom and workplace. Although informative, prior learning paradigms, unlike the Perseverance Task, notably do not give participants the option to quit participating and thus cannot speak to neural contributions to perseverance. Additionally, much of developmental psychology and neuroscience is focused on averages, but this obscures meaningful individual variation occurring during development. As such, the current dissertation considers several

individual difference measures that may add meaningful insight into the development and manifestation of mechanisms facilitating perseverance.

In the following chapters, I present three studies that bring together several cutting edge bio-behavioral methods to examine contributors to perseverance.

Summary of Study 1: Neural correlates of perseverance

The goal of psychology is to develop and test theories about how the mind works and how that functioning relates to behavior. fMRI can inform theories about cognition by answering the extent to which the way the brain responds to a given stimulus is relevant for behavior. The present study leverages fMRI to investigate neural activation to negative and positive performance feedback as it relates to subsequent perseverance. This study also includes a comparison of neural activation to hedonic reward versus positive performance feedback to test whether extrinsically versus intrinsically motivated states are associated with perseverance. Combining fMRI with a motivational model of perseverance will increase understanding of neural mechanisms underlying perseverance and the potential for development of empirically founded intervention programs targeted at boosting perseverance. If perseverance is not a static trait, but rather founded in motivation, it can be amplified by targeting motivational systems. For example, White and colleagues (2017) found that thinking about an archetype (i.e., Batman) who was good at working hard increased perseverance in 4- and 6-year-old children. Although not interpreted by the authors in the context of expectancy-value models, it is likely that the Batman intervention changed the motivational value of the task thereby increasing perseverance (e.g., attainment value is influenced by perceptions of idealized images of what one should be like; Eccles, 2009). Similarly, improvements in academic achievement have been observed using mindset interventions that reframe effort expenditure in terms of increasing expectancy of

success rather than signaling failure (Yeager & Dweck, 2012). The present work is a first step in identifying relevant neural systems to target (e.g., affective regulation of negative feedback versus increased saliency of reward associated with positive feedback).

Summary of Study 2: Developmental differences in perseverance behavior and neural correlates

Closely related literature on grit demonstrates an increase in self-reported grit with age. Duckworth and colleagues (2007) reported that grit increased monotonically with age in adulthood whereas Kannangara and colleagues (2018), in a study of undergraduate and postgraduate students, found grit was higher for those aged 31 and above compared to those between ages 16 and 21. In a longitudinal behavioral investigation of persistence on a challenging task in children, individual differences in the stability of persistence were observed suggesting for some children the capacity to persist changes dramatically from 5 to 10 years of age whereas for others trajectories are flat (Zhou et al., 2007). The authors speculate that development of effortful and reactive control, superordinate constructs that include persistence, may not have reached maturity in their sample resulting in divergent developmental trajectories of persistence. Notably, however, the puzzle box task used by Zhou and colleagues as an index of persistence was incentivized with external reward (see also Eisenberg et al., 1996; Eisenberg et al., 2004). Attaching external rewards has been shown to undermine intrinsic motivation (Deci et al., 1999). Framing a task in terms of extrinsic rather than intrinsic goals also undermines performance and learning (Vansteenkiste et al., 2004, 2008). This has relevance for theories of autonomy development in that intrinsic motivation seems to be tied to internal representations of motivational value for the self, irrespective of external valuation. A sense of autonomy, development of which increases during adolescence (Zimmer-Gembeck & Collins, 2003; Crone

& Dahl, 2012), is necessary for intrinsic motivation (Ryan & Deci, 2000) and thus, as autonomy increases, intrinsic motivation may also increase. These biological and psychosocial features of adolescence create an opportunity to (re)direct the orientation of intrinsic motivation toward achievement goals. The present work tests whether these age findings hold when examining perseverance behaviorally during an intrinsically motivated paradigm and whether neural development is associated with age-related disparities in perseverance behavior.

In the past decade, there has been a surge in research attempting to understand how the brain develops both structurally and functionally and what this development means for behavior. The brain is plastic and able to adapt to environmental input, especially during development (Fuhrmann et al., 2015). In adolescence, this plasticity supports increases in autonomy. Adolescents are more frequently actively choosing the environmental stimuli they experience in contrast with children (McElhaney et al., 2009). Returning to expectancy-values models of motivation, Wigfield (1994) proposes that over development, children and adolescents begin to attach more value to activities in which they do well. This may be an adaptive strategy for maintaining positive self-perceptions, but may also create a negative feedback loop whereby children and adolescents avoid challenging activities before competency is able to develop. Foregoing challenges in favor of more risk-averse activities could have lasting impacts for the development of neural systems supporting future perseverance. If the brain is plastic and perseverance is not fixed, then perseverance can be harnessed to achieve success: continual engagement of systems supporting perseverance can strengthen the responsivity of these systems during future perseverance attempts.

Summary of Study 3: Person-level factors associated with perseverance

After identification of candidate mechanisms and developmental inquiry as to the relative contribution of such mechanisms, the next step in elucidating contributors to a behavioral phenomenon is to investigate individual variability. As reviewed above, negative feedback can act as a social-evaluative threat and positive feedback is rewarding. Thus, several person-level factors associated with reward and threat were selected as potential contributors to perseverance.

Sex

Females tend to report higher sensitivity to punishment (Santesso et al., 2011; adolescents and adults, no age interaction), but females also report higher grit than male counterparts (Christensen & Knezek, 2014; note this effect is for total grit scores and consistency of interests with marginal significance for the perseverance facet). Sex in the full sample and sex by age interactions were investigated as a predictor of perseverance behavior and neural response to feedback.

Inflammation

Although conceptualizations of perseverance are generally that it is associated with positive outcomes, perseverance may have unintended negative consequences for some individuals (Destin, 2019). For example, pursuing goals and achieving academic and social competence despite economic or social adversity can lead to deleterious health outcomes including increased risk of cardiovascular disease (James et al., 1987), as well as elevated cortisol and blood pressure (Brody et al., 2013). Recent work on goal-disengagement also suggests perseverance may be costly at a physiological level (Miller & Wrosch, 2007). Although it is not clear that perseverance is stress-inducing, the finding that greater goal persistence is associated with higher levels of systemic inflammation in adolescents may be attributable to changes in the stress response system during this developmental stage. Neural development

during adolescence may amplify the sensitivity of stress responsivity having lasting effects for stress calibration (McEwen, 2007). Miller and Wrosch (2007) took a critical step in expanding health psychology inquiries beyond severe chronic stressors to normative differences in goal-directed behavior, but their findings are limited in a single assessment of chronic inflammation (C-reactive protein, CRP) and self-reported goal pursuit. The present work investigates links between task-based perseverance behavior and five markers of low-grade inflammation, including pro-inflammatory cytokines. Incorporating behavioral, neurobiological, and physiological queries of the antecedents and costs of perseverance is an integrative approach well suited for improving measurement and understanding of perseverance.

Impulsivity

According to the reward responsivity hypothesis, engaging in effortful self-control can lead to a dramatic increase in reward pursuit to counter negative feelings associated with self-control (Kelley et al., 2019). This self-control / reward-pursuit trade-off occurs because of the cognitive load associated with self-control, depleting resources necessary to continue regulating behavior. The effects of this cognitive depletion might be more pronounced for individuals high in impulsive behavioral tendencies given impulsivity interferes with executive function abilities involved in effortful control such as strategic thinking, attention, working memory, and problem solving (Romer et al., 2009). Thus, it is possible that adolescents who choose not to persist also report higher levels of impulsivity. Reward responsivity, a potential motivator of perseverance, also increases impulsivity (Braams et al., 2015; Galván et al., 2007). If positive feedback promotes feelings of reward, but negative feedback promotes feeling of failure, impulsive individuals may be more likely to seek additional reward by pursuing an easier task rather than

continuing to persevere on a more difficult one for which they are likely to received additional negative feedback.

Chapter 2

Perseverance engages neural systems tracking valence and information value

Introduction

Individuals vary in the extent to which they persevere in pursuit of goals. A first step in understanding whether perseverance is malleable is to understand whether responses to situational factors are associated with differences in perseverance: does what motivates some individuals to persevere act as a deterrent for others? Perseverance, or continued effort toward goal pursuit despite difficulty or challenge, is associated with numerous positive outcomes including psychological well-being (Duckworth et al., 2009; Lovering et al., 2015) and objective measures of success like academic achievement and job success (Littman-Ovadia & Lavy, 2016; Tang et al., 2019). Lack of perseverance may be especially detrimental in learning contexts that frequently require grappling with failure prior to success. For example, lack of persistence is associated with reduced learning, particularly conceptual learning which requires deeper processing of information (Vansteenkiste et al., 2006, 2008). After failure, perseverance may reflect a drive to acquire information in attempts to resolve uncertainty about how to achieve success (Loewenstein, 1994). Even without relevance to future success, information itself has value and can drive behavior in systematic ways similar to extrinsic rewards (Marvin & Shohamy, 2016). The current study examines neural response to performance feedback and reward, two situational factors that are known to influence motivation, to elucidate neural systems associated with perseverance in the face of failure.

Both positive and negative feedback can increase motivation. Positive feedback can increase expectancies of goal success by increasing a sense of self-efficacy or perceived competence in pursuing a goal (Bandura, 1997). However, as previously discussed, this increased goal expectancy may undermine effort expended. Negative feedback can also increase motivation by promoting goal adherence (Higgins, 1987). Self-discrepancy theory (Higgins,

1987) distinguishes goals that obtain pleasure and goals that avoid pain such that those focused on obtaining pleasure have a promotion orientation to increase the presence of positive outcomes, thereby encouraging persistence of goal pursuit. Thus, whether negative feedback is perceived as an informative signal that further effort is needed to achieve success or whether it is perceived as punishment thereby activating a desire to avoid further negative feedback may contribute to individual differences in perseverance. It remains unclear whether sensitivity to positive or negative feedback, or both, relate to perseverance decisions. The benefits of feedback for motivation are, in part, related to affective consequences of goal attainment as reward. Thus, reward responsivity, or the intensity of responding to reward-related stimuli, was selected as a second potential contributor to perseverance. Prior work assessing perseverance as a multi-faceted personality trait found individuals reporting greater persistence found less-arousing situations more intrinsically motivating and rewarding, as inferred by greater neural activation in the striatum and medial prefrontal cortex (mPFC), neural regions associated with reward responsivity (Gusnard et al., 2003). In the current study, responsivity of reward-related neural systems was assessed during receipt of performance-related feedback as well as during receipt of monetary reward.

Feedback sensitivity

Performance feedback about whether responses are correct or incorrect provides valuable information to help guide learning (DePasque & Tricomi, 2015; van Duijvenvoorde et al., 2008). In typical investigations of feedback, positive feedback is intended to encourage continuation of behavior whereas negative feedback signals a need for behavioral modification. This perspective is informative for understanding feedback-based learning but does not consider how feedback is used in the decision to continue pursuing skill acquisition (i.e., perseverance on a task). In the

case of perseverance, negative feedback does not just indicate a need for a new performance strategy but should also signal a need to continue working on the task in order to gain mastery.

The cost or negative aspect of engaging in a task, such as fear of failure and effort expenditure required, is a critical component of determining whether one continues with a task goal (Eccles et al., 1983). Feedback can inform cost analyses by updating estimations about whether one will succeed on a given task, which can in turn influence motivation and interact with enlistment of cognitive effort through cost signaling in the insula (Meyniel et al., 2013) and reward signaling in the striatum (Dobryakova et al., 2013). Although feedback itself has no extrinsic value, it can produce subjective feelings similar to rewards and punishments (Eisenberger, 2012). The salience of this affective component of performance feedback may guide computations motivating perseverance.

Prior work has shown that when adults receive negative performance feedback, neural regions associated with cognitive control and response selection, such as the anterior cingulate cortex (ACC) and the dorsolateral PFC (dlPFC), activate. The dlPFC has been found to be more responsive after negative feedback (versus positive feedback) in adults compared with adolescents, consistent with the assertion that the dlPFC is important for implementation of goal-directed and controlled behavior (van Duijvenvoorde et al., 2008). The responsivity of the dlPFC varies more dramatically with age, as discussed further below, whereas engagement of the ACC appears to develop earlier (van Duijvenvoorde et al., 2008; van den Bos et al., 2009). Individuals who report high sensitivity to punishment demonstrate increased ACC activation during monetary losses (Santesso et al., 2011), which may be a result of signaling in the amygdala (Klavir et al., 2013). The dorsal ACC is also thought to integrate signals relevant to effortful control and behavioral shifting in order to adjust to control-demanding tasks (Shenhav et al.,

2017). The dlPFC has weak direct amygdala input and as such, the amygdala likely influences the dlPFC via indirect transmissions through the cingulate (Ray & Zald, 2012). Signaling from the amygdala to the dlPFC through the ACC may be necessary for regulation of behavior in response to negative feedback. Thus, developmental changes in connectivity of this circuitry may contribute to the developmental differences in activation to negative feedback.

The insula, acting as part of both the salience network and central executive network (Seeley et al., 2007), is also activated by negative feedback (Späti et al., 2014) and plays a modulatory role in coordinating connectivity among neural networks during cognitive control (Menon, 2011). The insula reduces autonomic activity in response to challenge in adults and is functionally connected to the ACC (Strang et al., 2011). Affective components of physical and social pain, including receiving socioevaluative feedback (Eisenberger et al., 2011), are processed by the ACC and insula (Eisenberger, 2012). Together, the ACC and insula are considered a functional circuit involved in attention and affective processes (Dosenbach et al., 2006; Menon & Uddin, 2010), and are thus also potential candidates of individual differences in how negative feedback may manifest as a deterrent to perseverance.

Unsurprisingly, positive feedback is considered both rewarding and informative, and at a neural level positive feedback activates the striatum, especially the caudate. The relevance of feedback for adult striatal activity modulates with goals and expectations (DePasque Swanson & Tricomi, 2014). Reward signals converge in the striatum, which receives projections from prefrontal regions, including the OFC, mPFC, and ACC, as well as the amygdala (Haber & Knutson, 2010; Tottenham & Galván, 2016). Despite common conceptions of the amygdala as a center for processing aversive stimuli, positive feedback has also been shown to elicit greater activation in the amygdala than negative feedback (Bischoff-Grethe et al., 2009; Drueke et al.,

2015). The amygdala plays a key role in learning and the extent to which neurons in the amygdala adjust their activity to value of an external stimulus predicts learning in animals (Paton et al., 2006).

The basal ganglia, including the striatum, play key roles in adaptive behaviors guided by reward and punishment (Robinson et al., 2010). Self-reported grit has been linked to resting state functional connectivity between the striatum, PFC, ACC, and posterior cingulate cortex (PCC) (Myers et al., 2016). Corticostriatal connectivity is associated with selective inhibitory control (Majid et al., 2013), or the ability to ignore irrelevant stimuli, and striatal and PCC activity is associated with delayed gratification (Weber & Huettel, 2008). Both of these cognitive control processes are relevant for perseverance. Positive feedback activates regions implicated in reward processing like the striatum, mPFC, PCC, and medial temporal lobes (MTL) (DePasque & Tricomi, 2015). Positive feedback activates the striatum to a greater extent when learning new rules compared to applying previously learned rules, suggesting sensitivity to the informative value of feedback in these dopamine-rich neural regions (Peters & Crone, 2017). This enhanced striatal response to feedback was associated with better performance longitudinally in adolescents and young adults. When perceived as informative, negative feedback also elicits striatal activity (Lempert & Tricomi, 2016). Developmental differences have been observed with regard to how well individuals learn from positive versus negative feedback (van der Schaaf et al., 2011), but the implications for choice behavior have yet to be identified.

A feedback-based model of self-regulation proposed by Carver and Scheier (1990) suggests negative feedback may be more important for determining who will persevere. According to this model, individuals regulate their actions to minimize the gap between their actual performance and their desired goal. Positive feedback, either from internal or external

sources, encourages individuals to reduce effortful output because they are closer to reducing the discrepancy between performance and their goal. Negative feedback, in contrast, signals the discrepancy still exists and further effort is needed to achieve the desired goal (i.e., motivating goal-directed action). Thus, the way individuals respond to negative feedback as either indicating a reduced expectancy of success or a need for further effort should relate to perseverance behavior.

Reward sensitivity

Prior work in adults suggests perceived agency in achieving a reward differentially activates the striatum compared to passive receipt of reward (Tricomi et al., 2004). As such, it is important to disentangle neural contributions of performance feedback, which is implicitly tied to skill or accomplishment, from basal functioning of the reward system. Understanding the uniqueness and similarities of perseverance-related reward processing and reward processing more generally will aid conceptualizations of perseverance. This is particularly important given regions overlapping with those involved in feedback processing are also implicated in reward processing in adults and youth (Liu et al., 2011).

Using dynamic causal modeling, Cho and colleagues (2013) suggest that anticipation of reward and loss involves an alerting signal in the thalamus that converges with interoceptive information in the insula to shape action selection in the striatum in both adolescents and adults. A major function of the insular node of the salience network is salience detection or detection of behaviorally relevant stimuli. Signals converging in this region may have differential effects on subsequent action selection in the ACC, which is involved in response selection and conflict monitoring. Striatal activity also serves a key role in action selection by integrating cognitive and affective information processed by frontal and temporal regions to refine action selection and

promote approach toward motivationally appetitive stimuli (Floresco, 2015). In adults, these neural circuits are engaged by positive performance feedback even in the absence of external reward (Murayama et al., 2010) but also during passive receipt of rewards (Tricomi et al., 2004) and in reward-based learning (Daniel & Pollmann, 2010). Aberrant reward functioning is an important potential mechanism to investigate with regard to perseverance given motivational deficits have been linked to problems with persistence in clinical populations (Dovis et al., 2012). Additionally, the salience network modulates other core networks involved in cognitive information processing, and modulation by the insula may be relevant for how performance feedback is used to guide perseverance decisions.

Hypotheses

Positive feedback was expected to elicit greater activation in the amygdala, striatum, mPFC, PCC, and MTL compared with negative feedback. Negative feedback was expected to elicit greater activation in hubs of the salience network, namely the ACC and insula, compared with positive feedback.

Differential neural response to negative feedback versus positive feedback was expected to relate to perseverance. The importance of neural response to negative feedback for perseverance is grounded in work by Carver and Scheier (1990) indicating positive feedback signals the need for less self-regulation as goal attainment is more likely whereas negative feedback suggests greater investment needed to achieve a goal. Additionally, for individuals oriented to persevere, negative feedback is more likely seen as useful information as opposed to a threat (Lee & Kim, 2014).

Given increased activation in the insula after experiencing an aversive event is associated with higher sensitivity to the aversive stimuli (Galli et al., 2013), reduced activation in the insula

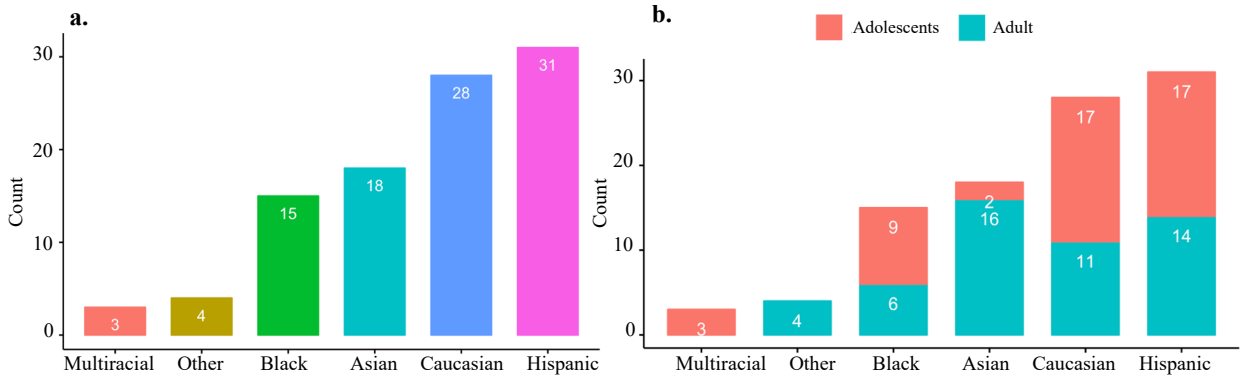
to negative feedback is hypothesized to relate to perseverance as opposed to quitting. Greater connectivity among nodes of the salience and central executive networks in response to negative feedback, as an indicator of increased ability to regulate response to aversive stimuli, is also hypothesized to relate to perseverance as opposed to quitting.

Methods for all studies

Participants

One-hundred adolescents and young adults ages 13-30 (61 females; M_{age}=18.330, *SD*=3.213) completed the Perseverance Task. Ninety-nine participants completed the task while undergoing fMRI (60 females; M_{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.

Ethnicity for the full sample and by age group are reported in Figures 2.1a-b. Sex by age group is reported in Figure 2.1c. Ethnicity did not significantly differ by age group, $t(97)=-.725$, $p=.470$. Sex was marginally associated with age group, $X^2(1, N=99)=2.835$, $p=.092$, such that the adult group consisted of more females than males.



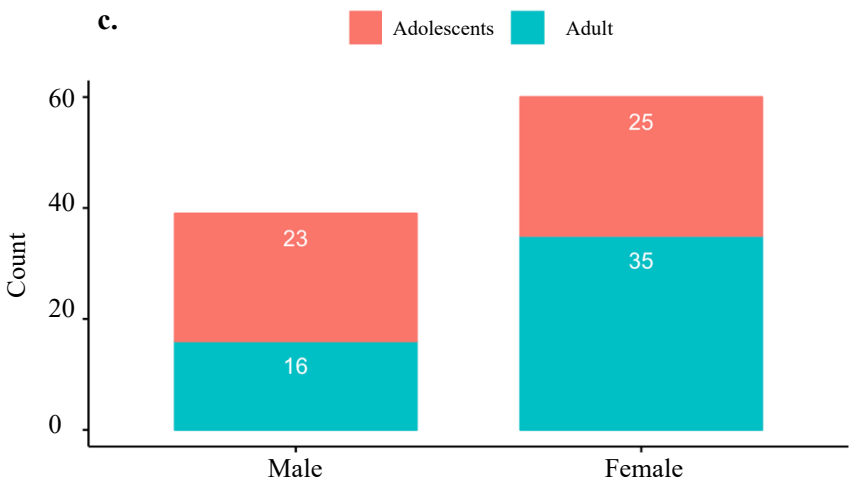


Figure 2.1. (a) Ethnicity reported for the full sample. **(b)** Ethnicity breakdown by age group. **(c)** Sex breakdown by age group. *N*=99. Adults, *n*=51; Adolescents *n*=48.

All participants were right-handed and free of metal. Additional exclusionary criteria included previous diagnosis of a psychiatric, neurological, or developmental disorder, or use of psychotropic medications. Participants visited the UCLA Staglin Center for Cognitive Neuroscience (CCN) where they performed tasks in the 3T Siemens Magnetom Prisma MRI scanner. Young adult and adolescent participants were scanned as part of two separate, larger studies.

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 (young adults) or a phone screening with a parent (adolescents). Young adult participants provided informed written consent. Adolescent participants provided informed written assent and their parent or guardian provided informed written consent. Participants were treated in accordance with the ethical standards of American Psychological Association.

Perseverance Task

Participants completed the Perseverance Task, which is a novel task I created and adapted for use with fMRI to assess intrinsically motivated behavioral perseverance (Figure 2.2a-c).

Participants received spoken instructions and completed one mental rotation practice trial outside of the scanner before beginning the experimental session. During the task, participants first completed a series of 50 mental rotation trials using stimuli created by Ganis and Kievit (2015) (Figure 2.2a). Participants were presented with pairs of objects, each made up of 7-11 cubes connected face-to-face to form a pipe-like object with 4 connected arms and two free ends. In each stimulus, one of the objects in the pair was rotated relative to the other (four angles disparities were used: 0, 50, 100 and 150 degrees) with shading and depth cues. Half of the shapes were matches, half were not matches. Ten trials were rotated 0 degrees, 15 rotated 50 degrees, 14 rotated 100 degrees, and 12 rotated 150 degrees. All shapes were white presented on a black background for 3500 ms. Duration of presentation was based on average RT for the most difficult shape rotation (150 degrees) identified in prior work with adults (3191 ms) (Ganis & Kievit, 2015). Additional time was added (309 ms rounding up to 3500 ms presentation) to ensure all participants could answer some trials successfully in order to achieve a sufficient number of positive feedback trials. Ensuring some trials were successful achieved two goals: (1) examination of positive versus negative feedback contrasts, and (2) minimize individuals perceiving the task as "unattainable" and consequently disengaging. Mental rotation was chosen as the challenge task rather than a task more familiar to participants (e.g., math problems) to reduce pre-task differences in ability beliefs, which have been shown to influence motivation (Eccles et al., 1998). Additionally, spatial reasoning skills have been linked to success in science, technology, engineering, and mathematics domains (STEM; Wai et al., 2009).

When the shapes offset, participants were given a decision screen during which they were instructed to make a button press to indicate whether they thought the shapes were identical, after mentally rotating one of them. Decision time was unlimited to prevent missing data and to ensure

negative feedback was provided after an answer was attempted rather than as a result of time, inattention, or refusal to answer.

After the decision was made, participants received quasi-manipulated feedback for 1500 ms indicating that their responses were either correct (positive feedback) or incorrect (negative feedback). Forty-percent of trials received negative feedback regardless of performance. The remaining 60% received accurate performance-based feedback. Manipulated feedback ensured all participants received negative feedback on a minimum number of trials to assess whether neural response to negative feedback was associated with perseverance behavior. To reduce the likelihood that participants were able to identify trials for which feedback was manipulated, manipulated negative feedback was randomly interspersed between accurate feedback trials and manipulated feedback was not given for the easiest trial type (0 degree rotation). Manipulated feedback was given for 6 trials rotated 50 degrees, 7 rotated 100 degrees, and 7 rotated 150 degrees. Inter-trial intervals (ITIs) of 1000 ms onset after the feedback screen and before the next mental rotation presentation.

Upon completing the 50 trials, participants made decisions as to whether they would continue on a path requiring more mental rotations (Path A, persevere) or quit for an easier and shorter path (Path B, quit) (Figure 2.2b). 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 and rather as a decision to "quit" (i.e., reduce effort). In everyday situations, the decision to quit a challenge is often accompanied by a break in effortful expenditure improving the ecological validity of the quit path. 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

persevered prior to the reward game (see below, Figure 2.2c). If participants chose to persevere (Path A), they completed an additional 5 mental rotations (100 and 150 degree 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. If participants chose Path A they received another 5 mental rotation trials, if they chose Path B the mental rotation tasks stopped and they continued to the reward game (Figure 2.2c). There were 3 options to switch paths after the initial perseverance choice.

Last, all participants completed a simple reward game where they overturned colored cups to receive money similar to a coin flip but without an observable reward probability (Figure 2.2c). Participants were told they would receive a percentage of their earnings. Half of the 20 trials had the red cup on the left, half had the blue cup on the left. Rewards varied in amount from $0.40 to $2.00 (randomly presented) and were presented for 2000 ms. All cups resulted in reward with amounts varying randomly. The reward game was administered to assess neural response to receipt of hedonic, extrinsic reward compared with neural response to positive performance feedback, which has been shown to elicit activation of neural systems associated with reward. After the reward game, Path A perseverers who had not yet chosen to switch were given one additional switch option that ended the game regardless of decision. Participants completed one functional run and duration of the run was participant-paced.

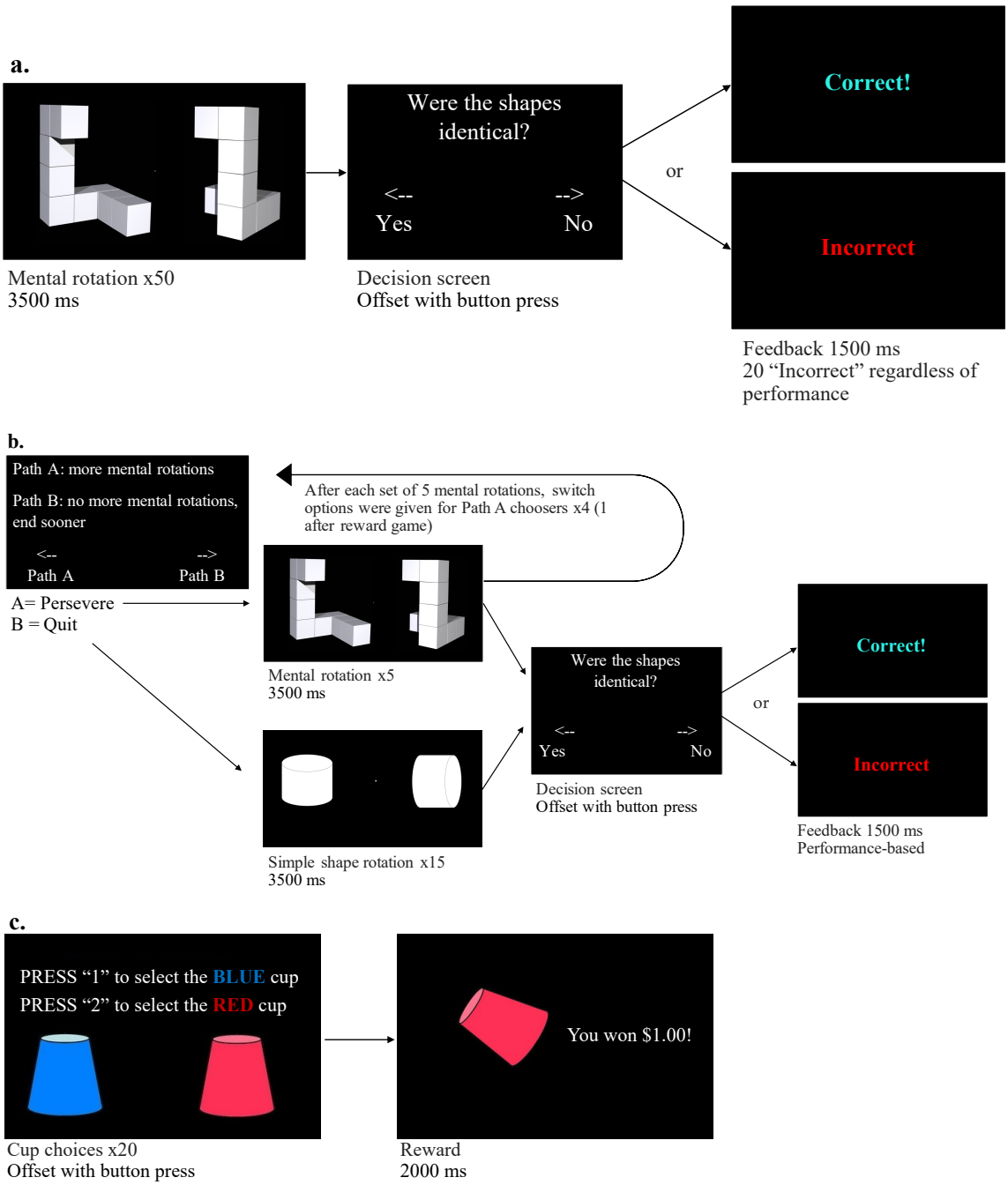


Figure 2.2. (a) Representative mental rotation trial on the Perseverance Task. **(b)** Path decisions after the initial mental rotation task resulted in two divergent tasks. For Path A, participants received additional mental rotation trials in blocks of 5 with an option to switch paths after each block. Switch options were presented 4 times and an additional 15 mental rotations were included in Path A. For Path B, participants received a set of 15 simple shape rotation trials

presented in a single block. All feedback for both paths was accurate performance-based. **(c)** All participants, regardless of path choice, completed a reward game. Participants chose to overturn either the blue or red cup and received money varying in amount.

Perseverance Task Questionnaire

Outside of the scanner after completion of the Perseverance Task, participants completed a questionnaire consisting of 13 questions regarding their choices and feelings about the Perseverance Task (see Appendix A).

Analytic plan

Behavioral data analyses were performed using R statistical software (version 3.6.1). Analyses predicting perseverance decisions were conducted using logistic regression (0=quit, 1=persevere). RT analyses were conducted using mixed effects linear regression lmer function in lme4 including random intercepts. For all analyses, perseverance decisions were coded as 0=quit, 1=persevere. RTs are reported in milliseconds (ms).

Two-tailed p-values were used to make significance inferences. P-values below .050 are considered to be statistically significant whereas p-values between .050 and .100 (inclusive) are considered marginally significant. For any mediation or moderation analyses, 95% confidence intervals that do not include 0 are regarded as having reached statistical significance.

fMRI methods

Neuroimaging analyses were executed in several stages. First, whole-brain analyses were conducted to assess differences in activation by task state across all participants. Next, whole-brain effects by perseverance decision (perseverance path choosers versus quit path choosers) were tested for each task contrast. Region-of-interest (ROI) analyses were then conducted to further probe perseverance decisions using a set of *a priori* regions. Beta-series correlation

(Rissman et al., 2004) analyses were used to assess differences in connectivity by group and task state. Representation similarity analyses (RSA) were conducted to test similarity in neural pattern representation of feedback and reward (Kriegeskorte et al., 2008).

fMRI data acquisition

The scan was conducted on a 3T Siemens Magnetom Prisma MRI scanner. Parameters for acquisition of the Perseverance Task were as follows: voxel size=3.0 x 3.0 x 4.0 mm, slices=34, slice thickness=4.0 mm, repetition time (TR)=2000 ms, echo time (TE)=30.0 ms, flip angle=90 degrees, interleaved slice geometry, 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 presented using E-Prime Professional 2.0 and 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 FEAT (FMRI Expert Analysis Tool) version 6.00, part of FSL version 6.0.1 (FMRIB Software Library, 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 (intra-modal 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). For participants exceeding 2.0 mm maximum absolute displacement in any direction, analyses were replicated removing those participants and results remained the same. Two participants exceeded 2.0 mm maximum displacement during the Perseverance Task (1 adolescent 2.778 mm and 1 adult 3.986 mm). Each participant's functional data was registered to their MPRAGE using boundary-based registration (Greve & Fischl, 2009) and then to MNI (Montreal Neurological Institute) 2.0 x 2.0 x 2.0 mm stereotaxic space with 12 degrees of freedom using FSL's registration method via FLIRT (FMRIB's Linear Image 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 (Table 2.1). 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 therefore served as an implicit baseline.

Table 2.1. Regressors for the Perseverance Task general linear model.

Event	Pre or post path decision	Regressor of interest or nuisance

Mental rotation stimuli	Pre	nuisance
Mental rotation decision	Pre	interest
Positive feedback	Pre	interest
Negative feedback	Pre	interest
Instructions	Pre and post	nuisance
Mental rotation / shape stimuli	Post	nuisance
Mental rotation / shape decision	Post	nuisance
Positive feedback	Post	nuisance
Negative feedback	Post	nuisance
Monetary reward gamble	Post	nuisance
Monetary reward receipt	Post	interest

Whole-brain analyses

For group-level analyses, FILM (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 $p<.05$. Outliers were de-weighted in the multisubject statistics using mixture modeling (Woolrich, 2008). All results are reported in MNI space. Contrasts of interest are listed in Table 2.2.

Table 2.2. Contrasts of interest for the Perseverance Task.

Contrast	Pre or post path decision
Positive > negative feedback	Pre
Negative > positive feedback	Pre
Mental rotation decision > baseline	Pre

Mental rotation decision after negative feedback > Mental rotation decision after positive feedback	Pre
Monetary reward receipt > baseline	Post
Monetary reward receipt > positive feedback	Post, pre, respectively

Parametric modulation analyses

Parametric modulation analyses were conducted to determine whether there were group 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., 2014).

Regions of interest

Key nodes in the salience network (ACC, insula), limbic network (striatum, mPFC), and executive network (dlPFC) were selected as ROIs (Figure 2.3a-d). First, ROIs were selected from an independent functional atlas (Shirer et al., 2012). This atlas comprised 90 functional ROIs defined using independent component analysis (ICA) based on whole-brain connectivity patterns during rest and three different cognitive tasks (episodic memory recall, music recall, and mental subtraction). Functional ROIs were then masked with corresponding anatomical regions from the Harvard-Oxford (HO) 50% probability structural atlas. The bilateral anterior insula and ACC were defined using the Shirer anterior salience mask overlayed with the HO insular cortex mask and the HO anterior cingulate gyrus mask, respectively; the bilateral dorsal striatum was defined using the basal ganglia Shirer mask overlayed with the HO caudate subcortical mask; the

mPFC was defined using the dorsal default mode network Shirer mask overlayed with the HO frontal pole mask; and the bilateral dlPFC was defined using the Shirer central executive mask overlayed with the HO inferior frontal gyrus, pars triangularis mask. ROIs were created in standard MNI T1 2mm space and masks were transformed to individual functional space using FLIRT linear registration.

For ROI activation analyses, activation values were extracted from the filtered 4D data at the group level using *fslmeants*.

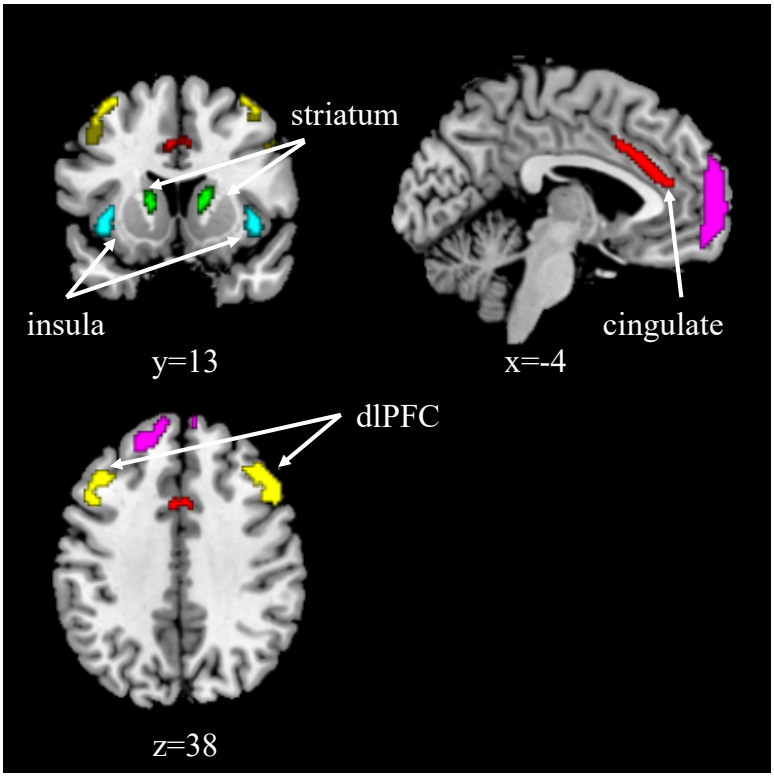


Figure 2.3. Regions of interest overlayed on standard MNI T1 2mm brain. Striatum shown in green (250 voxels), bilateral anterior insula shown in cyan (189 voxels), anterior cingulate shown in red (263 voxels), medial prefrontal cortex shown in violet (1230 voxels), and bilateral dorsolateral prefrontal cortex shown in yellow (1011 voxels).

Beta-series connectivity analyses

Functional connectivity was examined using a beta-series approach (Rissman et al., 2004) to construct a time-series for each *a priori* ROI (Figure 2.3). Magnitude of task-related BOLD response was estimated separately for each trial using the least squares single (LSS) method (Mumford et al., 2012). Each single-trial GLM included regressors for the event of interest, all other remaining events, and all other events of non-interest. ITIs were not explicitly modeled and therefore served as the implicit baseline. This approach yields a set of parameter estimates for each trial in every voxel across the whole-brain. These values can then be concatenated to form a time-series, also known as a beta-series. Beta-series within each ROI were extracted from each trial-specific GLM *Z* statistic image resulting in an n x p matrix for each subject where n is the number of trials and p is the number of ROIs. Correlation matrices were constructed using Pearson's correlation coefficient and standardized using the Fisher transform. When the beta-series between two ROIs shows a high correlation, these regions are inferred to demonstrate functional connectivity.

Representational similarity analyses

Using CoSMoMVPA (Oosterhof et al., 2016), RSA was conducted as a form of multivoxel pattern analysis (MVPA). Single-trial activation patterns were examined for positive feedback, negative feedback, and monetary reward receipt trials using least squares-single methods (Mumford et al., 2012). To preserve the fine-grained spatial details required for MVPA, data were not smoothed. Each single-trial GLM included regressors for the stimuli event of interest, all other remaining stimuli events, and all other events of noninterest. ITIs were not explicitly modeled and therefore served as the implicit baseline. For each participant, voxelwise patterns of activation represented by z-transformed parameter estimates were extracted on a trial-by-trial basis for each stimuli type. Pairwise Pearson correlation coefficients were calculated for

vectors for all trials, collapsed across stimuli type. Fisher's r-to-z transformation was then applied as a variance-stabilizing processing step. Higher values represented relatively greater similarity and lower values representing relatively greater dissimilarity.

Results

Perseverance behavior

Forty-two participants (42.42%, 20 females M_{age}=19.19, *SD*=3.78, range=14-30 years) chose to persevere (Path A). Fifty-seven participants (57.57%, 40 females M_{age}=17.75, *SD*=2.59, range=13-26 years) chose to quit (Path B).

Of the 42 participants who persevered, 12 chose Path A throughout the entire course of the task and 30 chose to switch at some point after the initial perseverance decision. Of the 30 perseverers who switched, 28 filled out the Perseverance Task Questionnaire. Only 4 of those participants cited frustration or task performance as a reason for switching whereas the remainder cited a desire for novelty, a feeling of competency, or some other strategy for wanting to switch (Table 3). Compounded with the small sample size of participants who persevered throughout the entire course of the task, this trend was not optimal for further assessment of between-subjects differences after the initial perseverance decision.

On average, participants were accurate on 39.69 (79.37%) of the first 50 mental rotation trials, range=23-50 *SD*=5.94. Of these trials, 20 were associated with negative feedback regardless of participant accuracy. Of those 20 manipulated feedback trials, participants answered an average of 15.72 (78.60%) correctly, range=8-20 *SD*=2.61. There were no significant sex differences in mental rotation accuracy, $t(97)=.906$, $p=.367$. Age was not significantly associated with mental rotation accuracy, Estimate=-.029, *SE*=.187, $t=-.152$, $p=.879$.

Accuracy was marginally associated with perseverance decision such that those who chose to persevere answered on average 2.363 more questions correct than those who chose not to persevere, Estimate=.072, *SE*=.037, *z*=1.929, *p*=.054 (Figure 2.4). This may signal that ability beliefs (Eccles et al., 1983) differed between the groups, contributing to motivational differences. However, feedback received was also only marginally associated with perseverance decision, Estimate=.102, *SE*=.057, *z*=3.170, *p*=.075, such that those who persevered received "success" feedback for 1.417 additional mental rotation trials compared to those who quit (Figure 2.5). This was due to the fact that 60% of feedback was performance-based and the perseverance group was marginally more accurate than the quit group. On average, participants received negative feedback on 26.030 trials (including trials for which feedback was manipulated), *SD*=3.864, range 20-37, and received positive feedback on 23.970 trials, *SD*=3.864, range=13-30. Feedback received did not moderate the association between perseverance decision and accuracy, $\text{Estimate}_{\text{interaction}}$=-.129, $SE_{\text{interaction}}$=.107, $t_{\text{interaction}}$=1.2016, $p_{\text{interaction}}$=.233.

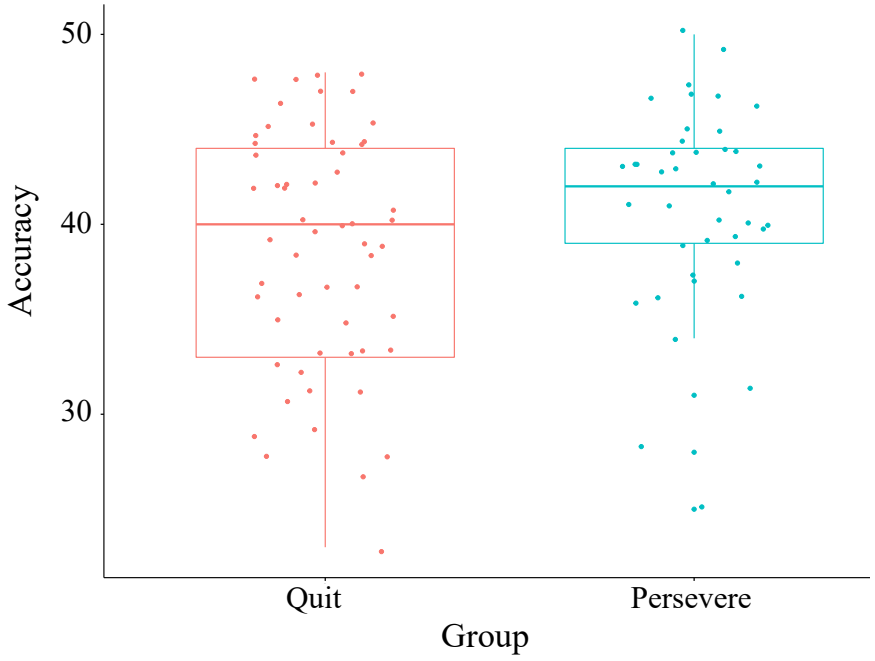


Figure 2.4. Accuracy on the first 50 mental rotation trials was marginally significantly different for those who chose to persevere and those who chose to quit. Y-axis reports actual accuracy regardless of feedback received.

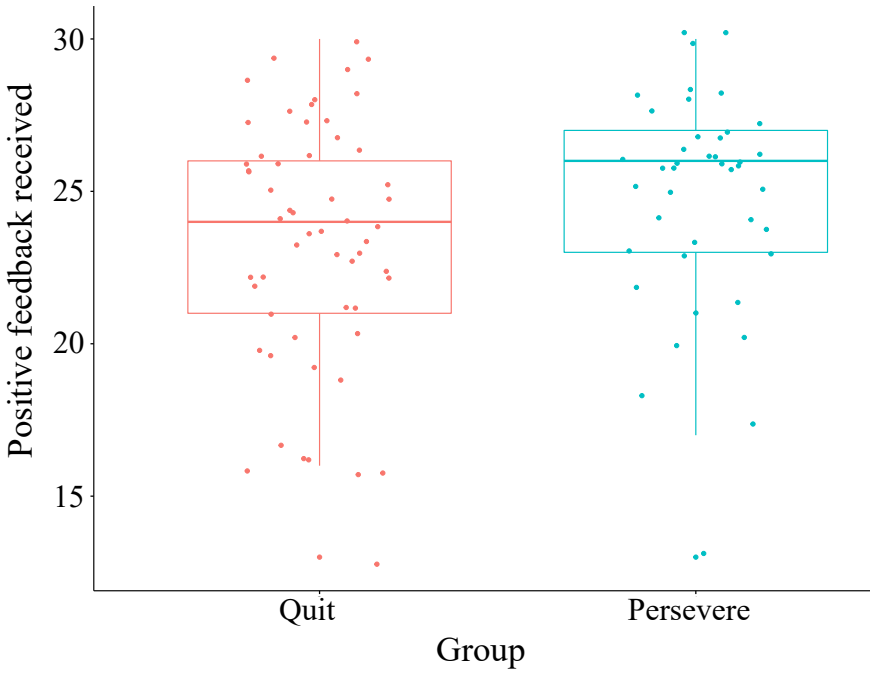


Figure 2.5. Feedback on the first 50 mental rotation trials was marginally significantly different for those who chose to persevere and those who chose to quit. Y-axis reports number of trials (out of 50) for which participants received feedback that their response was correct (max possible = 30 trials because of manipulated feedback).

On average, participants made mental rotation decisions in 993.794 ms after receiving positive success feedback and in 1032.996 ms after receiving negative feedback. RT after positive and after negative feedback were strongly correlated, $r(99)=.822$, $p<.001$, indexing an individual difference in RT. RT after negative feedback was not significantly related to perseverance decisions, Estimate=-72.670, *SE*=79.160, $t=-.918$, $p=.361$, nor was RT after positive feedback, Estimate=-105.810, *SE*=70.940, $t=-1.492$, $p=.139$. 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, $Estimate_{quadratic}$=8.008, $SE_{quadratic}$=2.531, $t_{quadratic}$=1.358, $p_{quadratic}$=.002 (Figure 2.6a). This association held controlling for perseverance decision and average RT across the full task, $Estimate_{quadratic}$=7.480, $SE_{quadratic}$=2.547, $t_{quadratic}$=2.937, $p_{quadratic}$=.004. Average RT after positive feedback was linearly associated with accuracy, Estimate=-6.253, *SE*=1.588, *t*=-3.937, *p*<.001 (Figure 2.6b). This association held controlling for perseverance decision and average RT across the full task, Estimate=-7.643, *SE*=3.230, *t*=-2.366, *p*=.020. Perseverance did not significantly moderate either RT – accuracy association, negative feedback RT: $Estimate_{interaction}$=.521, $SE_{interaction}$=1.274, $t_{interaction}$=.409, $p_{interaction}$=.683, 95% CI [-2.009, 3.051]; positive feedback RT: $Estimate_{interaction}$=5.455, $SE_{interaction}$=3.450, $t_{interaction}$=1.581, $p_{interaction}$=.117, 95% CI [-1.394, 12.305].

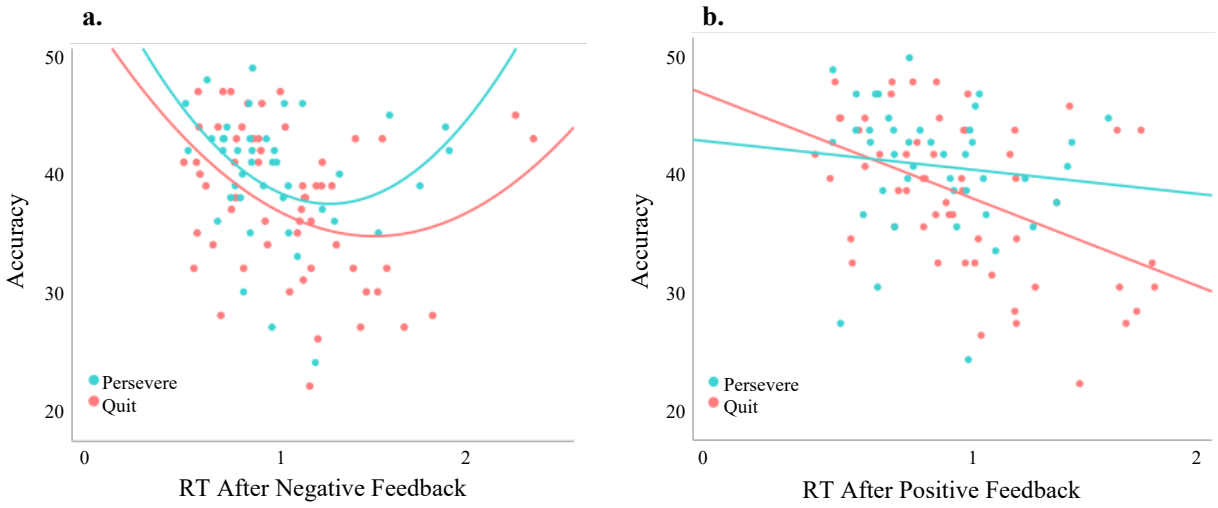


Figure 2.6. Reaction time after **(a)** receiving negative feedback quadratically associated with accuracy on the first 50 mental rotation trials, and **(b)** receiving positive feedback linearly associated with accuracy on the first 50 mental rotation trials. Y-axis=accuracy, X-axis=RT (sec).

Ninety-eight participants completed the Perseverance Task Questionnaire (see Appendix A; one participant who chose to persevere did not complete the questionnaire). Of those participants, 56 chose to quit whereas 42 chose to persevere. Seventy-four percent of participants who chose the perseverance path (n=31 out of 42) reported that they chose that path because it was more difficult (Figure 2.7) whereas 100% off participants who chose to quit (n=55 out of 55) reported they chose that path because it was easier (one participant who chose to quit reported "neither" reason for choosing the path and was therefore excluded from this analysis). Decisions associated with path difficulty significantly differed between the groups, X^2 (1, N=97)=59.663, p<.001. Sixty-four percent of participants who chose the perseverance path (n=27 out of 42) reported enjoying the mental rotation trials they got correct more than those that were challenging and 77% (n=43 out of 56) of participants who chose to quit reported the same, which did not significantly differ by group X^2 (1, N=98)=1.838, p=.175. Eighty-two percent of participants who chose to quit (n=46 out of 56) reported they enjoyed the monetary reward game more than the mental rotation task whereas only 41% of participants who chose to persevere reported enjoying the monetary reward game more (n=19 out of 42). Comparative task enjoyment significantly differed between the groups, X^2 (1, N=98)=14.635, p<.001. Several free-response questions were also asked and a sampling of participant answers by path is reported in Table 2.3.

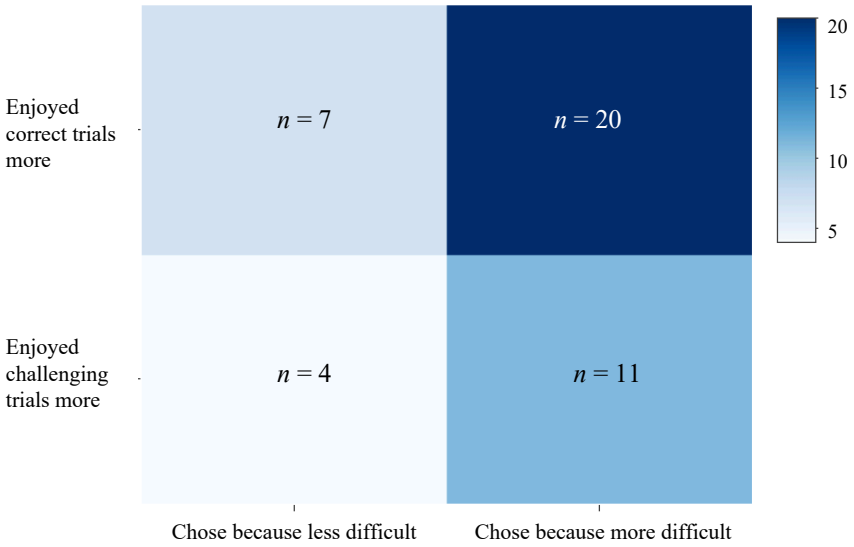


Figure 2.7. Data for participants who chose the perseverance path and responded to the Perseverance Task Questionnaire (*N*=42). *n* denotes number of participants in each cell. Y-axis represents which type of mental rotation trial participants reported they enjoyed most, those that they got correct or those that were challenging. X-axis represents explanation for path selection, because the path was more or less difficult.

Table 2.3. Sample free-response answers to Perseverance Task Questionnaire (Appendix A).

Question	Persevere Responses	Quit Responses
Why did you choose [the path you chose]?	"Because I'd been getting a lot of 'incorrect' responses that confused me, and I wanted to challenge the game" "I wanted to try to do better" "Because I was getting incorrect answers when I first played it and I wanted to get it right and prove to myself I could" "I wanted to understand what I was doing wrong. I wanted to understand what I didn't see before" "I felt as though I needed to try to get all of them right before giving up"	"It was easier and because I wanted to finish earlier" "The mental rotation questions were frustrating me" "I wasn't very good at the mental rotations, and got a lot wrong" "Because it seemed like the easier path" "The mental rotations were difficult for me to figure out, I kept getting many wrong"
What was the most enjoyable part of the mental rotation and	"Feeling good that I was able to get the mental rotations correct"	"The cups required little effort and earned money"

cups [monetary reward] tasks?	"Realizing I could hold the image and rotate it in my head" "Mental rotations was like a fun exercise for the brain" "It was a challenge and the farther I went along, the more I improved. This was a satisfying feeling" "probably getting the hard problems right"	"It was fun earning money with the cups, I didn't really like the mental rotation" "The most enjoyable part were the ones I got right" "Wouldn't call it enjoyable. I guess it was better if I got it right" "Earning money with the cups task"
What was the least enjoyable part of the mental rotation and cups [monetary reward] tasks?	"getting so many incorrect and feeling frustrated" "Getting the answer wrong" "Not showing me why I was wrong" "Getting the rotation wrong" "There was no skill or effort required in the cups task so it felt like a waste of time"	"Some of the mental rotations were fairly difficult and made me question my intelligence" "When I got a lesser amount of money" "The least enjoyable part were the ones I did not get right and the more difficult ones" "The least enjoyable part was getting it wrong and everything about the cups was enjoyable" "Challenging mental rotations"
How did you feel when you got a mental rotation answer correct?	"I felt good, smart" "Good, validated" "I felt excited and wanted to do more" "I felt as though I am smart, in order to get them right" "Proud because I kept getting more wrong in the beginning "	"smart and excited" "validated" "Less stressed" "I felt pretty good and I felt that it showed that I was smart" "I felt really great. I like being right"
How did you feel when you got a mental rotation answer incorrect?	"Ready for the next one" "A little bit of frustration but made me more engaged for the next one" "Same as when I got it right" "I felt a little discouraged at first, but it got me excited to get the next one right" "Like I was somehow failing"	"I felt frustrated with the answers I got wrong" "sad, disappointed" "I felt like giving up because I would get them incorrect frequently" "I felt terrible" "I felt ashamed I felt like I was dumb for getting it wrong"
How did you feel earning money during the cups	"Made me happy, relieved" "Excited"	"Good, not stressed" "Very little effort. I was ok with it"

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

All answers reproduced verbatim.

Neural response

Performance 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 reward-related regions including the ventral striatum and

medial prefrontal cortex (Table 2.4, Figure 2.8a). For positive versus negative feedback, participants who persevered compared to those who quit demonstrated heightened activation in the mPFC, a neural region implicated in a wide variety of functions including value representation and decision making (Table 2.4, Figure 2.8b) (Hiser & Koenigs, 2018; Piva et al., 2019).

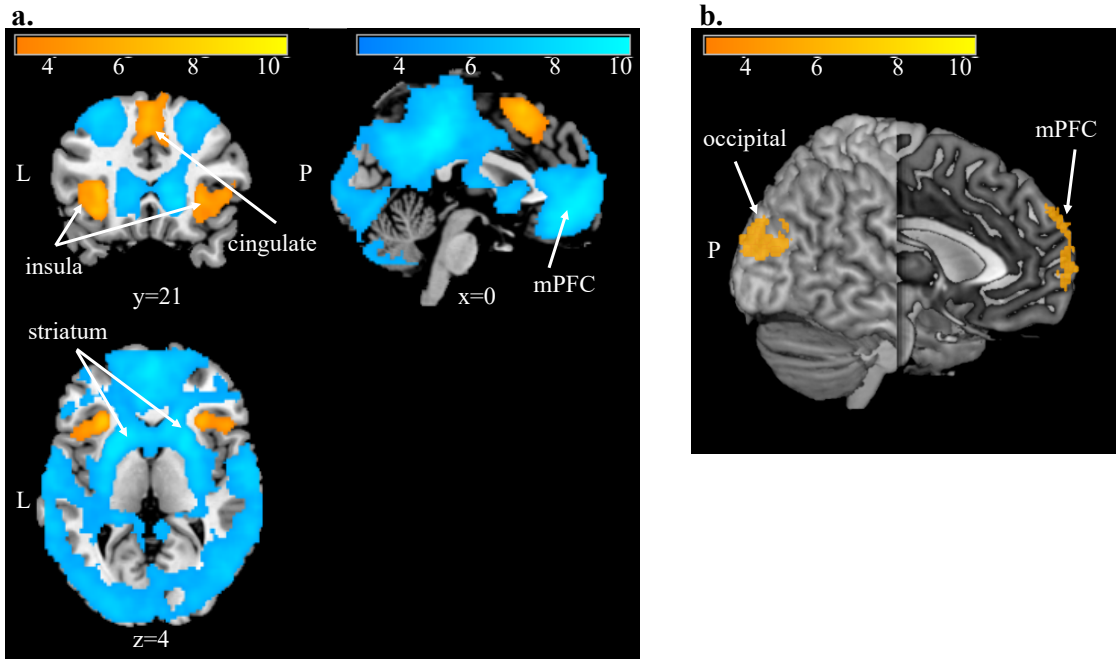


Figure 2.8. Visualization of significant activation for the contrast of **(a)** negative feedback > positive feedback (hot) and positive feedback > negative feedback (cool), all participants; **(b)** positive feedback > negative feedback for participants who persevered > participants who quit. Flame1, $Z>3.1$, FWE-corrected $p<.05$, outliers deweighted. Color bar indicates Z intensity values. Coordinates are in MNI space. L=left hemisphere, P=posterior. $N=99$.

Whole brain analyses were supplemented with ROI analyses using 8 *a priori* independent ROIs (Figure 2.3). Only the left insula, $t(97)_{\text{Linsula}}=2.337$, $p_{\text{Linsula}}=.021$, 95% CI[3.190, 39.135], and right dlPFC, $t(97)_{\text{RdlPFC}}=2.054$, $p_{\text{RdlPFC}}=.043$, 95% CI[3.190, 39.135], demonstrated significant differences by group such that the left insula was significantly more activated to

negative versus positive feedback for those who quit (M=20.354, SD=40.037) versus those who persevered (M=-.808, SD=50.020) and the right dlPFC was significantly more deactivated for those who persevered (M=-30.745, SD=70.775) versus those who quit (M=-2.906, SD=63.467). These associations did not survive $p<.006$ Bonferroni correction for 8 multiple comparisons at $\alpha=.05$.

Parametric modulation analyses revealed participants showed habituation (decreased response) to linear accumulation of negative feedback in the mPFC, thalamus, anterior cingulate gyrus, bilateral anterior insula, and occipital cortex. Sensitization (increased response) to accumulation of negative feedback was observed in the precentral gyrus, posterior cingulate gyrus, precuneus, and bilateral posterior insula. No regions showed sensitization to accumulation of positive feedback, but habituation was observed in the bilateral striatum, anterior cingulate gyrus, mPFC, bilateral angular gyrus, bilateral dlPFC, and occipital cortex (Table 2.4, Figure 2.9). No differential activation by group (persevere versus quit) at the whole-brain level was associated with accumulation of either negative or positive feedback.

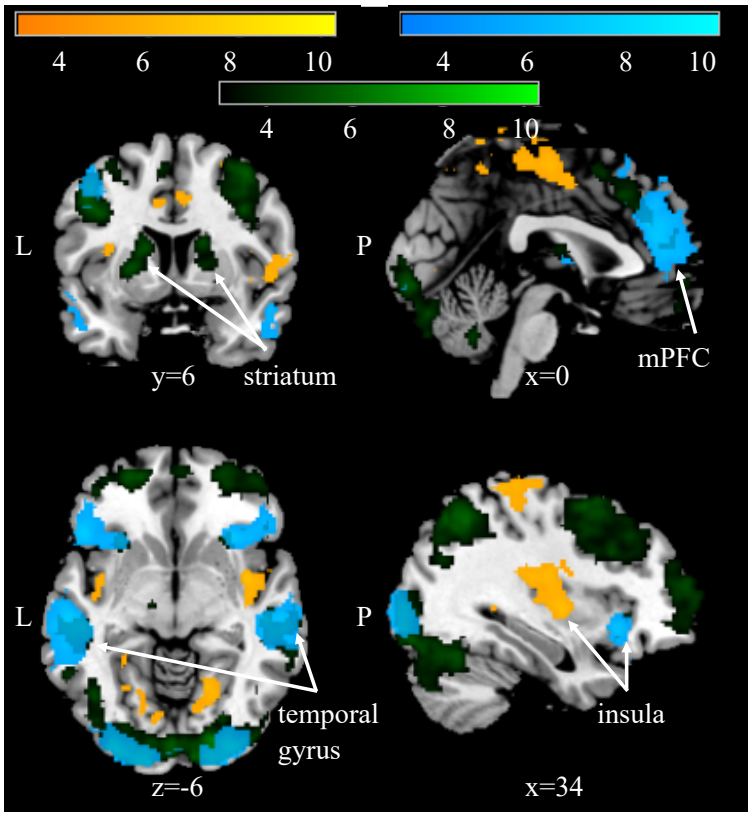


Figure 2.9. Visualization of significant activation for parametric modulation analyses of linear accumulation of negative feedback (habituation, cool; sensitization, hot) and positive feedback (habituation, green) versus baseline, all participants. Flame1, $Z>3.1$, FWE-corrected $p<.05$, outliers deweighted. Color bar indicates Z intensity values. Coordinates are in MNI space. L=left hemisphere, P=posterior. $N=99$.

On manipulated negative feedback trials, there was no differential activation on trials for which participants received negative feedback for accurate responses versus those for which participants received negative feedback for incorrect responses.

Table 2.4. Significant clusters from group level whole-brain analyses for feedback contrasts.

Cluster peak region[1]	Voxels	*p* value	Max Z value	R/L	Peak MNI coordinates X	Y	Z
Negative > positive feedback							

Superior frontal gyrus	1640	<.001	7.26	M	0	18	58
Insular cortex	692	<.001	7.23	L	-30	24	2
Insular cortex	579	<.001	6.11	R	32	24	4
Positive > negative feedback							
Cingulate gyrus; Precuneus	96558	<.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		978	L	-20	6	-10
Occipital cortex	LM		9.77	L	-42	-66	38
Positive > negative feedback, Persevere > quit							
Occipital pole	392	<.001	4.55	R	22	-98	20
Frontal pole	313	<.001	4.83	L	-14	60	32
Negative feedback habituation> baseline							
Paracingulate gyrus; Cingulate gyrus	3819	<.001	5.88	M	0	42	20
Superior temporal gyrus; Middle temporal gyrus	1829	<.001	7.18	L	-58	-30	0
Occipital pole	1704	<.001	6.54	L	-32	-94	-4
Insular cortex	1466	<.001	5.66	R	32	22	-6
Frontal orbital cortex; Frontal operculum cortex	1448	<.001	6.33	L	-48	24	-6
Occipital pole	1187	<.001	6.19	R	28	-94	-4
Middle temporal gyrus; Superior temporal gyrus	1040	<.001	5.73	R	56	-20	-8

Angular gyrus	803	<.001	5.82	L	-56	-58	32
Middle frontal gyrus	574	<.001	5.23	L	-42	6	46
Thalamus	155	.009	4.56	L	-6	-2	2
Negative feedback sensitization > baseline							
Superior parietal lobule	9942	<.001	5.97	R	16	-48	68
Insular cortex	2166	<.001	5.51	R	38	0	-6
Lingual gyrus	1992	<.001	5.75	L	-28	-50	2
Occipital pole	428	<.001	4.51	L	-12	-88	28
Lingual gyrus	218	.001	4.07	L	-16	-70	0
Positive feedback habituation> baseline							
Occipital fusiform gyrus	15556	<.001	6.93	R	20	-86	-8
Precentral gyrus; Middle frontal gyrus	5167	<.001	5.95	L	-46	2	38
Middle frontal gyrus	3070	<.001	5.96	R	40	4	54
Frontal pole	2120	<.001	5.67	R	26	56	8
Paracingulate gyrus	1915	<.001	5.72	R	6	32	32
Lateral occipital cortex	1835	<.001	6.13	R	38	-58	48
Frontal pole	1669	<.001	5.21	L	-24	54	-6
Cerebellum	223	<.001	4.58	M	0	-56	-34
Frontal pole; Frontal medial cortex	223	<.001	4.30	R	4	56	-6

Note: N=99. Z>3.1, FWE-corrected *p*<.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. [1]Regions based on the Harvard-Oxford Structural Atlas.

As expected, beta-series analyses connectivity analyses revealed all participants demonstrated strong positive connectivity among all 8 *a priori* ROIs (Figure 2.3) for negative feedback and positive feedback trials (Figure 2.10a-b). Connectivity significantly differed between negative and positive feedback trials for the mPFC – right insula, mPFC – left insula, mPFC – ACC, right dlPFC – right insula, and left dlPFC – ACC, such that connectivity was significantly higher for negative feedback compared to positive feedback (Table 2.5). Of these pairwise connections, the mPFC – right insula connectivity survived $p<.0018$ Bonferroni correction for 28 multiple comparisons at $\alpha=.05$.

There were no between-group differences in connectivity for negative or positive feedback (Figure 2.10c-f). For participants who persevered, mPFC – right insula and mPFC-ACC significantly differed between negative and positive feedback (Table 2.5). For participants who quit, right dlPFC – left insula, right dlPFC – ACC, right dlPFC – left striatum, and right dlPFC – right striatum significantly differed between negative and positive feedback (Table 2.5). Activation was greater during negative feedback for all significant connections.

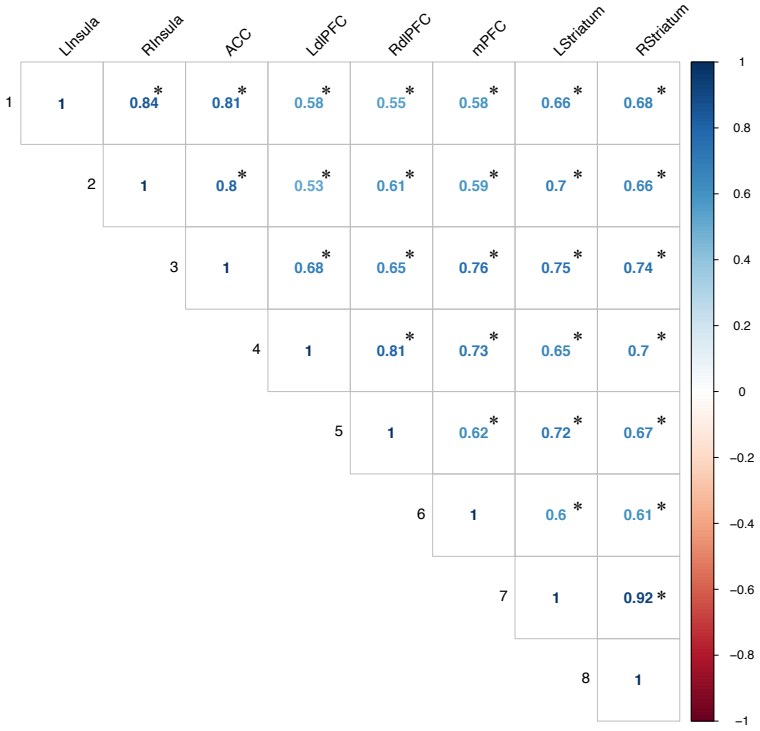
Table 2.5. Paired-t test results for significant connectivity differences between negative and positive feedback.

Connectivity pairs	*t*	*p* value	95% CI	*M* negative feedback	*M* positive feedback
All participants					
mPFC – right insula	-3.331	.001	[-.214, -.054]	.677	.543
mPFC – left insula	-2.150	.034	[-.159, -.006]	.665	.582
mPFC – ACC	-2.555	.012	[-.190, -024]	1.01	.901
right dlPFC – left insula	-2.443	.016	[-.165, -.017]	.659	.590
left dlPFC – ACC	-2.217	.029	[-.164, -.009]	.838	.751

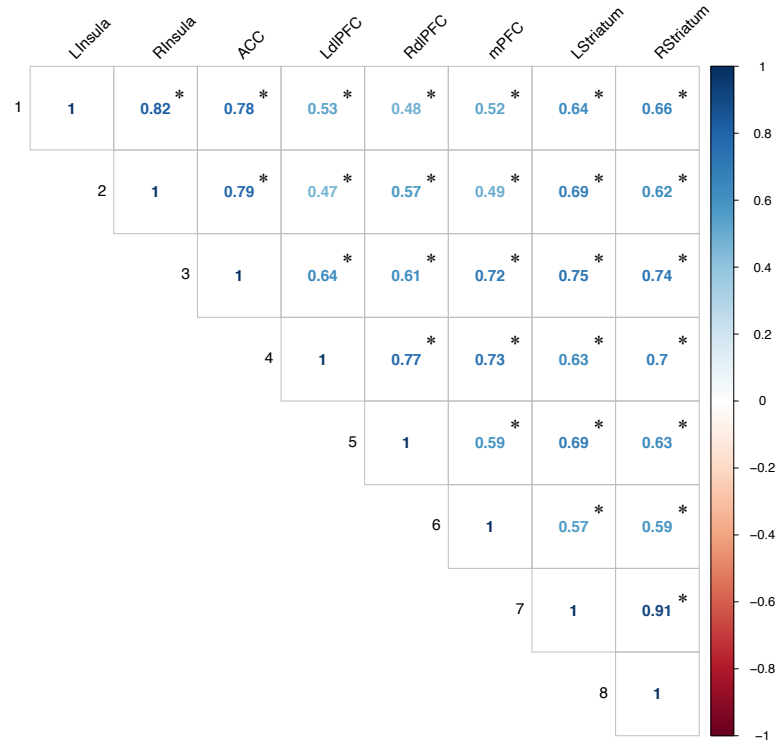
Persevere					
mPFC – right insula	-3.220	.003	[-.315, -.072]	.682	.488
mPFC – ACC	-2.339	.024	[-.270, -.020]	1.048	.903
Quit					
right dlPFC – left insula	-2.074	.043	[-.195, -.003]	.625	.526
right dlPFC – ACC	-2.055	.045	[-.220, -.003]	.786	.675
right dlPFC – left striatum	-2.617	.011	[-.205, -.027]	.932	.816
right dlPFC – right striatum	-2.340	.023	[-.207, -.016]	.835	.723

Note: N=99. Values are Fisher's z scores.

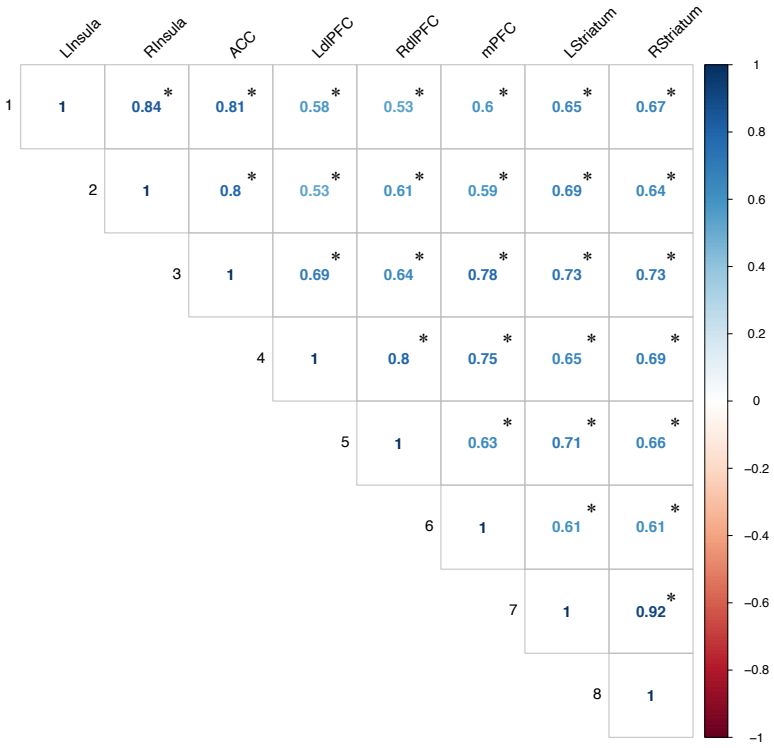
a. All participants, negative feedback



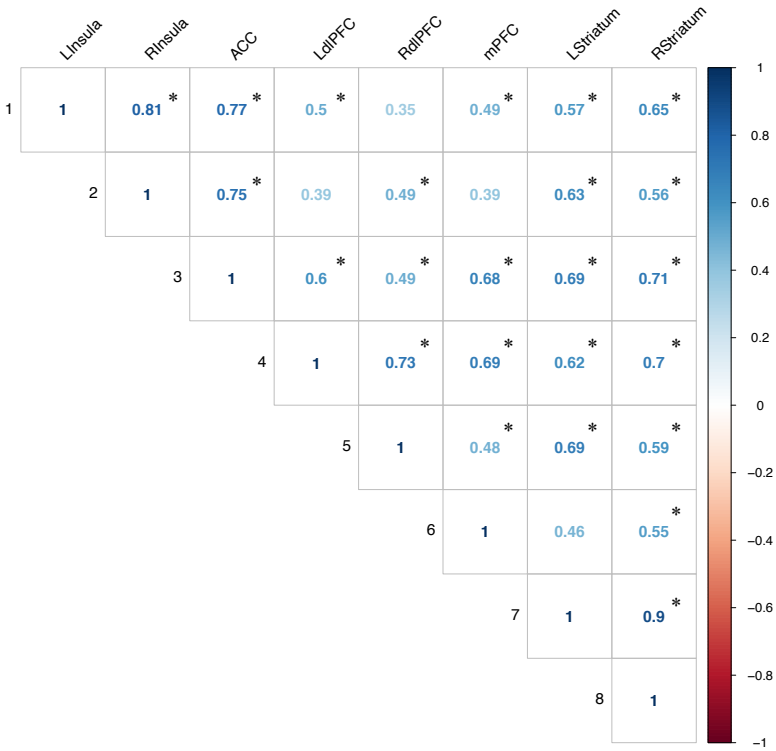
b. All participants, positive feedback



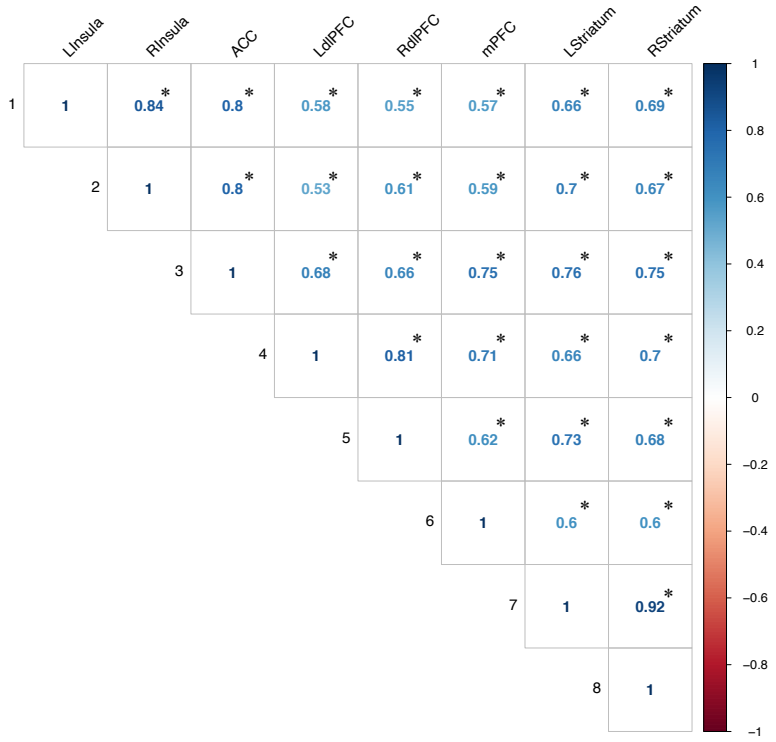
c. Persevere, negative feedback



d. Persevere, positive feedback



e. Quit, negative feedback



f. Quit, positive feedback

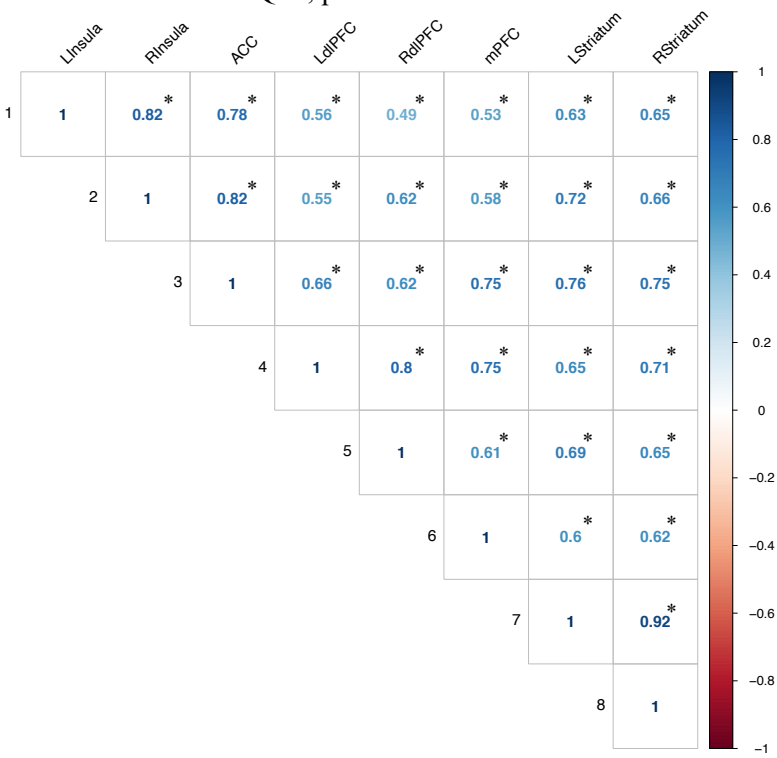


Figure 2.10. Correlations among regions of interest for **(a)** all participants in response to negative feedback; **(b)** all participants in response to positive feedback; **(c)** participants who persevered in response to negative feedback; **(d)** participants who persevered in response to positive feedback; **(e)** participants who quit in response to negative feedback; **(f)** participants who quit in response to positive feedback. Numeric values and color bar indicate Pearson's correlation coefficient (*r*). **p*<.0018*,* Bonferroni corrected within each matrix for 28 multiple comparisons at α=.05. *N*=99. L=left, R=right, ACC=anterior cingulate cortex, dlPFC=dorsolateral prefrontal cortex, mPFC=medial prefrontal cortex.

Recent work using dynamic causal modeling suggests an intrinsic valuation system for negative outcomes exists between the dlPFC and a fronto-insular network consisting of the mPFC, ACC, and insula (Zhang et al., 2018). In the present work, negative versus positive feedback resulted in differential activation by group in the mPFC, left insula, and right dlPFC. Post-hoc connectivity analyses were conducted to test whether connectivity between the bilateral dlPFC and the fronto-insular network comprised of the mPFC, ACC, and bilateral insula was associated with activation magnitude in the fronto-insular regions, covarying for perseverance decision. All contrasts were for negative feedback versus positive feedback. The multivariate result was significant, Pillai's Trace=.082, $F(3, 94)=2.781$, p=.045, η_p^2=.082. Univariate tests revealed individuals with greater connectivity demonstrated decreases in activation magnitude (Table 2.6, Figure 2.11). dlPFC connectivity with the mPFC-ACC-insula network did not significantly differ by group.

Table 2.6. Multivariate linear regression model of dlPFC and fronto-insular connectivity associated with activation in fronto-insular regions, covarying for perseverance decision.

	mPFC activation	ACC activation

	β	SE	t	p	β	SE	t	p
Intercept	-76.335	12.119	-6.299	<.001	-7.758	6.700	-1.158	.250
Connectivity	-40.920	19.793	-2.067	.041	-27.748	10.942	-2.536	.013
Perseverance decision	21.586	15.914	1.356	.178	10.952	8.798	1.245	.216
η_p^2	.043				.063			
$F(1, 96)$	4.274				6.431			

	Insula activation			
	β	SE	t	p
Intercept	.602	6.720	.090	.929
Connectivity	-27.183	10.976	-2.476	.015
Perseverance decision	21.027	8.825	2.383	.019
η_p^2	.060			
$F(1, 96)$	6.133			

Note. N=99. Perseverance decision: 0=quit, 1=persevere.

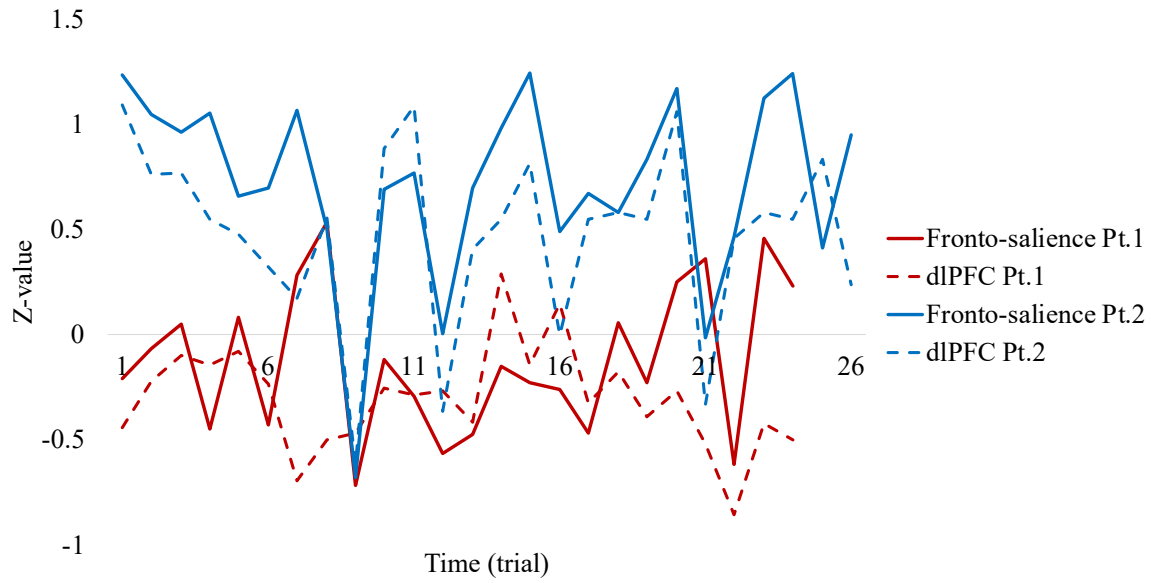


Figure 2.11. Sample time series for two participants showing strong connectivity between dlPFC activity and fronto-salience activity in blue, r=.745, p<.001, and weak non-significant connectivity in red, r=-.079, p=.701. dlPFC time series shown in dashed and fronto-salience timeseries shown in solid. N=99. x-axis=time, y-axis=Z-values from each ROI.

Mental rotations. Across all trials, mental rotation decisions evoked activation in anterior salience network hubs, including the ACC and bilateral insula, as well as regions of the visuospatial network involved in visuospatial attention (Table 2.7, Figure 2.12a). No differential activation by group was significant for mental rotation decisions versus baseline.

On trials after participants received negative feedback compared those after which they received positive feedback, greater activation was elicited in the mPFC, posterior cingulate gyrus, and dorsal striatum (Table 2.7, Figure 2.12b). These regions are associated with encoding outcomes necessary for altering goal-directed behavior (Pearson et al., 2011). No regions were activated to a greater extent for trials after positive feedback compared to after negative feedback. Compared to individuals who quit, individuals who persevered demonstrated greater activation in the parietal operculum cortex, a region evoked by cognitive tasks, including mental

rotation (Hugdahl et al., 2015) (Table 2.7, Figure 2.12c). None of the *a priori* ROIs demonstrated differential activation by group for the contrast of mental rotation decisions after negative feedback versus those after positive feedback.

Parietal operculum activation interacted with perseverance decision to predict RT after negative feedback, Estimate=.001, *SE*=.001, *t*=2.028, *p*=.045. For participants who quit, less activation was associated with slower RT, Estimate=-.001, *SE*=.001, *t*=-2.420, *p*=.019, but there was no significant difference in RT after negative feedback as a function of activation for participants who persevered, Estimate=.0001, *SE*=.0004, *t*=.299, *p*=.767 (Figure 2.13).

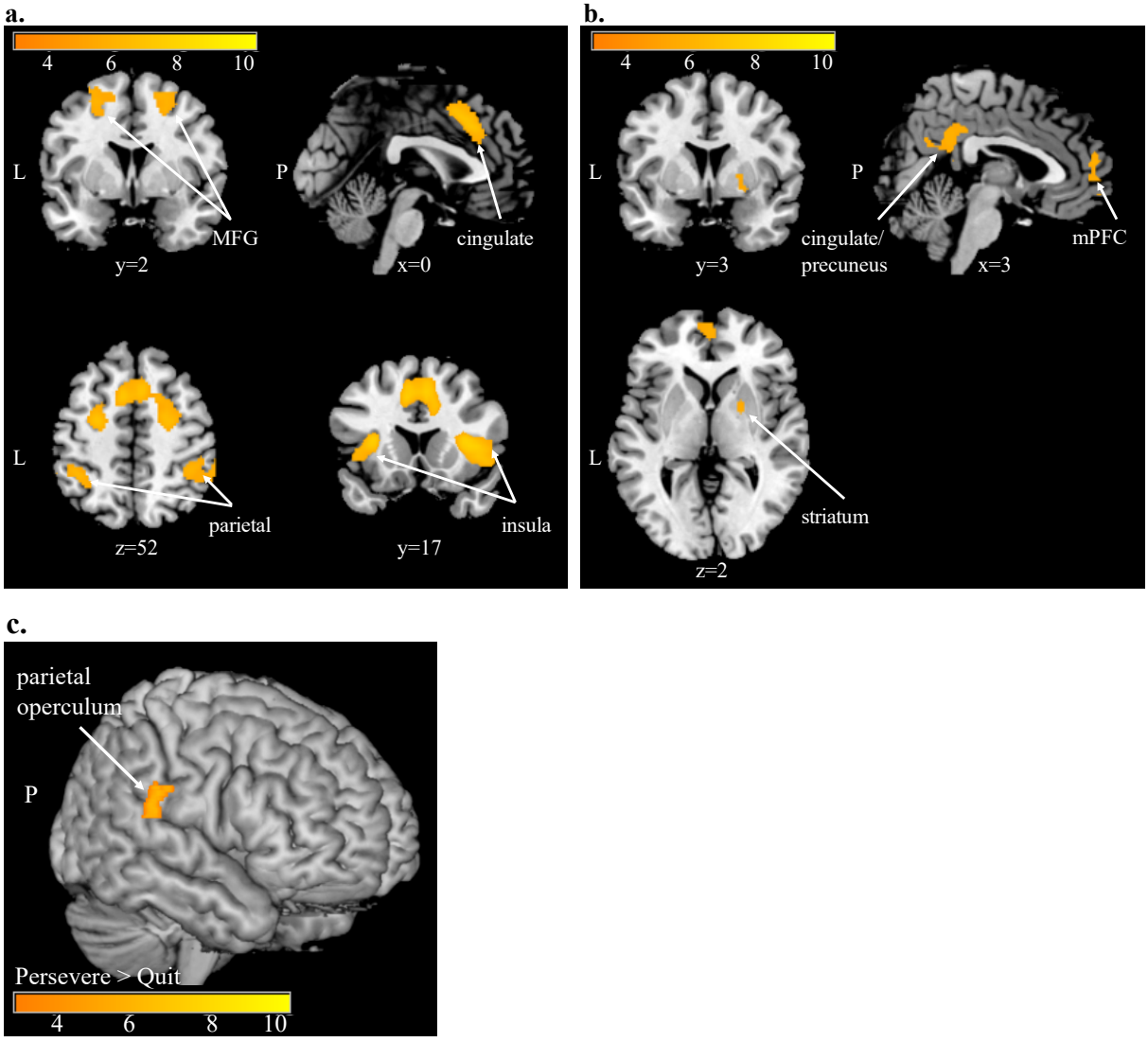


Figure 2.12. Visualization of significant activation for the contrast of **(a)** mental rotation decisions > baseline, all participants. MFG=middle frontal gyrus; **(b)** mental rotation decisions after negative feedback > mental rotation decisions after positive feedback, all participants; **(c)** mental rotation decisions after negative feedback > mental rotation decisions after positive feedback for participants who persevered > participants who quit. Flame1, Z>3.1, FWE-corrected p<.05, outliers deweighted. Color bar indicates Z intensity values. Coordinates are in MNI space. L=left hemisphere, P=posterior. N=99.

Table 2.7. Significant clusters from group level whole-brain analyses for mental rotation contrasts.

Cluster peak region[1]	Voxels	p value	Max Z value	R/L hemisphere	Peak MNI coordinates		
					X	Y	Z
Mental rotation decisions > baseline							
Cingulate gyrus; Paracingulate gyrus	2990	<.001	6.66	R	6	26	30
Frontal operculum cortex; Insular cortex	1240	<.001	6.95	R	32	20	10
Supramarginal gyrus; Superior parietal lobule	1004	<.001	4.81	R	38	-40	46
Frontal pole	981	<.001	5.60	R	34	54	26
Superior parietal lobule; Supramarginal gyrus	778	<.001	5.66	L	-36	-44	44
Frontal operculum cortex	441	<.001	6.39	L	-32	16	12
Frontal pole	216	.002	5.02	L	-34	52	22
Mental rotation decisions after negative feedback > after positive feedback							
Cingulate gyrus	717	<.001	4.12	R	4	-44	32

Frontal pole	293	<.001	4.19	R	2	56	14
Putamen	106	.033	3.77	R	22	2	2
Mental rotation decisions after negative feedback > after positive feedback, Persevere > Quit							
Parietal operculum cortex; Planum temporale	107	.032	4.19	R	64	-26	18

Note: N=99. Z>3.1, FWE-corrected *p*<.05, Flame1. R=Right hemisphere, L=Left hemisphere. Local maxima not listed. [1]Regions based on the Harvard-Oxford Structural Atlas.

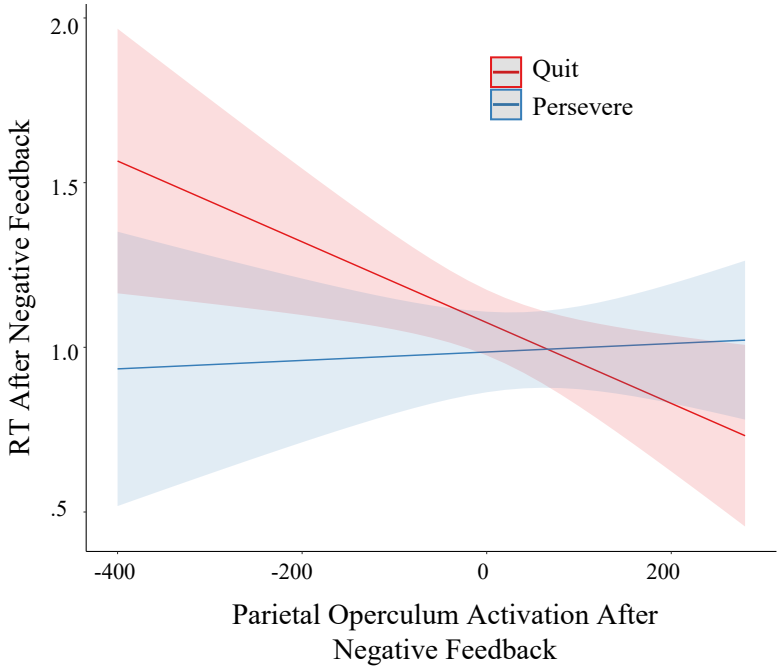


Figure 2.13. Reaction time after receiving negative feedback differed as a function of parietal operculum activation and perseverance decision. Y-axis=parietal operculum activation after negative feedback > positive feedback, X-axis=RT (sec) after negative feedback. Participants who persevered are depicted in blue and those who quit are depicted in red.

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 2.8, Figure 2.14). Participants who

quit compared to those who persevered 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 2.8, Figure 2.14).

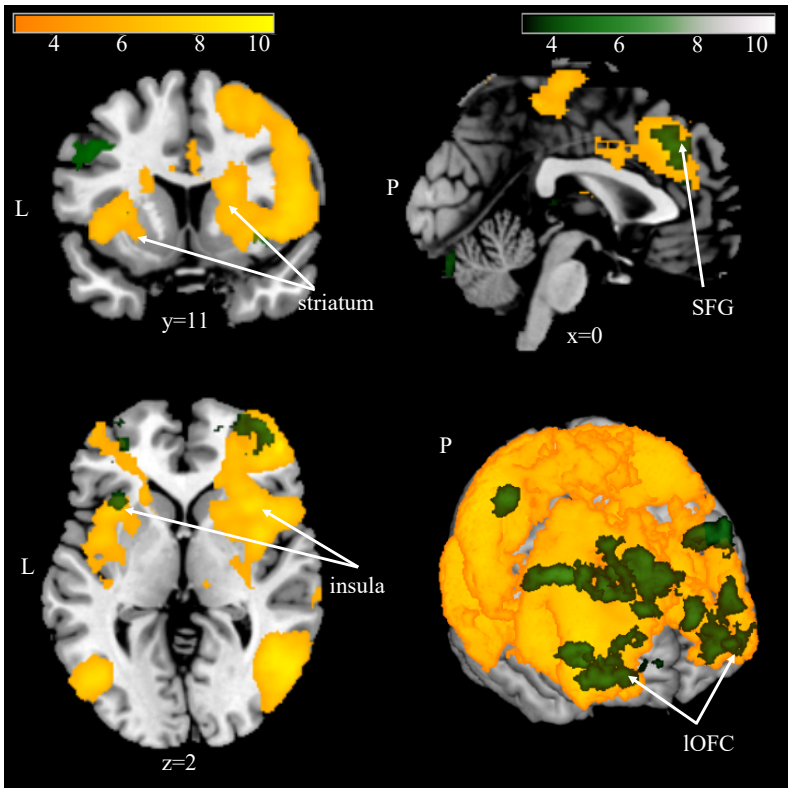


Figure 2.14. Visualization of significant activation for the contrast of monetary reward receipt versus baseline (all participants, hot; quit > persevere, green). Flame1, Z>3.1, FWE-corrected p<.05, outliers deweighted. Color bar indicates Z intensity values. Coordinates are in MNI space. L=left hemisphere, P=posterior, SFG=superior frontal gyrus, lOFC=lateral orbitofrontal cortex. N=99.

When compared with positive performance feedback, monetary reward evoked greater activation in the striatum, paracingulate gyrus, bilateral anterior insula, and other lateral cortical regions including the middle frontal gyrus (MFG) and occipital cortex (Table 2.8, Figure 2.15a). Positive feedback versus monetary reward receipt evoked greater activation in several cortical regions including the medial orbitofrontal cortex, ACC, bilateral posterior insula, and bilateral

superior temporal gyrus, as well as the bilateral hippocampus and bilateral amygdala (Table 2.8, Figure 2.15a). Participants who persevered compared to those who quit activated the ventromedial prefrontal cortex, lateral orbitofrontal cortex, SFG extending to the MFG, and right postcentral gyrus of the parietal lobe to a greater extent for positive feedback versus receipt of monetary reward (Table 2.8, Figure 2.15b).

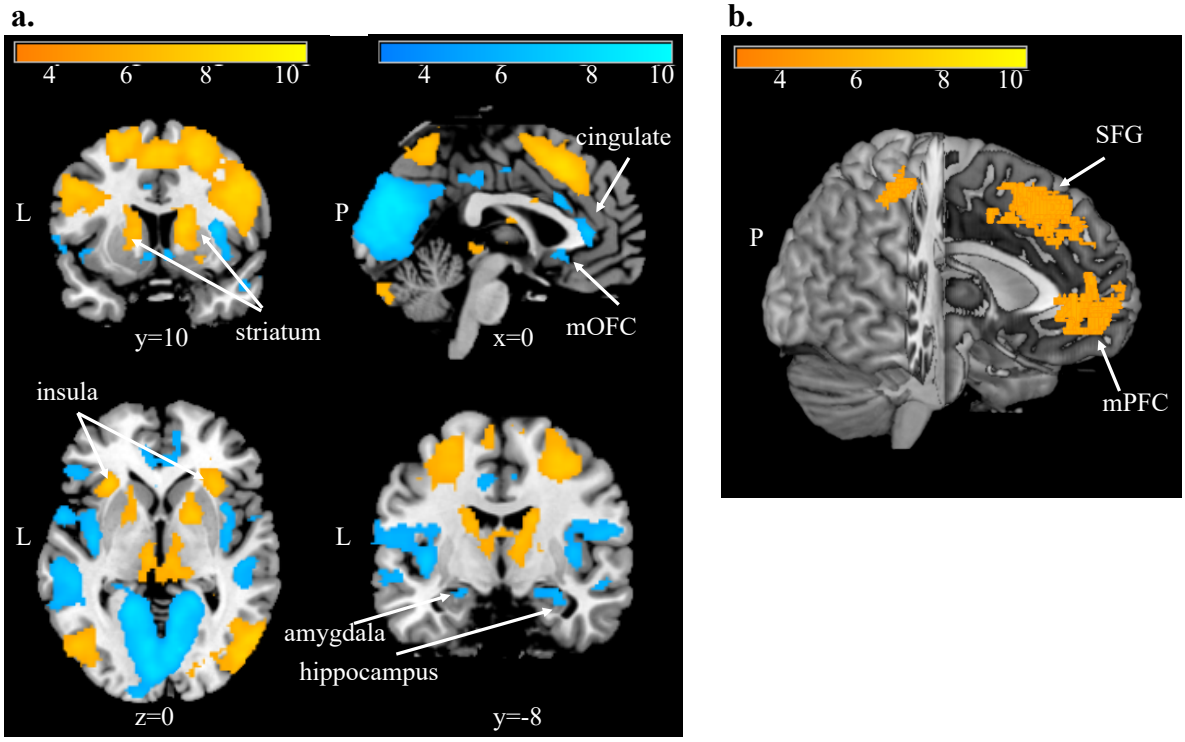


Figure 2.15. Visualization of significant activation for the contrast of **(a)** monetary reward receipt > positive feedback (hot) and positive feedback > monetary reward receipt (cool), all participants; **(b)** positive feedback > monetary reward receipt, persevere > quit. Flame1, Z>3.1, FWE-corrected p<.05, outliers deweighted. Color bar indicates Z intensity values. Coordinates are in MNI space. L=left hemisphere, P=posterior. N=99.

Table 2.8. Significant clusters from group level whole-brain analyses for reward contrasts.

Cluster peak region[1]	Voxels	*p* value	Max Z value	R/L hemisphere	Peak MNI coordinates		
					X	Y	Z

Monetary reward receipt > baseline							
Frontal pole	46587	<.001	10.40	R	46	46	6
Occipital cortex	1250	<.001	7.76	L	-44	-70	0
Cerebellum	1125	<.001	6.67	L	-38	-72	-28
Monetary reward receipt > baseline, Quit > Persevere							
Superior frontal gyrus	1092	<.001	4.50	R	4	36	46
Frontal pole	646	<.001	4.28	L	-28	64	4
Frontal pole	630	<.001	5.30	R	44	60	16
Occipital fusiform gyrus	583	<.001	5.33	L	-18	-80	-26
Middle frontal gyrus	396	<.001	4.69	L	-54	14	40
Insular cortex	189	.027	4.66	L	-32	20	-4
Frontal orbital cortex	171	.040	4.90	R	30	20	-10
Thalamus	166	.045	4.52	R	4	-24	10
Superior parietal lobule	162	.049	4.41	R	42	-38	56
Monetary reward receipt > positive feedback							
Superior frontal gyrus	32997	<.001	8.51	R	26	2	64
Frontal pole	169	.017	5.33	L	-30	52	20
Positive feedback > monetary reward receipt							
Cuneal cortex	12633	<.001	9.48	R	4	-80	26
Central opercular cortex	4472	<.001	6.59	L	-36	2	14
Central opercular cortex; Insular cortex	1543	<.001	7.25	R	36	8	10
Cingulate gyrus	1176	<.001	5.96	R	2	36	8

Superior temporal gyrus	651	<.001	6.05	R	48	-34	4
Inferior frontal gyrus; Frontal pole	338	<.001	5.48	L	-54	32	4
Hippocampus	295	<.001	5.16	R	32	-28	-8
Cingulate gyrus	154	.025	4.76	L	-8	-12	42
Positive feedback > monetary reward receipt, Persevere > Quit							
Superior frontal gyrus	1143	<.001	4.67	L	-16	18	44
Frontal orbital cortex	222	.004	4.24	L	-28	34	-6
Frontal pole	184	.011	4.25	R	40	60	2
Paracingulate gyrus; Frontal pole	168	.016	4.32	R	6	54	-2
Postcentral gyrus	147	.029	4.31	R	22	-38	54

Note: N=99. Z>3.1, FWE-corrected p<.05, Flame1. R=Right hemisphere, L=Left hemisphere, M=medial. Local maxima not listed. [1]Regions based on the Harvard-Oxford Structural Atlas.

Whole brain analyses were supplemented with ROI analyses using 8 *a priori* independent ROIs (Figure 2.3). The left insula, $t(97)_{\text{Linsula}}=2.025$, $p_{\text{Linsula}}=.046$, 95% CI[-154.478, -1.546], and mPFC, $t(97)_{\text{mPFC}}=2.239$, $p_{\text{mPFC}}=.027$, 95% CI[-241.328, -14.554], demonstrated significant differences by group such that the left insula was significantly more activated to positive feedback versus monetary reward receipt for those who persevered (M=55.088, SD=162.949) versus those who quit (M=-22.925, SD=206.722) and the mPFC was significantly more activated for those who persevered (M=63.370, SD=248.004) versus those who quit (M=-64.571, SD=302.785). The ACC, $t(97)_{\text{ACC}}=1.739$, $p_{\text{ACC}}=.085$, 95% CI[-134.030, 8.826], left striatum, $t(97)_{\text{Lstriatum}}=1.885$, $p_{\text{Lstriatum}}=.062$, 95% CI[-121.909, 3.136], right striatum, $t(97)_{\text{Rstriatum}}=1.695$, $p_{\text{Rstriatum}}=.093$, 95% CI[-102.897, 8.109], and right dlPFC, $t(97)_{\text{RdlPFC}}=1.875$, $p_{\text{RdlPFC}}=.064$, 95% CI[-157.086, 4.450], all demonstrated marginally significant associations for the contrast of

positive feedback versus monetary reward receipt such that participants who persevered (M_{ACC}=38.088, SD_{ACC}=162.276; $M_{Lstriatum}$=-27.148, $SD_{Lstriatum}$=143.598; $M_{Rstriatum}$=-41.288, $SD_{Rstriatum}$=159.900; M_{RdlPFC}=-71.065, SD_{RdlPFC}=222.347) demonstrated greater activation in all regions compared to those who quit (M_{ACC}=-24.513, SD_{ACC}=187.006; $M_{Lstriatum}$=-86.535, $SD_{Lstriatum}$=162.696; $M_{Rstriatum}$=-88.683, $SD_{Rstriatum}$=118.481; M_{RdlPFC}=-147.383, SD_{RdlPFC}=182.129). These associations did not survive p<.006 Bonferroni correction for 8 multiple comparisons at α=.05.

As detailed above, all participants demonstrated strong positive functional connectivity among the 8 *a priori* independent ROIs (Figure 2.3) for positive feedback trials and there were no between-group differences in connectivity for positive feedback (Figure 2.10b,d,f). Participants demonstrated moderate to strong positive connectivity for the receipt of monetary reward (Figure 2.16a). Connectivity significantly differed between positive feedback and monetary reward receipt for numerous regions (Table 2.9). Those surviving Bonferroni correction for 28 multiple comparisons at α=.05 (p<.0018) were the mPFC – left dlPFC, mPFC – right dlPFC, ACC – right insula, and ACC – right striatum.

Compared with positive feedback, participants who persevered demonstrated significant differences in connectivity to monetary reward receipt in several regions with the mPFC – left dlPFC surviving multiple comparison correction (Table 2.9; Figure 2.16b). In response to monetary reward receipt compared with positive feedback, participants who quit demonstrated significant differences in mPFC – right dlPFC and mPFC – left dlPFC connectivity surviving multiple comparison corrections (Table 2.9; Figure 2.16b-c). For all significant differences, connectivity was stronger during positive feedback than monetary reward receipt. There were no significant between-group differences in connectivity for receipt of monetary reward.

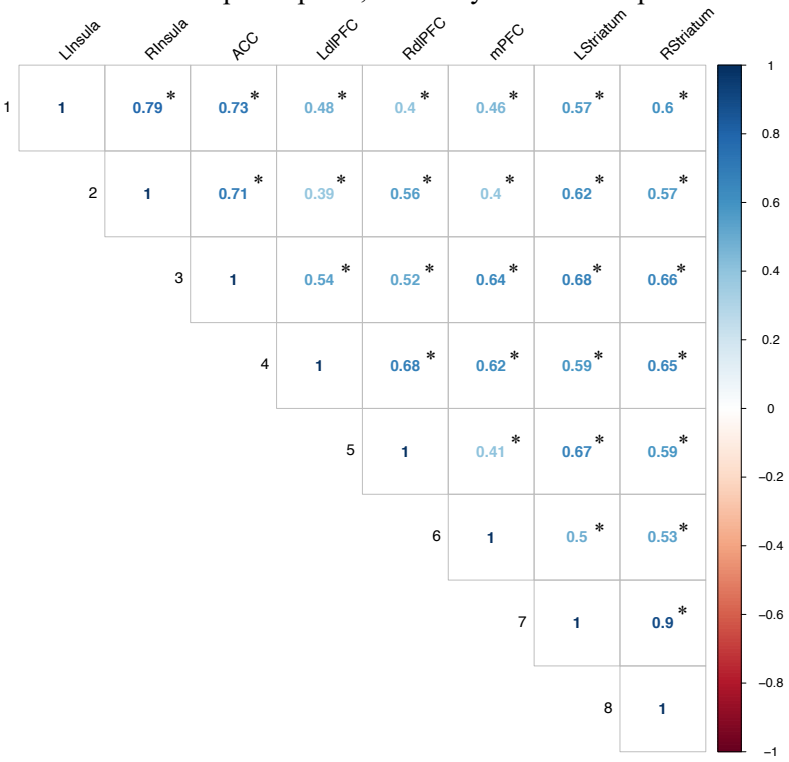
Table 2.9. Paired-t test results for significant connectivity differences between positive feedback and monetary reward receipt.

Connectivity pairs	*t*	*p* value	95% CI	*M* positive feedback	*M* monetary reward
All participants					
mPFC – right insula	2.256	.026	[.014, .224]	.543	.423
mPFC – ACC	3.025	.003	[.048, .233]	.901	.760
mPFC – left dlPFC	4.741	<.001	[.121, .296]	.938	.729
mPFC – right dlPFC	5.189	<.001	[.153, .342]	.679	.431
ACC – right insula	3.205	.002	[.069, .292]	1.067	.8863
ACC – left insula	2.394	.019	[.022, .238]	1.050	.920
ACC – left striatum	2.807	.006	[.041, .241]	.965	.824
ACC – right striatum	3.367	.001	[.064, .247]	.946	.791
left dlPFC – ACC	2.811	.006	[.042, .246]	.751	.607
right dlPFC – ACC	2.535	.013	[.029, .238]	.713	.579
left dlPFC – right dlPFC	3.784	<.001	[.091, .293]	1.029	.836
left striatum – right insula	2.321	.022	[.015, 198]	.840	.733
left striatum – left insula	2.050	.043	[.003, .205]	.753	.649
left striatum – right striatum	2.211	.029	[.011, .196]	1.556	1.452
Persevere					
mPFC – left dlPFC	3.445	.001	[.103, .395]	.965	.716
mPFC – right dlPFC	2.806	.008	[.061, .375]	.683	.465
ACC – right insula	2.100	.042	[.008, .386]	1.022	.825
ACC – left dlPFC	2.025	.049	[.0004, .324]	.790	.627
ACC – right dlPFC	2.424	.020	[.035, .380]	.764	.557

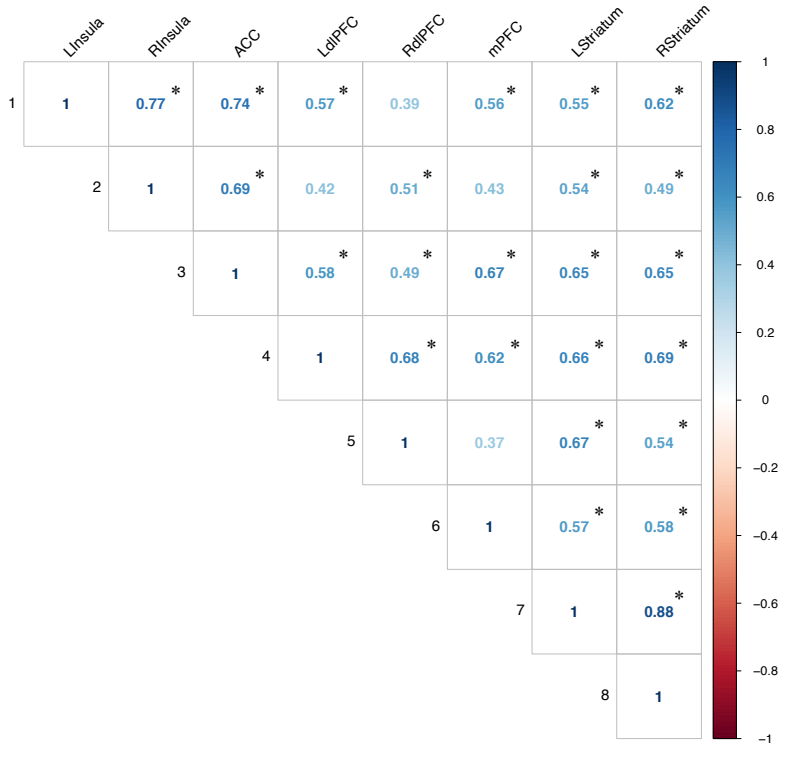
ACC – left striatum	2.150	.038	[.011, .337]	.955	.781
ACC – right striatum	2.106	.041	[.007, .332]	.944	.775
Left insula – right insula	2.240	.031	[.020, .386]	1.200	.996
Left dlPFC – right dlPFC	2.772	.008	[.055, .348]	1.054	.853
Quit					
mPFC – right insula	2.329	.023	[.023, .303]	.583	.420
mPFC – ACC	2.503	.015	[.030, .267]	.899	.751
mPFC – left dlPFC	3.249	.002	[.005, .069]	.917	.738
mPFC – right dlPFC	4.464	<.001	[.148, .390]	.675	.406
mPFC – left striatum	2.451	.017	[.030, .296]	.664	.501
mPFC – right striatum	2.067	.043	[.004, .257]	.686	.556
ACC – right insula	2.409	.019	[.028, .307]	1.100	.932
ACC – right striatum	2.660	.010	[.036, .254]	.948	.803
Left dlPFC – right insula	2.049	.045	[.003, .293]	.518	.369
Left dlPFC – right dlPFC	2.625	.011	[.036, .254]	1.010	.824
Left striatum – right striatum	2.685	.010	[.039, .269]	1.576	1.422

Note: N=99. Values are Fisher's z scores.

a. All participants, monetary reward receipt



b. Persevere, monetary reward receipt



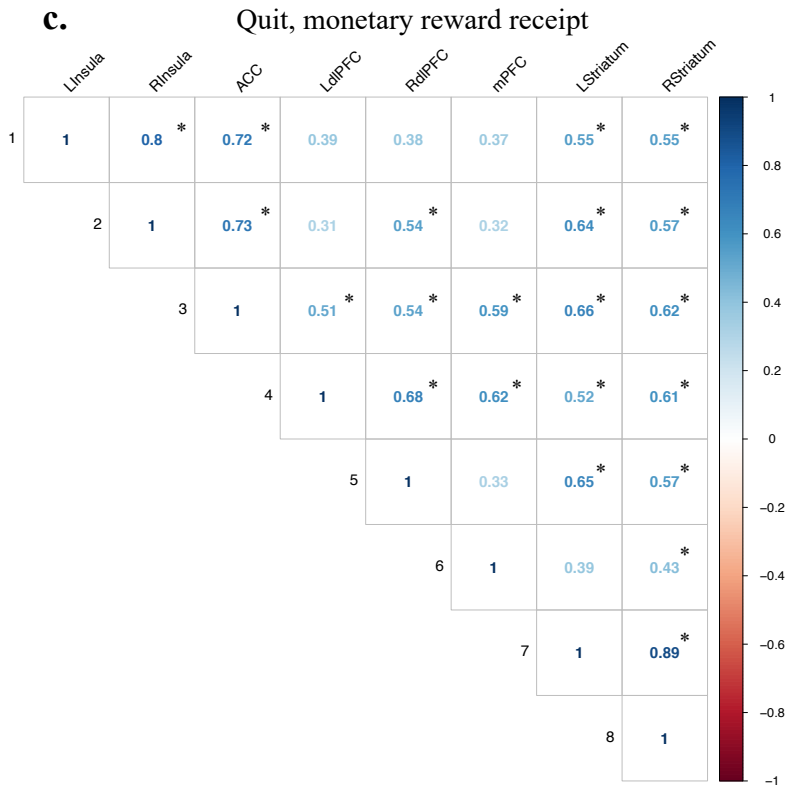


Figure 2.16. Correlations among regions of interest for **(a)** all participants in response to monetary reward receipt; **(b)** participants who persevered in response to monetary reward receipt; **(c)** participants who quit in response to monetary reward receipt. Numeric values and color bar indicate Pearson's correlation coefficient (*r*). **p*<.0018, Bonferroni corrected *p*-value within each matrix for 28 multiple comparisons at α=.05. *N*=99. L=left, R=right, ACC=anterior cingulate cortex, dlPFC=dorsolateral prefrontal cortex, mPFC=medial prefrontal cortex.

Positive feedback and monetary reward elicited activation in overlapping regions of the striatum and right dlPFC (Figure 2.17). Functioning of cortico-striatal circuits, including the dlPFC and striatum, are implicated in goal-directed behavior and attention allocation (Morris et al., 2016). RSA, as a form of MVPA, was used to elucidate the extent to which perceptually different stimuli were represented in similar ways at the neural level (Etzel et al., 2013; Xue et al., 2010). Specifically, RSA was performed for the striatum and dlPFC to determine whether

positive feedback stimuli were represented at a neural level more similarly to negative feedback or to monetary reward receipt. Paired samples *t*-tests revealed similarity between positive and negative feedback was greater than similarity between positive feedback and monetary reward receipt for both the striatum and dlPFC: striatum: $t(98)=21.191$, $p<.001$, 95% CI [-.279, -.231], $M_{RSAposfdbk\_negfdbk}=.467$, $SD_{RSAposfdbk\_negfdbk}=.136$, $M_{RSAposfdbk\_rwd}=.212$, $SD_{RSAposfdbk\_rwd}=.072$; dlPFC: $t(98)=14.503$, $p<.001$, 95% CI [-.280, -.214], $M_{RSAposfdbk\_negfdbk}=.173$, $SD_{RSAposfdbk\_negfdbk}=.017$, $M_{RSAposfdbk\_rwd}=.098$, $SD_{RSAposfdbk\_rwd}=.010$. This difference was evident in all participants regardless of perseverance decision, with no differences in similarity by decision.

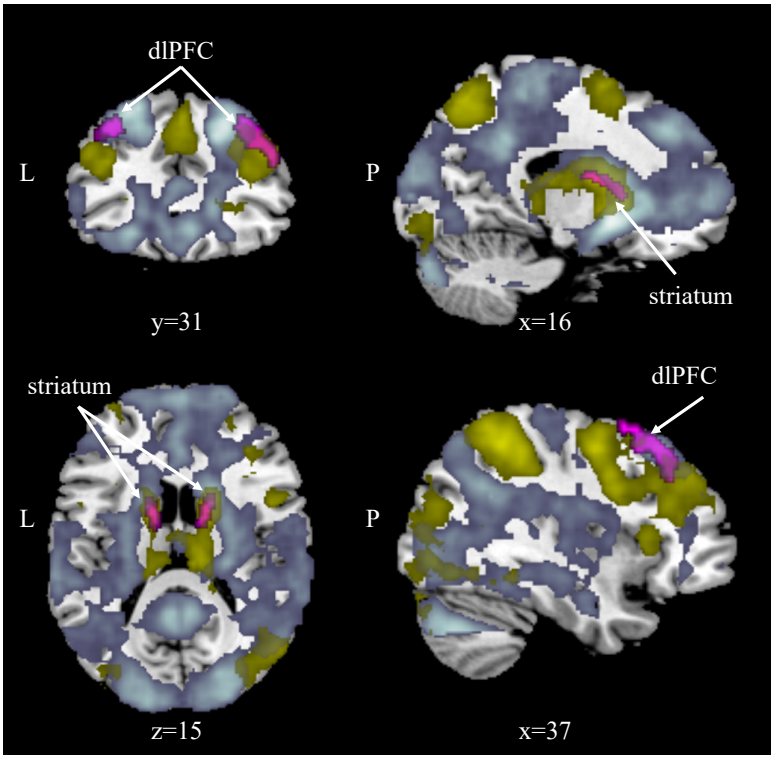


Figure 2.17. Visualization of significant activation for **(a)** positive feedback > negative feedback (gray), and monetary reward receipt > positive feedback (yellow) with striatum and dorsolateral prefrontal cortex (dlPFC) regions of interest overlayed in violet. Analyses thresholded using

Flame1, Z>3.1, FWE-corrected p<.05, outliers deweighted. Coordinates are in MNI space. L=left, P=posterior. N=99.

Discussion

The present work is a first step in identifying neural systems associated with intrinsically motivated choice to pursue challenge after failure. Forty-two percent of participants chose to persevere. There are several mechanisms that may explain this choice including information seeking or curiosity (Marvin & Shohamy, 2016), conserved approach behavior despite negative feedback (Förster et al., 2001), or signals indicating a need for increased effort to attain a goal (Lunenburg, 2011). Neural findings provide evidence for all of these mechanisms. Perseverance was associated with enhanced recruitment of task-relevant resources after negative feedback and increased activation in value coding systems after positive feedback, pointing to perseverance as a process involving value-guided goal pursuit. Individuals who persevered also demonstrated greater activation in attentional control and value systems to positive feedback compared with monetary reward. Self-report provides converging evidence that individuals who persevered made explicit choices to pursue challenge despite enjoying being correct as much as those who quit. In contrast, individuals who quit demonstrated reduction in control processes in response to negative feedback and reported aversive responses to failure. These findings support the proposal that perseverance is associated with motivation to achieve success whereas quitting is motivated by a desire to avoid failure (Chapter 1, Figure 1.1).

Theoretical models based on advances in cognitive and affective neuroscience identify interactions between multiple processes that underlie motivated behavior, including drive for reward, value-based decision making, and goal-directed control (e.g., Kim, 2013). These models demonstrate flexible responsivity in the brain depending on motivational signals via situational

factors like feedback and reward, as well as their interactions with goal expectancy. The Perseverance Task in this study tapped neural systems underpinning all of these processes. Although understanding of striatal contributions to generating and maintaining motivation is largely based on extrinsic reward and decisions to approach or avoid behavior to acquire reward, the present study identifies a similar role for the striatum in intrinsic motivation. The dlPFC, mPFC, and ACC are implicated in executive functioning associated with goal pursuit (e.g., maintaining value information, calculating estimated effort costs) and were also recruited during the Perseverance Task. The Perseverance Task elucidates how motivationally-relevant neural systems respond to varying situational factors and results point to the importance of both valuation and control processes for perseverance decisions.

As hypothesized, negative versus positive performance feedback elicited greater activation in salience network hubs, namely the ACC and insula, whereas positive feedback elicited activation in distributed neural regions including dopamine rich regions of the reward system (mPFC, striatum). Both the insula and striatum activate to rewards with increasing motivational value (Knutson & Greer, 2008), and the insula and striatum are associated with increased motivation following negative evaluation (Prévost et al., 2018). The striatum is suggested as a mediator of effort-based motivation responsible for translating motivational signals into action (Clithero et al., 2011). Monetary reward receipt versus baseline elicited activation in reward-related regions of the striatum, lateral OFC, and insula with activation in the dlPFC and striatum overlapping for positive feedback versus negative feedback and monetary reward versus positive feedback. When compared directly, positive feedback recruited the medial OFC, hippocampus, amygdala, temporal gyrus, and posterior insula to a greater extent than monetary reward. Monetary reward recruited the dlPFC, striatum, and anterior insula to a

greater extent than positive feedback. These results establish that both valence and informational value have consequences for recruitment of motivational neural systems.

Although RT was not significantly related to perseverance decisions, 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 & 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). Prior work supports the interpretation of faster RT after feedback as indicative of greater motivation (Tricomi et al., 2006). 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. Faster RT after positive feedback has been understood to indicate goal adherence and commitment toward goal striving whereas slower RT after positive feedback indicates a temporary state of post-fulfillment inhibition of a goal that was previously achieved (Förster et al., 2005). This interpretation aligns with the theory that positive feedback signals the individual is close to goal attainment and can consequently reduce self-regulation (Carver & Scheier, 1990). Associations between accuracy and RT after both positive and negative feedback remained significant controlling for average RT on the overall task indicating a behavioral shift following feedback rather than an underlying individual difference.

At the neural level, all participants demonstrated increased activation in the mPFC and striatum on mental rotation trials after receiving negative versus positive feedback. Activation of, and connections between, the mPFC and striatum after negative feedback are associated with computing prediction errors and subsequent learning (e.g., Schönberg et al., 2007; Park et al.,

2012). Differential activation after negative feedback was observed by group such that participants who persevered demonstrated greater activation in the parietal operculum cortex on trials after negative feedback compared to positive feedback. The parietal operculum is involved in cognitive task performance, including mental rotation and has been shown to co-activate with the anterior insula and ACC when a task is increasingly effortful (Engström et al., 2013). For participants who quit, reduced activation in the parietal operculum after negative feedback was associated with slower RT, likely reflecting attentional disengagement or interference as a function of feedback valence. These findings reflect a key principle of Goal Setting Theory that negative performance feedback signals a need for increased effort to achieve performance goals (Lunenburg, 2011).

Participants who persevered demonstrated greater activation in the mPFC, a neural region implicated in reward and value representation, during receipt of positive versus negative feedback. In comparison to monetary reward, positive feedback elicited greater activation in the mPFC, bilateral OFC, SFG, and parietal lobe for participants who persevered compared to those who quit. ROI analyses indicated the insula and mPFC were also more activated to positive feedback compared to monetary reward. This converges with prior work identifying differential activation depending on perceived agency in achieving a reward compared to passive receipt of reward in adults (Tricomi et al., 2004). Together, these findings suggest perseverance is associated with increased value signal of positive feedback compared with negatively valenced information (negative feedback) and other types of non-informative reward (money earned by chance).

Participants who quit demonstrated increased activation in the insula and deactivation in the dlPFC to negative versus positive feedback. The dlPFC is regarded as having an inhibiting

role on the salience network in a variety of contexts (Bräscher et al., 2016). Amount of accumulated feedback across the task was not associated with perseverance decisions. Thus, habituation did not account for reduced insula activation for those who persevered in response to negative feedback. The dlPFC flexibly controls engagement of reward-related neural systems like the striatum and mPFC depending on the relative importance of information during learning (Li et al., 2011). Performance approach goals associated with challenge avoidance are associated with reduced dlPFC activity after negative feedback (Lee & Kim, 2014). Those who quit were less likely to recruit these control processes when confronted with negative feedback than those who persevered. There was no neural evidence to suggest participants experienced a prediction error on manipulated feedback trials, supporting the interpretation that motivational contributors rather than task design underlie perseverance decisions.

Connectivity between frontal regulatory regions (dlPFC) and salience regions was greater for negative feedback compared to positive feedback across all participants. The frontoparietal CEN, anchored in the dlPFC, plays an active role in manipulating attention and working memory during decision-making and goal-directed behavior (Menon, 2010). The dlPFC integrates motivational processes during goal pursuit, with greater connectivity between the dlPFC and ACC, a key node of the salience network, shown to play a role in maintaining goal pursuit (Spielberg et al., 2012). Greater coupling between the mPFC and salience regions was also observed for negative versus positive feedback and coupling within this network has been previously interpreted as reflecting integration of negative emotion-related information (Zhang et al., 2018). The dlPFC exerts control over this intrinsic valuation system comprised of the mPFC, ACC, and insula, (Zhang et al., 2018) and the dlPFC overrides the strong desire to avoid future loss. In the Perseverance Task, connectivity among this network in response to negative

feedback versus positive feedback was associated with less activation magnitude in the ACC, mPFC, and insula for the same contrast. Perseverance was associated with reduced insula activation and increased dlPFC activation, but connectivity was not significantly differentiated by perseverance decision, which may be a result of no explicit threat of loss in this task. However, this connectivity-activation association may reveal one individual difference contributor to activation differences observed in this study, specifically dlPFC control over salience regions associated with detecting and assigning value to motivationally-relevant stimuli. A lack of differential connectivity between the dlPFC and striatum to feedback valence is consistent with prior work on achievement goal orientation demonstrating the dlPFC was not recruited as a control mechanism for striatal processing during feedback. Participants demonstrated significantly greater connectivity between the dlPFC and mPFC as well as the ACC and insula, and the ACC and striatum in response to positive feedback versus monetary reward. There were no significant pairwise connectivity differences to positive feedback versus monetary reward that differed by group.

Positive performance feedback after mental rotations elicited more similar multivoxel patterns of activation to negative performance feedback than it did with monetary reward receipt across both groups. The manner in which these representations were calibrated at the individual level did not relate to perseverance decisions. However, this finding elucidates otherwise opaque representations of feedback and reward: It was previously unclear whether the way individuals represent positively valenced performance feedback was more similar to negatively valenced feedback or positively valenced non-informative reward. Univariate activation obscures this association: positive and negative feedback evoke different *amounts* of activation in the dlPFC

and striatum, but the *way* these regions encode performance feedback is more similar than that of positive feedback and reward.

Accuracy was marginally associated with perseverance. However, there were many participants who quit after achieving high accuracy and those who persevered after comparatively low accuracy. Importantly, because of the use of quasi-manipulated feedback, all participants received feedback that they were at least 40% inaccurate on prior trials. This feedback could be perceived as an informative signal that further effort is needed to overcome the present challenge or a punishment signaling success was unattainable prompting disengagement. Individuals who persevered reported a challenge-oriented motivation: 74% perseverers reported they chose their path because it was more difficult whereas 100% of those who quit reported they chose their path because it was easier. Perseverers also reported enjoying mental rotation trials more than monetary reward trials (82%) whereas only 41% of those who quit reported enjoying mental rotation trials more than monetary reward trials. The groups did not differ in the extent to which they enjoyed getting mental rotation trials correct, with a majority of participants in both groups enjoying those they got correct more than those that were challenging. Participant reported motivation indicates there are psychological factors that relate to behavior in addition to observed neural differences between the groups.

Notably, it was not that participants who quit did not value getting answers correct, but that they reported more aversive feelings to getting answers wrong whereas those who persevered perceived negative feedback as a challenge. Although not directly assessed in this study, it is likely that expectations of goal attainment and competency beliefs interacted with feedback valence to differentiate decisions. Over the course of goal-pursuit relevance of positive versus negative feedback shifts. Positive feedback acts to instantiate goal commitment early on

and negative feedback provides signals for increase effort after goal commitment is established (Fishbach et al., 2010). Free-response questions elucidate additional potential factors at play. For example, expectations that quitting will bring stress relief. Twenty-five percent of participants who quit reported reflecting on their decision with disappointment or another negative appraisal. It may be that reflection could help individuals who are less motivated to persevere by illustrating that quitting is not always accompanied by relief. Offering "opt-in" options to reflect this subset of regretful quit decisions would be a fruitful future avenue for further exploration. Opportunities for choice updating also allows for value updating through decision-making trial and error.

Interpretation of the current findings should be made in the context of study specifics. Several factors that may influence motivation were not assessed including two prominent in the motivation and achievement literature: achievement goals (Lee & Kim, 2014) and growth mindset (Yeager & Dweck, 2012). A strength of the current study is the use of an intrinsically motivated task, but future work would benefit from investigating intra-individual differences in behavior under different reward contingencies. Given the task was not individualized to each participant's interests, it is possible some participants may not have been engaged or motivated by the task. Recent meta-analytic findings on grit point to the importance of passion in combination with perseverance in goal attainment (Jachimowicz et al., 2018). The current study did not assess interest in the goal provided: improving mental rotation skills. However, there are several factors that point toward the ecological validity of a task that does not attempt to tap "passion". First, in academic domains, children and adolescents are often required to pursue mastery without regard for task-level interest. The potential long-term goals motivating performance in this context are academic success, educational attainment, social approval,

among others. Those same motivational factors may have been at play in the current study even if the task itself was not of personal relevance to the participant. Additionally, perseverance is a necessary component to measures of objective success, even if it is not sufficient in the absence of passion, and is thus still worthy of in-depth investigation.

Intrinsically motivated perseverance as evaluated in the current study is associated with functioning of motivational systems in the brain. Several regions of executive control and reward systems were associated with perseverance behavior. Specifically, greater activation in the mPFC for positive versus negative feedback and greater dlPFC and reduced insula activation for negative versus positive feedback. Perseverance was also associated with differential activation during mental rotation depending on prior feedback, which was related to RT differences demonstrating behavioral adjustment following negative feedback. Comparisons of monetary reward and positive feedback lend further insight suggesting perseverance is associated with differential valuation of positive stimuli depending on the informative nature of the stimuli. These findings indicate perseverance is not a static trait, but rather may be malleable by targeting motivation and enhancing value for informative feedback.

Chapter 3

Prefrontal regulation of intrinsic value systems underpins age-related differences in perseverance

Introduction

Ongoing neurobiological maturation during adolescence provides a unique opportunity to study developmental differences in perseverance. Several neural systems associated with psychological and behavioral phenomena proposed to be important for perseverance undergo continued development during this time, including prefrontal regions implicated in behavioral, cognitive, and emotion regulation (Miller & Cohen, 2001; Casey et al., 2008), as well as dopaminergic systems important for intrinsic motivation (Casey et al., 2008). Functioning of the insula and connectivity with the insula and other nodes of the salience network also develop throughout adolescence (Smith et al., 2014; Strang et al., 2011), and connectivity between subcortical nodes of the salience network strengthen over development (Solé-Padullés et al., 2016). During adolescence, ongoing neural development contributes to the cognitive control necessary to modify behavior given motivational demands, learn from informative negative feedback, and regulate affective response to negative feedback. These are all skills that are likely to promote perseverance, but it remains unknown whether developmental differences in neural functioning during adolescence relate to perseverance behavior.

Much of the focus of seminal adolescent neuroimaging investigations was to identify contributors of heightened risk-taking behavior by examining neural response to reward (May et al., 2004; Ernst et al., 2005; Galván et al., 2006; Fareri et al., 2008; Chein et al., 2011). Perhaps most widely studied, corticostriatal connectivity continues to develop during adolescence. In the presence of external rewards, selectively titrating cognitive control according to changing motivational demands (i.e., high versus low stakes) increases from adolescence to adulthood, an effect which is mediated by functional connectivity in corticostriatal circuitry (Insel et al., 2017). More recent investigations expanded these inquiries to domains of learning (Davidow et al.,

2016; McCormick & Telzer, 2017; Peters & Crone, 2017) and positive behaviors like prosociality (Telzer et al., 2010, 2013; van Hoorn et al., 2014). Specifically, feedback learning literature identifies enhanced performance during adolescence, suggesting adolescence as a developmental period of optimal feedback learning (Davidow et al., 2016; McCormick & Telzer, 2017; Peters & Crone, 2017). Together, this knowledge suggests an important role of the striatum in reward-based motivation, feedback learning, and risk taking resulting in both positive and negative outcomes. However, it has yet to be determined whether these features of adolescence are associated with intrinsically motivated perseverance.

Changes in the connectivity of corticostriatal circuitry may also explain age-related differences in response to feedback. During feedback learning, adolescents do not demonstrate differential dlPFC recruitment for negative versus positive feedback, unlike adults (van Duijvenvoorde et al., 2008). This lack of differential recruitment suggests the ability to learn from negative feedback is still developing during adolescence, due, in part, to maturation of corticostriatal circuitry (DePasque & Galván, 2017; van Duijvenvoorde et al., 2016; van den Bos et al., 2009). Adults are able to utilize a broader assortment of increasingly complex learning strategies relying on cognitive control systems whereas adolescents rely upon striatal mechanisms supporting more straightforward reinforcement learning (DePasque & Galván, 2019; Decker et al., 2015). The extent to which the insula is functionally connected with prefrontal circuitry in adolescents may also play a role in the ability to regulate behavior and emotions in response to negative aspects of challenge (Strang et al., 2011). The current program of work introduces a novel task that incorporates an option to quit or persist. A precursor to real-world feedback learning is the willingness to engage in a behavior that may result in a negative

outcome. By using this task in a developmental investigation of perseverance, the current work can better determine whether, and how, response to feedback relates to perseverance.

Other neural regions implicated in cognition and emotion develop during adolescence and may also contribute to perseverance. For example, the insula has been implicated in attention (Cole & Schneider, 2007; Menon & Uddin, 2010), motivation (Naqvi & Bechara, 2009; Cho et al., 2013), inhibitory control (Cai et al., 2014), and risk and error processing (Preuschoff et al., 2008; Ullsperger et al., 2010), all of which play a role in theoretical accounts of perseverance. In response to cognitive challenge, adults engage a more distributed network of prefrontal regions compared to adolescents, including the anterior insula. Increased insula activation in adults is tied to lower autonomic reactivity to challenges compared with adolescents (Strang et al., 2011). Importantly, the insula projects outputs to cortical and subcortical regions, including the PFC and striatum (Augustine, 1996; Ghaziri et al., 2018), which are important for purposeful behavior and are central components of recognized models of adolescent decision making. A recent theoretical review calling for consideration of the insula in investigations of adolescent decision making emphasizes that the extent to which the insula engages with cognitive and affective processing areas of the brain appears to be dependent on age (Smith et al., 2014). A developmental inquiry can better illuminate how individual differences in perseverance relate to relative maturity of neural regions tied to cognitive and affective processing, like the striatum and insula.

Hypotheses

Given ongoing development from adolescence to adulthood of neural systems implicated in cognitive control and affect regulation necessary to guide motivated behavior, age was expected to be positively correlated with perseverance such that older participants would exhibit more perseverance than younger participants.

Age was expected to be positively associated with greater neural response to negative feedback in salience and CEN regions compared with positive feedback, with adults demonstrating greater engagement in these regions compared to adolescents. Adolescents were expected to exhibit heightened striatal activation to positive feedback compared with adults.

The insula sends outputs to both cortical and subcortical neural structures important for deliberative and affective processing and was thus hypothesized to be a region of relevance for perseverance behavior. Salience-CEN connectivity during receipt of negative feedback was expected to mediate associations between age and perseverance, with greater connectivity indicative of perseverance as opposed to quitting.

Methods

Details for the Perseverance Task and general analytic plan are discussed in detail in "Methods for all studies" in Chapter 2.

Age was used as a continuous predictor in all behavioral analyses (see "Methods for all studies", Chapter 2). Linear and quadratic age effects were examined given extensive evidence of non-linear developmental changes from early adolescence to adulthood. Where quadratic effects were not significant, linear effects are reported.

Pubertal status was assessed using the Pubertal Development Scale (Petersen et al., 1988) for adolescent participants (n=45, missing data n=3). Puberty category scores were computed ranging from pre-pubertal to post-pubertal. For males, body hair growth, voice change, and facial hair growth scales were used. For females, body hair growth, breast development, and menarche scales were used.

A single-group average with additional covariate design was used with age as a demeaned regressor (mean centered across all participants) to examine the possible association

between age and neural activation during the Perseverance Task at a whole-brain level. Whole brain analyses were supplemented with ROI and beta-series connectivity analyses (see "fMRI Methods", Chapter 2).

Mediation analyses using perseverance decision as the dependent variable were estimated using methods appropriate for dichotomous outcomes (MacKinnon & Dwyer, 1993). Mediation analyses with continuous variables were conducted using Hayes PROCESS macro for SPSS (Hayes, 2013) with 5000 bootstrapped samples and significance determined at 95% bias-corrected confidence intervals. Continuous variables defining products were mean centered. A completely standardized index of mediation (ab_{cs}) was calculated for comparability with direct effects with continuous dependent variables (Preacher & Kelley, 2011).

Participants

Ninety-nine adolescents and young adults ages 13-30 (60 females; M_{age}=18.353, *SD*=3.22) were included in analyses. Forty-eight of the 99 participants were high-school adolescents ages 14 to 18 years and 51 participants were post-high school young adults ages 18 to 30 years. Of the 45 adolescents for whom pubertal status information was obtained, 86% (*n*=18) of males were categorized as post-pubertal and 13.6% (*n*=3) were categorized as late pubertal whereas 100% of females (*n*=24) were categorized as post-pubertal.

Results

Perseverance behavior

Age was not significantly associated with mental rotation accuracy, Estimate=-.029, *SE*=.187, *t*=-.152, *p*=.879, nor was it significantly associated with amount of negative feedback received (including manipulated feedback trials), Estimate=.029, *SE*=.122, *t*=.242, *p*=.809. Age

was not significantly associated with RT after negative feedback, Estimate=-67.120, *SE*=81.610, *t*=-.822, *p*=.413, or positive feedback, Estimate=-105.810, *SE*=70.940, *t*=-1.492, *p*=.139.

Age was significantly positively associated with perseverance decisions, Estimate=.147, *SE*=.068, *z*=2.159, *p*=.031 (Figure 3.1). This effect held controlling for performance accuracy, Estimate=.152, *SE*=.068, *z*=2.241, *p*=.025.

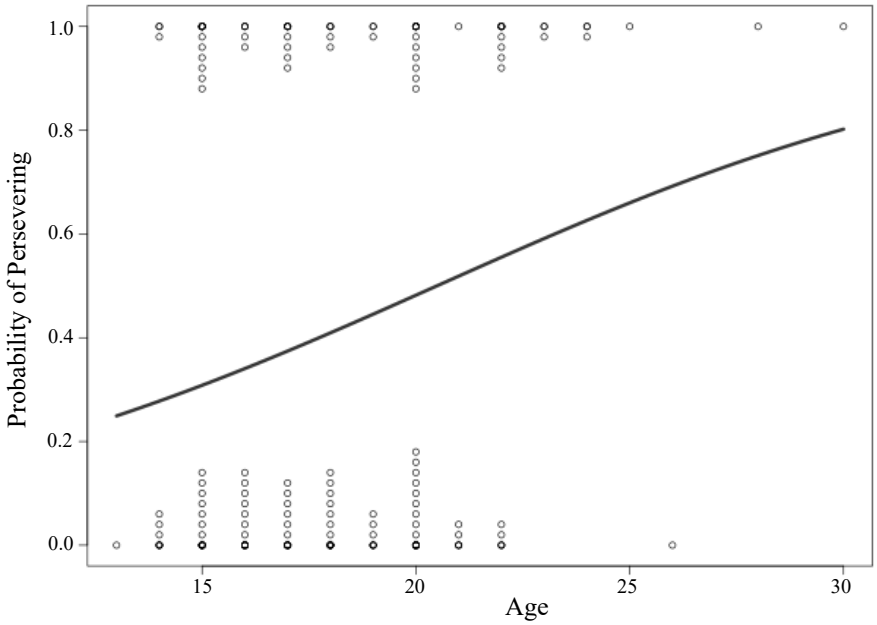


Figure 3.1. Age was significantly associated with perseverance decisions such that older participants had a higher probability of choosing the perseverance path, controlling for performance accuracy. Quit=0, Persevere=1.

Age was associated with several components of self-reported motivation (Perseverance Task Questionnaire; Appendix A; one participant who chose to persevere did not complete the questionnaire). Age was not significantly associated with whether participants reported that they made their path choice because that path was more or less difficult, Estimate=.059, *SE*=.067, *z*=.758, *p*=.384. Age was significantly associated with enjoying mental rotation trials that received positive feedback versus those that were challenging, Estimate=.180, *SE*=.073, *z*=6.005, *p*=.014, such that older participants were more likely to report liking challenging trials than

younger participants. Reported enjoyment of challenging versus correct trials was not associated with perseverance, X^2 (1, N=98)=1.838, p=.175, and age did not significantly moderate this association, Estimate$_{interaction}$=.005, $SE_{interaction}$=.142, $z_{interaction}$=.032, $p_{interaction}$=.975, 95% CI[-.273, .282]. Comparative task enjoyment was significantly associated with age, Estimate=.239, SE=.077, z=9.534, p=.002, such that older participants were more likely to report liking mental rotation trials as opposed to monetary reward trials. Comparative task enjoyment significantly differed between the groups, X^2 (1, N=98)=14.635, p<.001, and remained significantly associated with perseverance decision controlling for age, Estimate=-1.574, SE=.486, z=10.468, p=.001. Comparative task enjoyment significantly mediated the age – perseverance association, proportion of effect mediated=.577, Sobel z=2.241, SE=.168, p=.025.

Neural response

Performance feedback. Using age as a demeaned regressor in whole-brain analyses, feedback elicited differential activation such that older participants exhibited less activation in the right SFG to negative versus positive feedback (Table 3.1, Figure 3.2). Activation in the SFG was significantly associated with perseverance decisions, Estimate=-.007, SE=.003, z=4.930, p=.026, such that those who persevered had reduced SFG activation to negative versus positive feedback. SFG was not a significant mediator of the age – perseverance association, indirect effect=.048, SE=.035, 95% CI[-.011, .126] 5000 bootstrapped samples. SFG activation was positively associated with activation in the 8 *a priori* ROIs for negative versus positive feedback, all surviving Bonferroni correction and remaining significant partialling out age effects, rs>.409-.587, ps<.001.

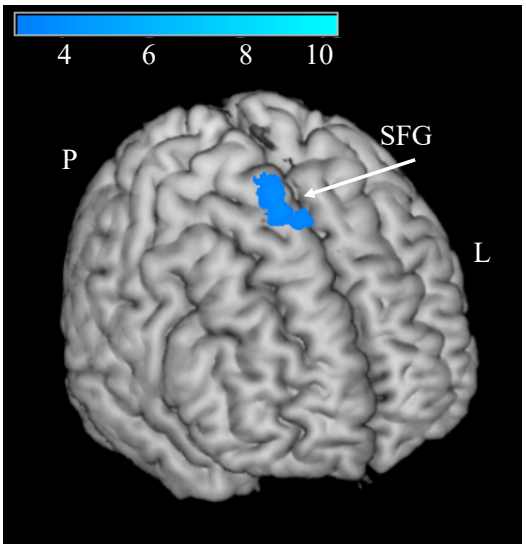


Figure 3.2. Visualization of significant activation of the negative age association for the contrast of negative feedback > positive feedback. Flame1, *Z*>3.1, FWE-corrected *p*<.05, outliers deweighted. Color bar indicates *Z* intensity values. L=left hemisphere, P=posterior. *N*=99.

Table 3.1. Significant age-related clusters from group level whole-brain analyses for feedback contrasts.

Cluster peak region[1]	Voxels	*p* value	Max Z value	R/L	Peak MNI coordinates X	Y	Z
Negative > positive feedback, negative association with age							
Superior frontal gyrus; Supplementary motor cortex	183	.005	4.02	R	8	4	70

Note: N=99. Z>3.1, FWE-corrected *p*<.05, Flame1. R=Right hemisphere. Local maxima not listed. [1]Regions based on the Harvard-Oxford Structural Atlas.

ROI analyses (Chapter 2, Figure 2.3) revealed age associations for negative versus positive feedback in the ACC, Estimate=-3.710, *SE*=1.354, *t*=-2.740, *p*=.007, and right insula, Estimate=-2.665, *SE*=1.298, *t*=-2.053, *p*=.043, such that younger participants demonstrated greater activation. The left insula was marginally significantly associated with age, Estimate=-2.602, *SE*=1.411, *t*=-1.844, *p*=.068, such that younger participants demonstrated greater

activation to negative versus positive feedback. These associations held controlling for amount of negative feedback received, which did not differ by age: ACC, Estimate=-3.675, *SE*=1.354, *t*=-2.715, *p*=.008; right insula, Estimate=-2.577, *SE*=1.253, *t*=-2.057, *p*=.042; left insula, Estimate=-2.554, *SE*=1.405, *t*=-1.818, *p*=.072. Activation in these regions did not mediate the age-perseverance association. These associations did not survive $p<.006$ Bonferroni correction for 8 multiple comparisons at $\alpha=.05$.

Parametric modulation analyses revealed no differential activation by age at the whole-brain level was associated with linear accumulation of either negative or positive feedback presented over the course of the task. Age was not associated with activation on manipulated feedback trials for which participants received negative feedback for accurate responses versus those for which participants received negative feedback for incorrect responses.

For negative feedback, beta-series connectivity analyses revealed left dlPFC – right striatum connectivity showed significant differential connectivity by age, $Estimate_{quadratic}=.776$, $SE_{quadratic}=.335$, $t_{quadratic}=2.319$, $p_{quadratic}=.023$ (Figure 3.3a). Left dlPFC – right striatum connectivity was significantly associated with RT after negative feedback such that greater connectivity was associated with longer RTs, Estimate=.301, *SE*=.112, *t*=2.689, *p*=.008. This association held controlling for age and average RT, Estimate=.144, *SE*=.063, *t*=2.281, *p*=.025. Connectivity was not significantly associated with longer RT after positive feedback controlling for age and average RT, Estimate=.063, *SE*=.053, *t*=1.185, *p*=.239. Comparative task enjoyment significantly moderated the age association with dlPFC – striatum connectivity, controlling for perseverance decision, $Estimate_{interaction}=.060$, $SE_{interaction}=.022$, $t_{interaction}=2.697$, $p_{interaction}=.008$, 95% CI[.016, .104]. Older participants who enjoyed mental rotations more than earning money

showed greater dlPFC – striatum connectivity than those who reported enjoying earning money more than mental rotations (Figure 3.3b).

No pairwise connections differed by age for positive feedback.

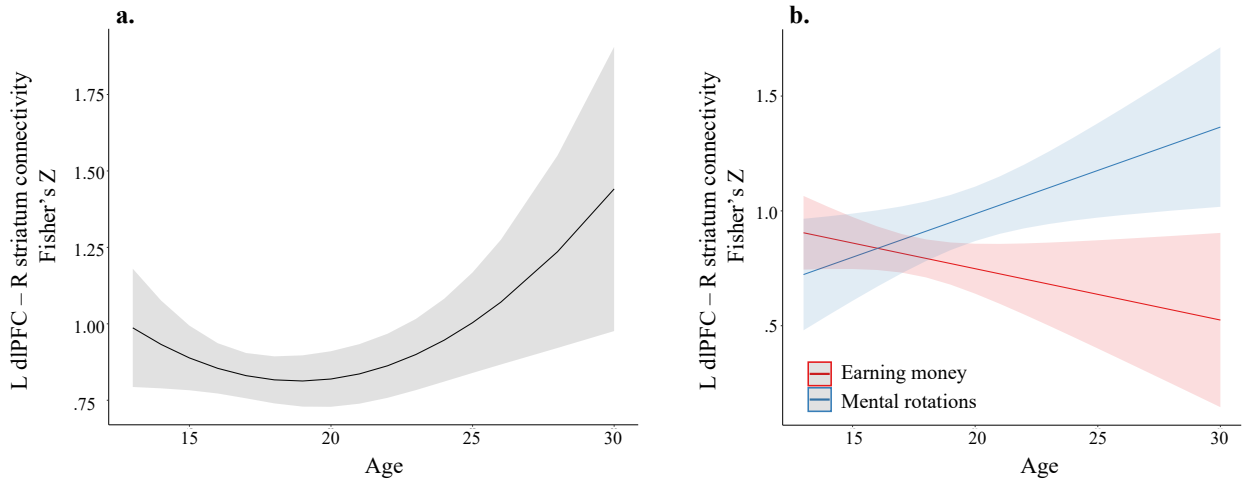


Figure 3.3. (a) Age was quadratically associated with connectivity between the left dorsolateral prefrontal cortex (dlPFC) and right striatum in response to negative feedback. **(b)** Comparative task enjoyment moderated the age – connectivity association such that older participants were differentiated in dlPFC – striatum connectivity to negative feedback based on whether they reported enjoying mental rotations more than earning money. *N*=99.

Age moderated the association between perseverance decision and connectivity of the dlPFC and fronto-insular network consisting of the mPFC, ACC, and insula in response to negative feedback. Older participants demonstrated perseverance at lower levels of connectivity whereas younger participants only chose to persevere if they had increased levels of dlPFC and fronto-insular connectivity (Table 3.2; Figure 3.4). In other words, decreased connectivity to negative feedback was associated with quitting in all participants whereas increased connectivity was associated with perseverance across the entire age range and moderate levels of connectivity demonstrated the biggest differentiation by age.

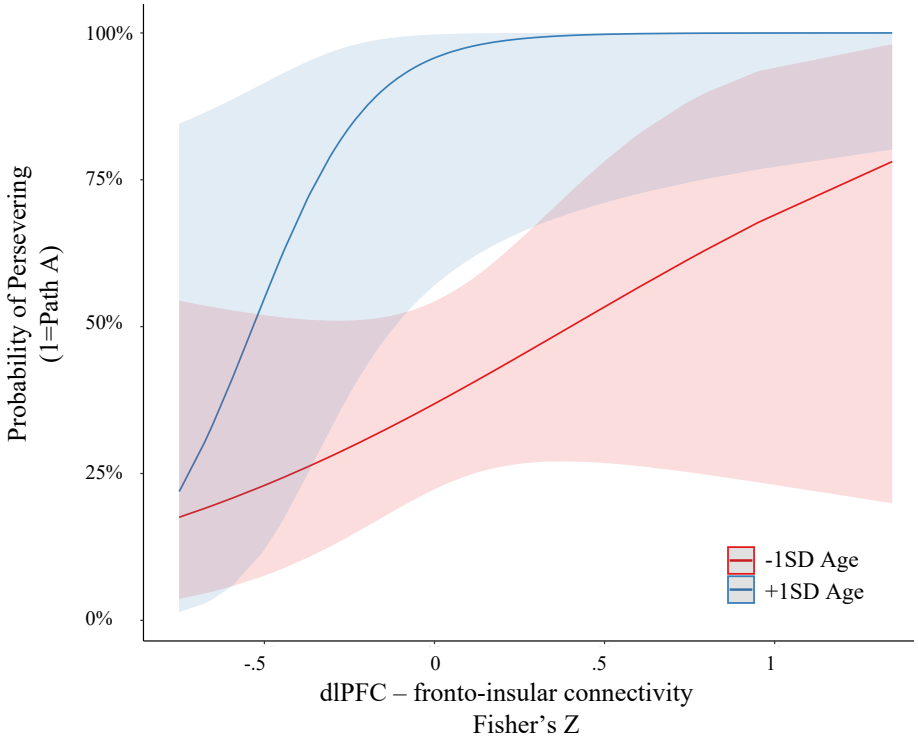


Figure 3.4. The interaction between age (quadratic) X connectivity in response to negative feedback between the dorsolateral prefrontal cortex (dlPFC) and fronto-insular network was associated with perseverance decisions. *N*=99.

Table 3.2. Logistic regression results for significant differences in perseverance decisions as a function of age and connectivity differences between the dorsolateral prefrontal cortex and fronto-insular network in response to negative versus positive feedback.

	Estimate	*SE*	t	*p*
Intercept	-.078	.259	-.302	.763
Connectivity	.645	.636	1.014	.311
Age	10.809	4.306	2.510	.012
Age^2	9.757	4.981	1.959	.050
Age*connectivity	11.928	8.460	1.410	.159
Age^2*connectivity	28.139	10.780	2.610	.009

Note: N=99. Perseverance decision, 0=quit, 1=persevere. Connectivity values are Fisher's z scores. Age in years.

Mental rotations. Age was not significantly associated with mental rotation decisions versus baseline at the whole-brain level nor was age associated with differential response on trials after participants received negative feedback compared those after which they received positive feedback. ROI analyses revealed several significant positive associations with age. Older participants demonstrated greater activation in the ACC, Estimate=5.174, *SE*=2.305, *t*=2.244, *p*=.027, left insula, Estimate=5.615, *SE*=2.788, *t*=2.014, *p*=.047, right insula, Estimate=7.959, *SE*=2.614, *t*=3.045, *p*=.003, and mPFC Estimate=6.556, *SE*=3.049, *t*=2.150, *p*=.034, for the contrast of mental rotation decisions after negative feedback versus those after positive feedback. The right insula survived $p<.006$ Bonferroni correction for 8 multiple comparisons at $\alpha=.05$. Activation in these regions did not mediate the age – perseverance association.

Reward. Activation to monetary reward receipt versus baseline was not significantly associated with age at the whole-brain level. Age was positively associated with neural response to positive feedback versus monetary reward receipt in the left occipital cortex such that older participants evinced greater activation (Table 3.3, Figure 3.5). Age-related activation in the occipital cortex was not significantly associated with perseverance decision, Estimate=-.001, *SE*=.001, *z*=1.222, *p*=.269.

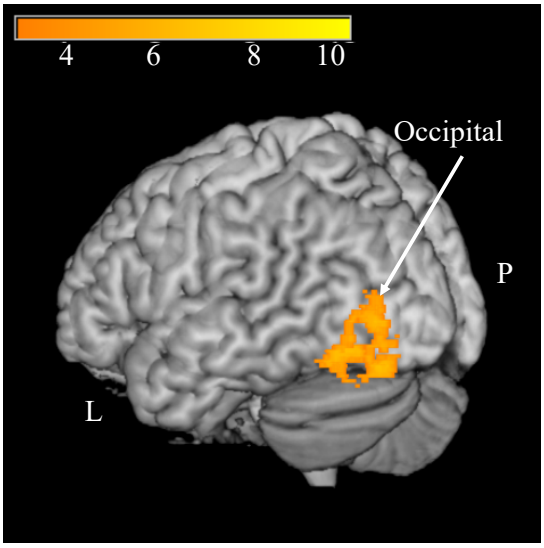


Figure 3.5. Visualization of significant activation of the positive age association for the contrast of positive feedback > monetary reward receipt. Flame1, *Z*>3.1, FWE-corrected *p*<.05, outliers deweighted. Color bar indicates *Z* intensity values. L=left hemisphere, P=posterior. *N*=99.

Table 3.3. Significant age-related clusters from group level whole-brain analyses for reward contrasts.

Cluster peak region[1]	Voxels	*p* value	Max Z value	R/L	Peak MNI coordinates X	Y	Z
Positive feedback > monetary reward receipt, positive association with age							
Occipital cortex; Occipital fusiform gyrus	441	<.001	5.01	L	-42	-74	-12

Note: N=99. Z>3.1, FWE-corrected *p*<.05, Flame1. L=Left hemisphere. Local maxima not listed.
[1]Regions based on the Harvard-Oxford Structural Atlas.

ROI analyses revealed a significant positive association between age and right striatum activation to positive feedback versus monetary reward receipt, Estimate=9.262, *SE*=4.274, *t*=2.167, *p*=.033. The right dlPFC was marginally significantly positively associated with age, Estimate=12.307, *SE*=6.266, *t*=1.964, *p*=.052, as was the right insula, Estimate=8.427, *SE*=4.923, *t*=1.712, *p*=.090. These associations did not survive *p*<.006 Bonferroni correction for

8 multiple comparisons at α=.05. Striatal activation to positive feedback versus monetary reward receipt was significantly positively correlated with occipital activation extracted from whole-brain analyses, partialling out effects of age: $r_{Rstriatum}(99)$=.938, $p_{Rstriatum}$<.001; $r_{Lstriatum}(99)$=.947, $p_{Lstriatum}$<.001.

For monetary reward receipt, the right insula and mPFC showed significant differential connectivity by age, $Estimate_{quadratic}$=-1.003, $SE_{quadratic}$=.417, $t_{quadratic}$=-2.404, $p_{quadratic}$=.018 (Figure 3.6a). The interaction of age X perseverance decision was associated with right insula – mPFC connectivity to monetary reward, $Estimate_{interaction}$=-.066, $SE_{interaction}$=.028, $t_{interaction}$=-2.405, $p_{interaction}$=.018. Late adolescents demonstrated highest levels of insula – mPFC connectivity with reductions into early adulthood. Reduced activation was associated with perseverance among older participants whereas increased activation was associated with quitting (Figure 3.6b).

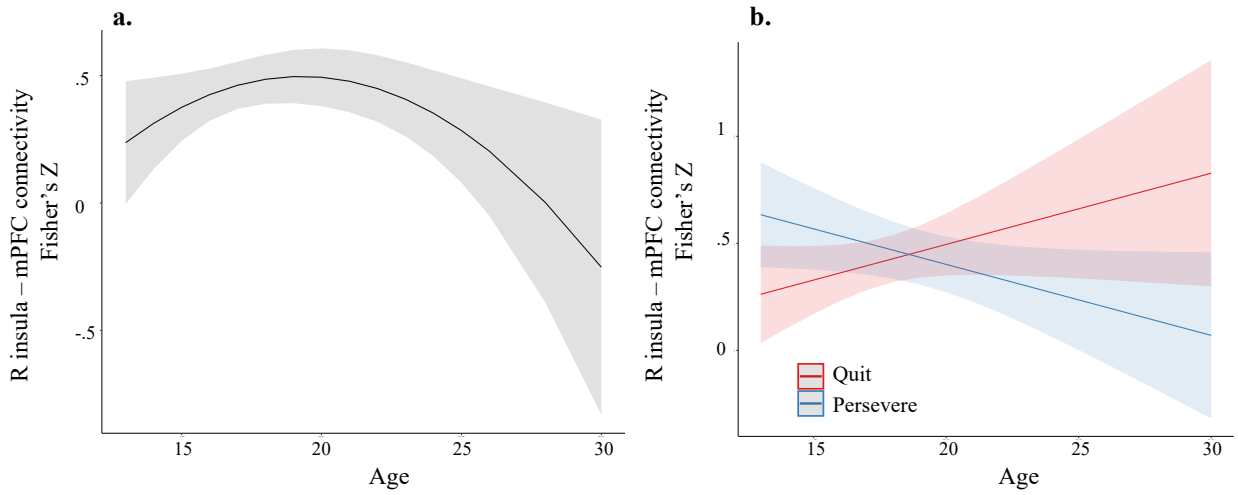


Figure 3.6. (a) Age quadratically associated with connectivity between the right insula and medial prefrontal cortex (mPFC) in response to monetary reward receipt. **(b)** The interaction of age X perseverance decision was associated with right insula and mPFC connectivity in response to monetary reward receipt. *N*=99.

Discussion

This study investigated neural differences associated with multiple facets of a perseverance task in a sample of adolescents and young adults. Analyses resulted in a number of age-related findings. First, age was associated with perseverance behavior as well as activation and connectivity to negative performance feedback. Second, regions of the fronto-insular network were differentially activated for mental rotation trials after negative feedback and age significantly moderated the association between perseverance decisions and dlPFC connectivity with this network. Lastly, age was associated with neural response to positive feedback and monetary reward receipt in regions associated with reward processing and motivated attention.

As hypothesized, older participants were more likely to persevere than younger participants, an effect which held controlling for performance accuracy. Older participants compared to younger participants reported greater enjoyment of challenging trials and the mental rotation task. In contrast, younger adolescents reported enjoying earning monetary reward more than challenge. Favoring the mental rotation task to the monetary reward game mediated the age-perseverance association. Valuation of challenge increased with age and this shift accounted for older participants persevering more than younger participants. These findings align with established understanding of unique facets of adolescence. Adolescents demonstrate enhanced neural and behavioral sensitivity to monetary reward receipt relative to children and adults (Galván et al., 2006; Geier et al., 2010; Van Leijenhorst et al., 2010). Additionally, adolescents demonstrate a higher tolerance for uncertainty and, thus, reduced motivation to engage in behavior that reduces uncertainty (van den Bos & Hertwig, 2017). Together, these developmental phenomena may contribute to adults enjoying the mental rotation task, which omitted monetary incentive and included uncertainty about future competency, more than

adolescents. It is possible that perseverance was motivated by a desire to resolve performance uncertainty, which would indicate that uncertainty tolerance may be detrimental for adolescent motivation in some contexts.

Age was associated with neural response to performance feedback. Younger participants demonstrated increased activation of the SFG in response to negative versus positive feedback. Age-related SFG activation was associated with perseverance such that reduced activation was associated with persevering. The ability to use performance feedback to guide decision-making is crucial for adaptive behavior. Both positive and negative feedback are important for performance, signaling need for behavior continuation or adjustment, respectively. Performance monitoring is particularly important during adolescence as younger individuals grapple with new, and often challenging, learning experiences. When processing reward signals under conditions of ambiguity, adolescents and young adults exhibit greater SFG activation (Blankenstein et al., 2018). Greater SFG activation in response to negative feedback for younger participants in this study may reveal less clear representation of the value of negative feedback. For example, younger participants may interpret negative feedback as both motivating (i.e., positive value) and aversive (negative value). If feedback is motivating, it signals the need for behavior modification (i.e., increased attention / effort, change in strategy, etc.) to achieve success. However, if feedback is aversive, it signals the goal may be unattainable and effort should be reduced. Greater SFG activation was associated with quitting, potentially because of ambiguous or conflicting signaling about whether task performance could be improved. Understanding whether the value of negative feedback changes with age is worthy of more detailed future exploration. Additionally, anxiety in response to negative stimuli is associated with increased activation in the right SFG, which has been interpreted to reflect increased

attention to negative stimuli (Spielberg et al., 2013). In the present study, ambiguity in the value of negative feedback may bias attention toward negative feedback consequently activating the SFG in younger participants. The posterior SFG subregion observed in this study is also part of the cortico-striato-thalamo-cortical loop that serves motor control (Li et al., 2013). Thus, SFG activation in the current study can be interpreted as a marker of increased effort mounting an appropriate response after negative feedback in younger participants.

Older participants demonstrated reduced activation magnitude in the ACC and insula when presented with negative feedback but greater activation magnitude in the ACC and insula on mental rotation trials after negative feedback. Thus, responsivity of these regions in older participants varied with the immediate utility of negative information. The ACC and insula are key nodes of the salience network activating in response to salient stimuli (Menon & Uddin, 2010). The anterior insula updates motivational states with specific associated goals and dynamically responds to motivational orientation (Calcott & Berkman, 2015; Wager & Barrett, 2017). The insula's role in a wide range of mental states including negative affect and risk prediction (Preuschoff et al., 2008; Uddin et al., 2017) indicate that it contributes to learning after negative experiences to guide future behavior (Lawrence et al., 2014). The ACC is also implicated in a wide range of cognitive functions and is theorized to learn about and maintain high-level action contingencies that motivate goal-directed action (Holroyd & Yeung, 2012). Dynamic responsivity of these regions may contribute to developmental improvements in behavioral flexibility across multiple domains.

For monetary reward receipt, the right insula and mPFC showed significant differential connectivity by age such that older adolescents demonstrated the highest levels of connectivity with reductions into early adulthood. Reduced connectivity was associated with perseverance

among adult participants whereas increased connectivity was associated with quitting. Thus, adults demonstrating greater connectivity in this circuitry resembled an adolescent profile of connectivity and also chose to quit. Emotion processing is associated with activation in the insula and mPFC, with the insula processing emotion perception and the mPFC evaluating emotion signals (Pavuluri & May, 2015). Affective bias toward reward-processing during adolescence may account for stronger connectivity of these regions, which are implicated in risk taking and reward processing (McCormick et al., 2019; Smith et al., 2014). Older participants who chose to quit demonstrated greater engagement of this reward-sensitive circuit in response to receiving money. The Perseverance Task did not offer any monetary reward for continued engagement indicating neural circuits responding to extrinsic versus intrinsic incentives play a role in motivating decisions to persevere.

Direct comparisons of monetary reward receipt with positive feedback illustrated a shift toward increased valuation of positive feedback compared with hedonic reward with age. Age was positively associated with left occipital cortex activation to positive feedback versus monetary reward receipt. Reward-stimulus associations influence representation of sensory information in the occipital cortex in order to guide subsequent behavior (Serences, 2008; Anderson et al., 2014). Thus, older participants may have formed stronger representations for positive feedback than monetary reward. Older participants also demonstrated greater striatal activation to positive feedback compared with monetary reward, which was positively correlated with occipital cortex activation, bolstering this interpretation. Together, these findings highlight the importance of considering how various types of positive stimuli are processed when conducting developmental investigations of decision-making.

Connectivity between the dlPFC and striatum in response to negative feedback showed associations with age such that late adolescents demonstrated lowest levels of connectivity. dlPFC – striatum connectivity was associated with slowed RT after negative feedback, and slowed RT after negative feedback was associated with greater accuracy. dlPFC regulation of the striatum slows preparatory motor and motivation signals (Staudinger et al., 2011), thus explaining deliberative behavior after negative feedback. Prior work with high and low value rewards suggests the dlPFC contributes to successful regulation of reward by promoting low-value reward cues in the striatum (Staudinger et al., 2011). Although Staudinger and colleagues interpreted slowed RT as a decrease in motivation to large rewards, slowed RT after negative feedback in this study promoted accuracy. Regulating striatal response through dlPFC connectivity during negative feedback may aid in perseverance by promoting approach behavior while limiting impulsivity. Whether participants reported enjoying mental rotations more than earning money moderated the association between age and dlPFC – striatum connectivity. For older participants, enjoying mental rotations trials was associated with higher connectivity. Again, this suggests dlPFC – striatum connectivity may have altered reward signals associated with negative feedback in a way that promoted perseverance.

dlPFC regulation of the fronto-insular network was also relevant for behavior. The age X connectivity interaction in response to negative versus positive feedback was associated with perseverance decisions. Older participants displayed perseverance behavior even at lower levels of connectivity, but younger participants only showed a greater than chance probability of persevering at high levels of connectivity. This network is involved in multiple aspects of processing the utility of and controlling response to negative consequences. The insula and ACC, anchors of the salience network, play a crucial role in detecting and responding to goal-relevant

information (Chen et al., 2016; Seeley et al., 2007), and connectivity between the insula and ACC drives behavioral adaptation after negative feedback (Ham et al., 2013). The salience network dynamically interacts with other intrinsically connected neural networks during cognitive control, including the central executive network, centered in the dlPFC, and the default mode network, including the mPFC (Menon, 2011). dlPFC control over the fronto-insular network guides decision making when potential loss is present (Zhang et al., 2018). Attenuated dlPFC and salience network coupling has been observed in anxious individuals, suggesting the dlPFC plays a role in regulating behavior in response to emotional cues (Simmons et al., 2010). Negative feedback can be interpreted to indicate additional effort is required in order to succeed at a given task or signal abandonment if a task is deemed too difficult or feelings of competence are undermined (Swift & Peterson, 2018). Younger participants required greater dlPFC regulation of the fronto-insular loss evaluation system to motivate perseverance behavior.

The current findings should be considered in the context of certain potential limitations. Age was not associated with accuracy or RT on the Perseverance Task. Several features of the task were designed to eliminate age-related differences in performance. For example, display time of mental rotation trials was lengthened based on RT in prior work and a separate decision screen was provided. Lack of performance differences improves interpretability of findings and separability of perseverance from performance, but also requires future work to determine whether performance proficiency is associated with development of perseverance. The results may differ for a task that involves more complex skills yet to fully develop during adolescence or under different task demands (see Swift & Peterson, 2018). Lack of convergence with prior work on performance feedback processing in adolescents and adults may be a result of task and sample specifics. For example, van Duijvenvoorde and colleagues (2008) found differential recruitment

of the dlPFC by age such that negative feedback evoked greater dlPFC activation than positive feedback in adults but not in adolescents. In contrast, no age-related differences in dlPFC activation magnitude were observed in the present study for the contrast of negative versus positive feedback. However, the current study included twice as many participants, age was assessed continuously, and mid- to late-adolescents were included in a contrast with early adolescents ages 11 to 13 years in the prior work. Additionally, greater dlPFC – striatum connectivity in response to negative feedback was observed for adults compared with adolescents, providing some converging evidence that feedback-related dlPFC functioning differs with age. While this study included a relatively large sample of adolescents and adults, replication in a wider age range and longitudinal inquiries will further illuminate neural systems that underpin the development of perseverance.

Several findings elucidate how age-related differences in neural response contribute to perseverance behavior. Older participants were more likely to persevere, reported greater enjoyment of challenge, demonstrated reduced activation in effort-related neural regions and regions of the salience network in response to negative feedback, and increased activation in value-driven attentional regions in response to positive feedback. Adolescent-like profiles of insula – mPFC connectivity in response to monetary reward were associated with quitting among adults whereas increased dlPFC connectivity with fronto-insular network nodes was associated with perseverance among adolescents. dlPFC – striatal connectivity further illuminated mechanisms promoting increases in challenge enjoyment with age. Promotion of value signals in response to negative feedback through dlPFC – striatal connectivity evinced a quadratic pattern across the sample age range consistent with understanding of prefrontal – subcortical connectivity development. These findings implicate complicated interactions among neural

systems involved in valuation, control, and attention in distinguishing who perseveres at different developmental stages.

Chapter 4

Trait and biological factors underlie perseverance behavior

Introduction

Biological factors and personality traits may contribute to decision-making by influencing neural processing of situational factors at the neural level. Performance feedback and reward were identified as situational factors of relevance to perseverance in Study 1, and value encoding of these factors was shown to differ as a function of age in Study 2. In the current study, sex, inflammation, and impulsivity were tested as individual difference factors given hypothesized associations with perseverance as well as neural response to feedback and reward. Variation of biological and trait factors across individuals can affect decision-making. For example, established sex differences in punishment and reward sensitivity may relate to affective processing of performance feedback and reward thereby contributing to sex differences in perseverance decisions (e.g., Jansen et al., 2014). Inflammation is also associated with alterations to affect and cognition with enhanced sensitivity to negative stimuli and reduced motivation for positive reward (e.g., Harrison et al., 2016). Responsivity to performance feedback and reward also differ as a function of impulsivity (e.g., Franken et al., 2008), a trait-like individual difference related to decision-making. The association between these individual differences factors and perception of motivationally-relevant stimuli suggest potential relevance for perseverance behavior. Further, understanding how individual difference factors contribute to perseverance and neural functioning can illuminate meaningful variability in group differences observed in Studies 1 and 2.

Sex

The closest related literature on sex differences in perseverance comes from research on grit. Adolescent females report higher levels of grit than males, but these effects are larger for the consistency of interest facet than perseverance of effort facet (Christensen & Knezek, 2014).

Counter sex differences have been observed in other potentially relevant constructs. For example, females consistently report higher sensitivity to punishment, across adolescence and adulthood with no moderating effect of age (Santesso et al., 2011; Cross et al., 2011). Greater sensitivity to punishment may mean that females place greater motivational relevance on negative feedback or that they are more avoidant of behaviors that may result in future punishment. Females also report that impulse control is more disrupted by negative affect (UPPS-P Negative Urgency) than males, although this effect is small and confined to adolescents (Cross et al., 2011). Together, greater sensitivity to punishment and negative urgency suggest females would be less likely to persevere than males, irrespective of age.

Inflammation

Although specific behaviors are often conceptualized as either positive or negative, rarely does a benefit come without any cost. For example, exploratory behavior adaptive for learning and social exploration during adolescence also promotes health-compromising risk taking. In the context of the present work, perseverance is most frequently portrayed as a positive behavioral adaptation necessary for success, but perseverance may also carry costs. Lucas and colleagues (2015) found that adults reporting low grit and those reporting high grit were both able to persist on a laboratory task when the outcome was positive, but that only higher grit individuals continued increasing effort when failing. This persistence led grittier individuals to complete fewer anagram problems because they continued to work on unsolvable problems that should have been passed over, increased effort when losing a game, and persisted at playing the game when given the opportunity to quit resulting in greater opportunity for monetary loss. The authors termed these patterns “costly persistence” (Lucas et al., 2015). Evidence suggests perseverance may also be accompanied by physiological costs. Miller and Wrosch (2007) found

that adolescents who self-reported difficulty disengaging from unattainable goals showed higher concentrations of C-reactive protein (CRP), a marker of chronic inflammation. The theory of goal disengagement as an adaptive response is somewhat controversial (see Seligman, 1975 for an association with goal disengagement and maladaptive psychological outcomes), but importantly Miller and Wrosch identified an association between physical health (i.e., inflammation) and sustained goal pursuit. Unlike examinations of inefficient allocations of effort (e.g., Lucas et al., 2015), which are subjective and may differ in their categorization as a "negative consequence" depending on the circumstances[4], biomarkers can better illuminate whether perseverance is associated with objective costs (i.e., adverse health consequences). Inflammatory cytokines are particularly well-suited because proinflammatory cytokines like IL-6, which stimulates production of CRP, show persistent elevation despite repeated exposure to the same stimuli (Breines et al., 2014). This pattern of responsivity differs from other biomarkers like cortisol, which shows a habituation response after repeated exposure (Petrowski et al., 2012). Examining perseverance behavior and inflammation is a first step to building a theoretical framework of mechanisms through which perseverance gets under the skin. One potential candidate is regulation of affective responses to negative feedback. According to Social Self Preservation Theory, social-evaluative threat (i.e., negative performance feedback) can elicit increased proinflammatory cytokine production (Dickerson et al., 2004). Inflammation is a proximal biological pathway to understanding health consequences of perseverance, and inflammation during development can have lasting consequences in adulthood (Allen et al., 2018; Slopen et al., 2013). Combined with a neurobiological account, investigating inflammation

[4] For example, performance-based costs can be interpreted as negative if considered in the short-term (i.e., number of questions answered) or beneficial if assessed in the long-term (i.e., skill mastery) or by different metrics of success (i.e., more difficult questions answered correctly).

and behavioral perseverance during adolescence can provide a more fulsome model of what biological systems perseverance involves, including potential costs.

Impulsivity

Individuals vary in their abilities to make deliberate decisions, and those high in impulsivity are characterized as making rash decisions. Affective states may interact with trait levels of impulsivity to affect self-regulation, thereby influencing decision making. In the present study, several facets of impulsivity indexed by the UPPS-P Impulsive Behavior Scale (Whiteside & Lynam, 2001) were assessed for associations with perseverance. The negative urgency and positive urgency subscales of the UPPS-P measure the tendency to act rashly under conditions of negative and positive emotions, respectively. Predispositions to make impulsive decisions in these circumstances may be relevant for perseverance given choices are accompanied by weighting of potential future success and failure, which evokes affective responses. The lack of premeditation subscale assesses the tendency to act without thinking, which has been associated with disadvantageous decision making (Zermatten et al., 2005). Negative urgency and lack of premeditation have also been associated with maximizing rewards and less avoidance of potential punishment, which can be an effective short-term strategy (Hulvershorn et al., 2015), but may be maladaptive for long-term goal pursuit associated with perseverance.

Impulsivity may be tempered by self-control (Matta et al., 2012). Engagement of the PFC, as well as connectivity with the basal ganglia, has been associated with regulating impulsive behaviors (Kim & Lee, 2011). However, greater responsivity in regions associated with reward, such as the striatum and mPFC, has been linked to greater impulsivity (Hariri et al., 2006). These neural systems are differentially evoked by negative and positive feedback and develop throughout adolescence. Perseverance, by definition, requires self-control necessary for

an individual to engage in repetitive or frustrating behaviors (e.g., striving despite failure). Self-control, like perseverance, predicts positive life outcomes (de Ridder et al., 2012) and academic achievement (Duckworth & Carlson, 2013). Self-control has also been shown to be effective in helping individuals refrain from setting unattainable goals (Baron et al., 2016), which has benefits for physiological health (Miller & Wrosch, 2007).

Hypotheses

Females were hypothesized to be less likely to persevere compared to males. Perseverance was hypothesized to be associated with greater inflammation as measured by pro-inflammatory cytokines. Greater impulsivity was expected to be associated with quitting as opposed to perseverance.

Methods

Details for the Perseverance Task and general analytic plan are discussed in detail in "Methods for all studies" in Chapter 2.

Adolescents and adults completed the task as part of two separate studies. Sex and impulsivity data were collected for both adults and adolescents. Inflammation data were only collected for adolescent participants. Participants completed all self-report measures online prior to their scan visit via Qualtrics survey software.

Skewed variables were log-transformed for analyses. Analyses including inflammation control for body mass index (BMI). BMI was assessed at the scan visit. Height (in meters) and weight (in kilograms) were measured and BMI was calculated using the standard formula BMI = weight / height^2, which was then log-transformed.

Mediation analyses using perseverance decision as the dependent variable were estimated using methods appropriate for dichotomous outcomes (MacKinnon & Dwyer, 1993). Mediation

analyses with continuous variables were conducted using Hayes PROCESS macro for SPSS (Hayes, 2013) with 5000 bootstrapped samples and significance determined at 95% bias-corrected confidence intervals. Continuous variables defining products were mean centered. A completely standardized index of mediation (ab_{cs}) was calculated for comparability with direct effects with continuous dependent variables (Preacher & Kelley, 2011).

Inflammation

Venous blood was drawn into a Serum Separator Tube (Becton-Dickinson) by antecubital venipuncture. Following the manufacturer's instructions, the tube was centrifuged at 1200 x g for 10 minutes, after which the serum was harvested, divided into aliquots, and frozen at -80°C until the end of the study. At that time the samples were thawed, and five commonly assessed biomarkers of low-grade inflammation were measured as pre-determined in consultation with Professor Gregory E. Miller at Northwestern University: CRP, interleukin-6 (IL-6), interleukin-8 (IL-8), interleukin10 (IL-10), and tumor necrosis factor-α (TNF-α). CRP was measured in duplicate by high-sensitivity immunoturbidimetric assay on a Roche/Hitachi cobas c502 analyzer. The average intra-assay coefficient of variation was 2.5%. This assay's lower limit of detection is 0.2 mg/L. The cytokines were measured in duplicate by electrochemiluminescence on a SECTOR Imager 2400A (MesoScale Discovery) with a Human Pro-Inflammatory 4-Plex Ultra-Sensitive assay (MesoScale Discovery), following instructions provided by the manufacturer (Fu et al., 2010). The kit's lower limits of detection range from 0.10 pg/mL (IL-8) to 0.80 pg/mL (IL-10). Across runs, the average intra-assay coefficients of variation were 3.02% (IL-6), 3.69% (IL-8), 4.22% (IL-10), and 3.69% (TNF-α).

Impulsivity

Impulsivity was assessed using the self-report UPPS-P questionnaire (Lynam et al., 2006). The scale is comprised of five factors of impulsivity (59 items). The scale scales reflect distinct personality traits that lead to impulsive-type behavior. Each item is answered using a four-point Likert scale ranging from 1=”agree strongly” to 4=”disagree strongly”. First, negative urgency (12 items) reflects a tendency to act rashly when experiencing negative affect. Second, lack of premeditation (11 items) is the tendency to act without thinking. Third, sensation seeking (12 items) is the tendency to seek out novel or thrilling experiences. Fourth, lack of perseverance (10 items) is the inability to remain focused on a task. Fifth, positive urgency (14 items) is the tendency to act rashly when experiencing positive affect (Cyders et al., 2007). The negative urgency and positive urgency subscales are considered first-order factors representing emotion based rash actions. The lack of premeditation and lack of perseverance subscales are considered first-order factors representing deficits in conscientiousness. Sensation seeking is a first-order factor of sensation seeking. These traits are detectible in adolescence (Zapolski et al., 2010) and stable over time (Cyders et al., 2007; Smith et al., 2007) with higher scores reflecting more impulsive behaviors.

Results

Sex

Sex was marginally significantly associated with perseverance decisions, X^2 (1, N=99)=3.437, p=.064, such that 53.846% (n=21 out of 39) of males (M_{age}=18.857, SD=4.292, range=14-30, 11 adolescents, 10 adults) but only 35.000% of females (n=21 out of 60) chose to persevere (M_{age}=19.524, SD=3.265, range=14-25, 7 adolescents, 14 adults). Sex remained marginally associated with perseverance decisions, controlling for performance accuracy,

Estimate=-.741, *SE*=.427, *z*=3.005, *p*=.083. Age did not significantly moderate the sex-perseverance association, Estimate=.101, *SE*=.146, *z*=.690, *p*=.490.

Neural response in the right striatum to positive feedback versus monetary reward significantly differed by sex such that females showed greater differential activation than males with higher activation magnitude to monetary reward receipt than positive feedback, $t(97)=2.082$, $p=.040$, $M_{female}=-91.605$, $SD_{female}=148.199$, $M_{male}=-33.147$, $SD_{male}=116.091$, 95% CI[2.725, 114.192].

Inflammation

CRP, IL-6, IL-8, IL-10, and TNF-α were assayed for 46 adolescent participants (23 females, $M_{age}=15.848$, $SD=1.135$, range=14-18 years). Scores were log transformed to address skew and *Z*-scores were computed to increase comparability across inflammation markers. Three participants were excluded from further CRP analyses because of unidentifiable assay scores ($n=43$). Ranges and correlations are provided in Table 4.1. The sample yielded sufficient variability for planned analyses (Figure 4.1).

Table 4.1. Descriptive statistics and correlations for inflammatory markers.

Marker	Min	Max	1 corr	2 corr	3 corr	4 corr	5 corr
1. CRP	-1.051	3.606	—				
2. IL-10	-1.004	3.395	.415**	—			
3. IL-6	-1.846	2.832	.355*	.295*	—		
4. IL-8	-2.240	3.759	.131	.258†	.044	—	
5. TNF-α	-1.288	5.265	.025	.201	-.040	.152	—

Note: Average=0, *SD*=1. *$p<.05$, **$p<.01$, ***$p<.001$, $^{\dagger}p<.10$. $n=46$, CRP $n=43$.

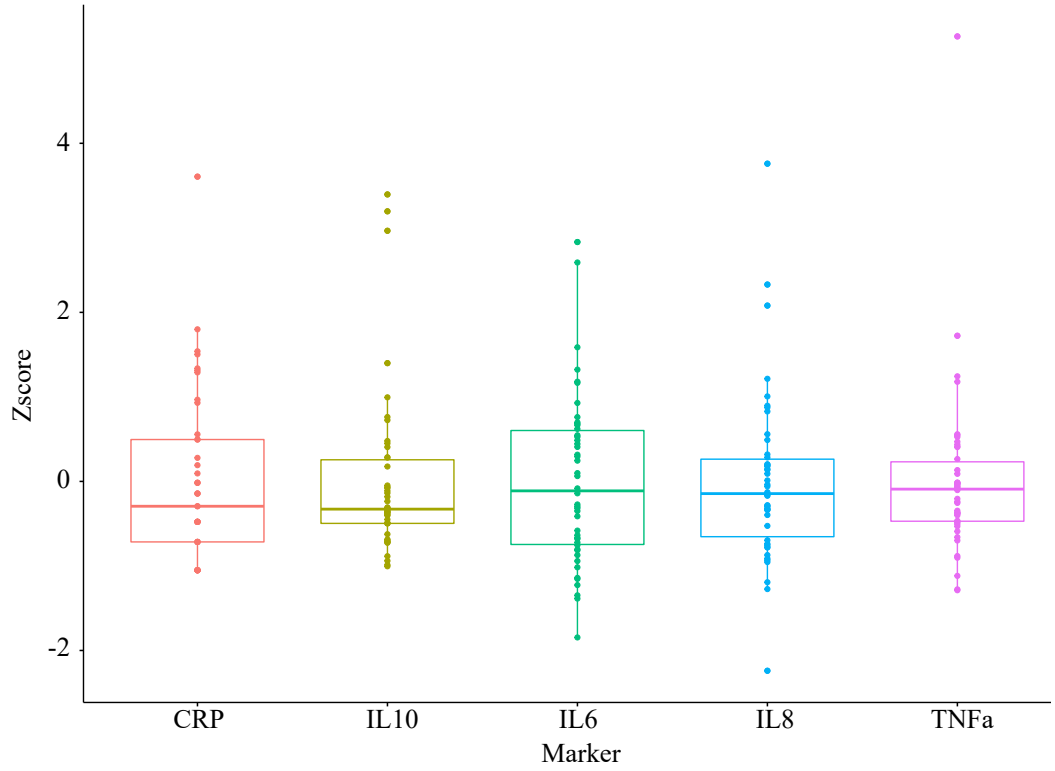


Figure 4.1. Boxplot distribution of log transformed, z-scored inflammatory marker concentrations.

BMI was calculated, log transformed, and used as a covariate in analyses because adipose tissue produces and releases pro- and anti-inflammatory factors (Fontana et al., 2007). Controlling for BMI, age was not significantly correlated with any inflammatory marker, rs<|.231| ps>.141. TNF-α was the only marker that significantly differed by sex such that males had higher levels, $t(44)=2.296$, $p=.026$, $M_{female}=-.324$, $SD_{female}=.715$, $M_{male}=.324$, $SD_{male}=1.147$, 95% CI[.079, 1.215].

Of the participants for whom inflammation data were collected, 39.13% chose Path A ($n=18$, 7 females, $M_{age}=15.778$, $SD=1.166$, range 14-18 years) and 60.87% chose Path B ($n=28$, 16 females, $M_{age}=15.893$, $SD=1.133$, 14-18 years). Controlling for BMI, IL-6 was associated with perseverance decisions such that individuals who persevered had higher levels of IL-6 (Figure 4.2), Estimate=.933, $SE=.412$, $z=2.266$, $p=.024$. IL-6 was also significantly associated

with participant report of whether they chose their path because it was more or less difficult, controlling for BMI, Estimate=.996, *SE*=.425, *z*=5.481, *p*=.019. Participants with higher IL-6 also reported reduced lack of premeditation, Estimate=-.126, *SE*=.060, *t*=-2.092, *p*=.043.

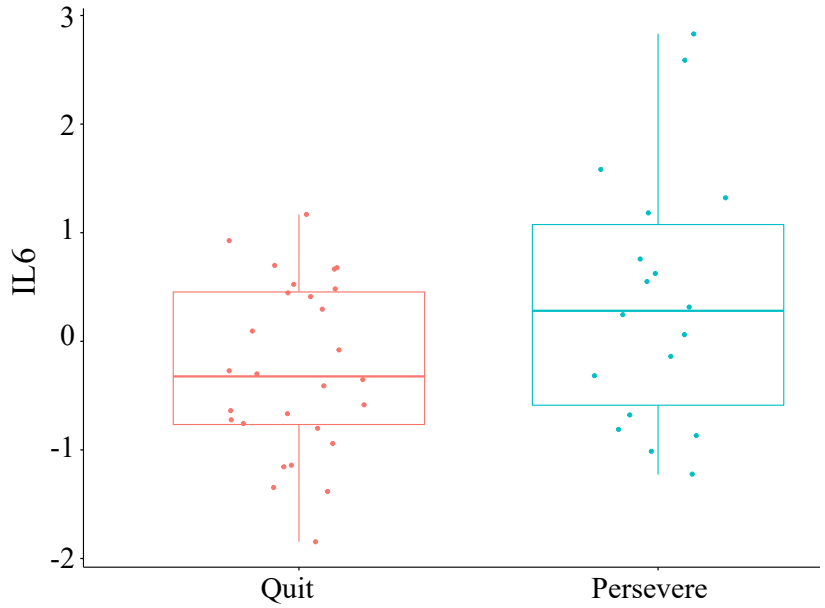


Figure 4.2. Boxplot distribution of log transformed, z-scored IL-6 concentration values by perseverance decision.

IL-6 was negatively associated with activation in the insula in response to negative versus positive feedback (Figure 4.3): left insula Estimate=-12.946, *SE*=6.138, *t*=-2.109, *p*=.041; right insula Estimate=-13.541, *SE*=4.488, *t*=-3.017, *p*=.004; bilateral insula (pictured) Estimate=-13.264, *SE*=4.591, *t*=-2.889, *p*=.006. The insula – inflammation association held controlling for perseverance but did not interact with perseverance decisions. In this sample (*n*=46) insula activation was negatively associated with perseverance Estimate=-.024, *SE*=.012, *z*=4.330, *p*=.037, consistent with findings from the larger sample (see Chapter 1). No associations were significant between IL-6 and neural response to reward.

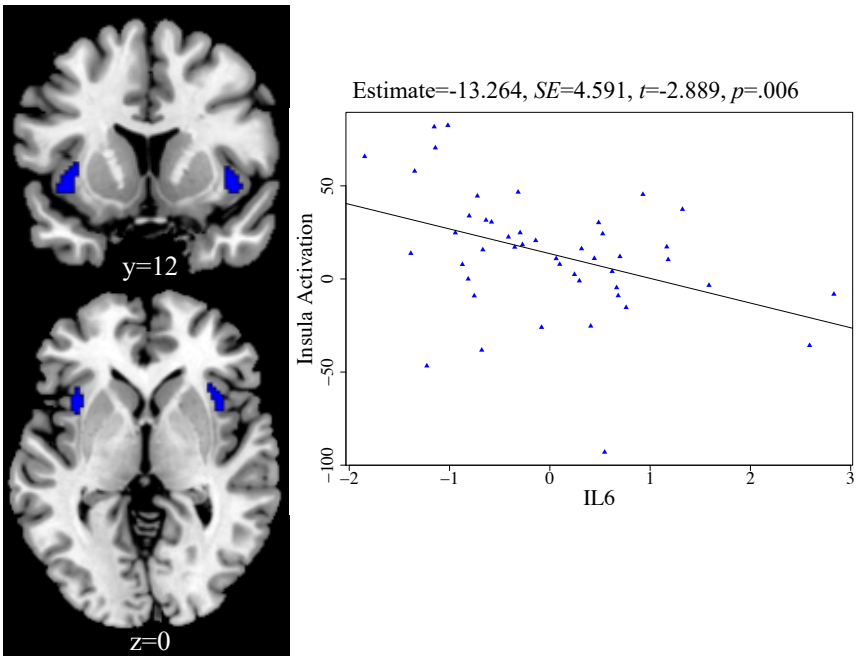


Figure 4.3. IL-6 was negatively associated with activation in response to negative versus positive feedback in the bilateral insula (blue).

TNF-α was negatively associated with activation in the left dlPFC and mPFC in response to positive feedback versus monetary reward receipt (Figure 4.4): left dlPFC Estimate=-131.660, *SE*=40.240, *t*=-3.272, *p*=.002; mPFC Estimate=-85.780, *SE*=38.290, *t*=-2.240, *p*=.030. These associations held controlling for sex, which was significantly associated with TNF-α. TNF-α interacted with perseverance decision to predict mPFC activation in response to positive feedback versus monetary reward receipt, such that there was no significant association for participants who quit but a negative association for those who persevered (Figure 4.5): $\text{Estimate}_{\text{interaction}}$=-244.370, $SE_{\text{interaction}}$=121.910, $t_{\text{interaction}}$=-2.004, $p_{\text{interaction}}$=.052. The interaction and dlPFC activation main-effect association remained significant when removing one outlier with a TNF-α z-score of greater than 5 (*n*=45): left dlPFC Estimate=-191.411, *SE*=65.893, *t*=-2.905, *p*=.006; interaction Estimate=-278.390, *SE*=137.190, *t*=-2.029, *p*=.049.

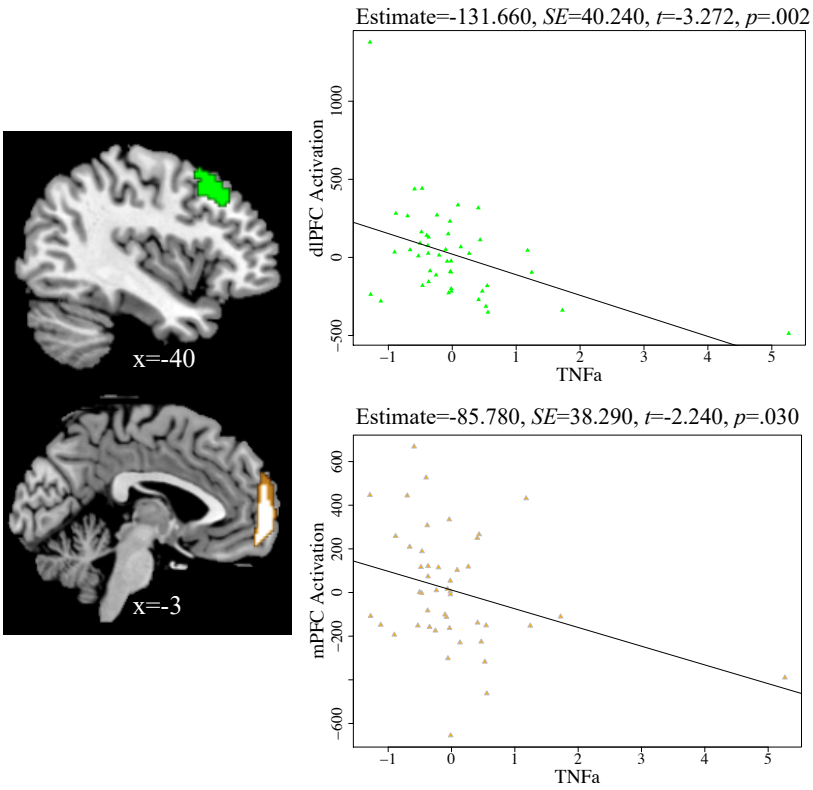


Figure 4.4. TNF-α was negatively associated with activation in response to positive feedback versus monetary reward receipt in the left dorsolateral prefrontal cortex (dlPFC, green) and medial prefrontal cortex (orange).

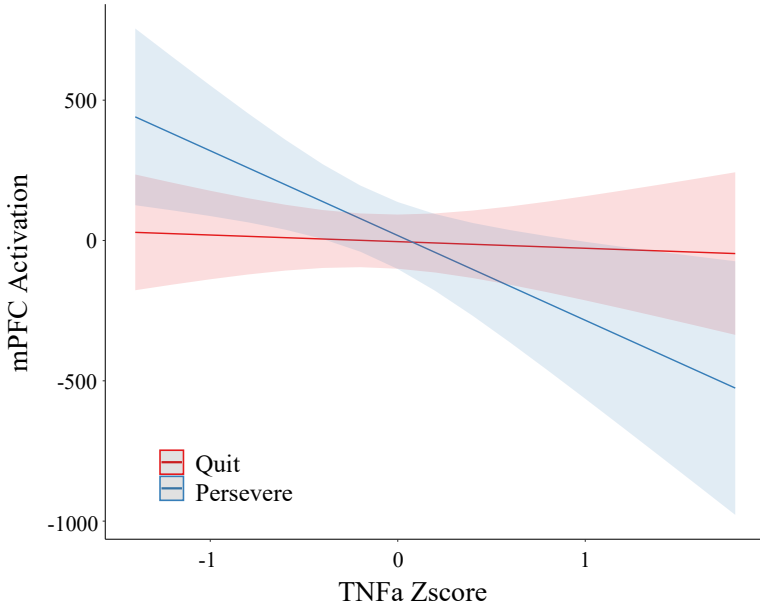


Figure 4.5. TNF-α X perseverance decision interaction associated with medial prefrontal cortex (mPFC) activation in response to positive feedback versus monetary reward receipt.

IL-8 was positively associated with activation in the ACC in response to negative versus positive feedback, Estimate=14.366, *SE*=5.792, *t*=2.481, *p*=.017 (Figure 4.6). The ACC – IL-8 association held controlling for perseverance but did not interact with perseverance decisions.

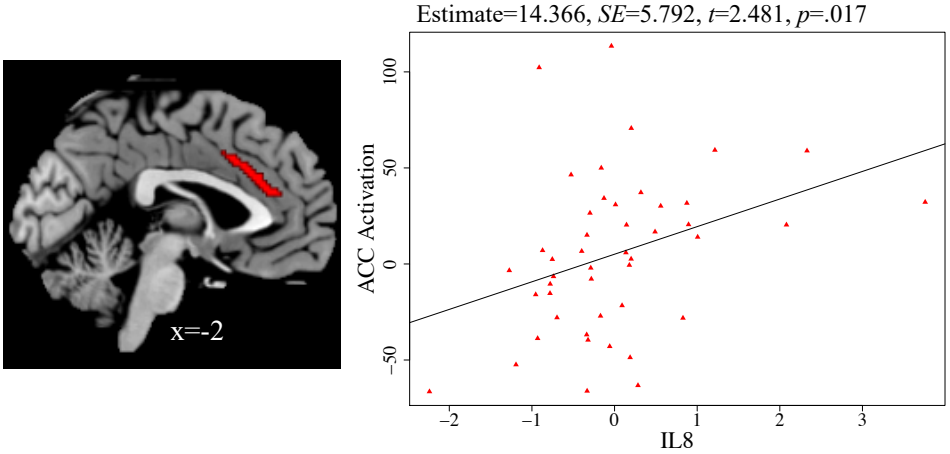


Figure 4.6. IL-8 was positively associated with activation in response to negative versus positive feedback in the anterior cingulate cortex (ACC, red).

Impulsivity

Impulsivity data were collected for 96 participants (59 females, M_{age}=18.469, *SD*=3.195) as indexed by the self-report UPPS-P Impulsive Behavior Scale (Whiteside & Lynam, 2001). Average scores and correlations are provided in Table 4.2.

Table 4.2. Descriptive statistics and correlations for the UPPS-P scale.

Scale	Mean (*SD*)	1 corr	2 corr	3 corr	4 corr	5 corr
1. Negative urgency	2.220 (.537)	—				
2. Lack of premeditation	1.892 (.391)	.204*	—			
3. Sensation seeking	2.780 (.598)	.122	.179†	—		
4. Lack of perseverance	1.979 (.447)	.413***	.319**	-.020	—	

5. Positive urgency	1.864 (.563)	.672***	.062	.316**	.292**	—

Note: Possible min=1, possible max=4. *p<.05, **p<.01, ***p<.001, $^{\dagger}p$<.10. n=96

Of the participants who completed the UPPS-P (n=96), 40 (41.667%) chose to persevere and 56 (58.333%) chose to quit. Lack of premeditation differed by perseverance decision such that individuals who persevered had lower scores reflecting more deliberative thinking, $t(94)=1.928$, $p=.057$.

Impulsivity and age. Age was significantly correlated with lack of premeditation, $r(96)=-.294$, $p=.004$, and lack of perseverance, $r(96)=-.216$, $p=.035$, such that younger participants scored higher on both subscales. Age and lack of premeditation interactions were not significant predictors of perseverance, $\text{Estimate}_{\text{interaction}}=.178$, $SE_{\text{interaction}}=.178$, $z_{\text{interaction}}=.999$, $p_{\text{interaction}}=.318$. Age and lack of perseverance interactions were not significant, $\text{Estimate}_{\text{interaction}}=-.029$, $SE_{\text{interaction}}=.168$, $z_{\text{interaction}}=-.175$, $p_{\text{interaction}}=.861$.

Impulsivity and sex. Positive urgency significantly differed by sex, $t(94)=2.607$, $p=.011$, $M_{\text{female}}=1.749$, $SD_{\text{female}}=.503$, $M_{\text{male}}=2.048$, $SD_{\text{male}}=.613$, such that males scored higher. Sex and positive urgency interactions were marginally significantly associated with perseverance, $\text{Estimate}_{\text{interaction}}=-1.473$, $SE_{\text{interaction}}=.831$, $z_{\text{interaction}}=-1.773$, $p_{\text{interaction}}=.076$, such that males were more likely and females were less likely to persevere at high levels of positive urgency.

Impulsivity and neural response. Greater lack of premeditation was associated with increased neural response to negative versus positive feedback in the ACC, insula, and dlPFC (Figure 4.7): ACC Estimate=27.150, SE=11.590, t=2.342, p=.021; left insula Estimate=25.510, SE=11.470, t=2.224, p=.029; right insula Estimate=25.150, SE=10.860, t=2.316, p=.023; bilateral insula (pictured) Estimate=27.320, SE=10.130, t=2.500, p=.014; left dlPFC

Estimate=23.750, *SE*=15.250, *t*=1.557, *p*=.123; right dlPFC Estimate=41.990, *SE*=16.220, *t*=2.589, *p*=.011; bilateral dlPFC (pictured) Estimate=34.090, *SE*=14.580, *t*=2.339, *p*=.021.

Age was negatively associated with activation in the insula and ACC to negative feedback (Chapter 3). Lack of premeditation significantly mediated age associations with neural response to feedback in the insula (bilateral tested), *n*=96, R^2=.088, *F*(2,93)=4.483, *p*=.014, indirect effect=-.731, SE=.412, 95% CI[-1.637, -.050], ab_{cs}=-.059, *SE*=.036, 95% CI[-.139, -.004]. The indirect effect of age through lack of premeditation was not significant for the ACC.

Lack of premeditation did not interact with perseverance decision to predict neural response to feedback, but lack of perseverance and neural response associations remained significant controlling for perseverance decision. No associations were significant between lack of premeditation and neural response to reward.

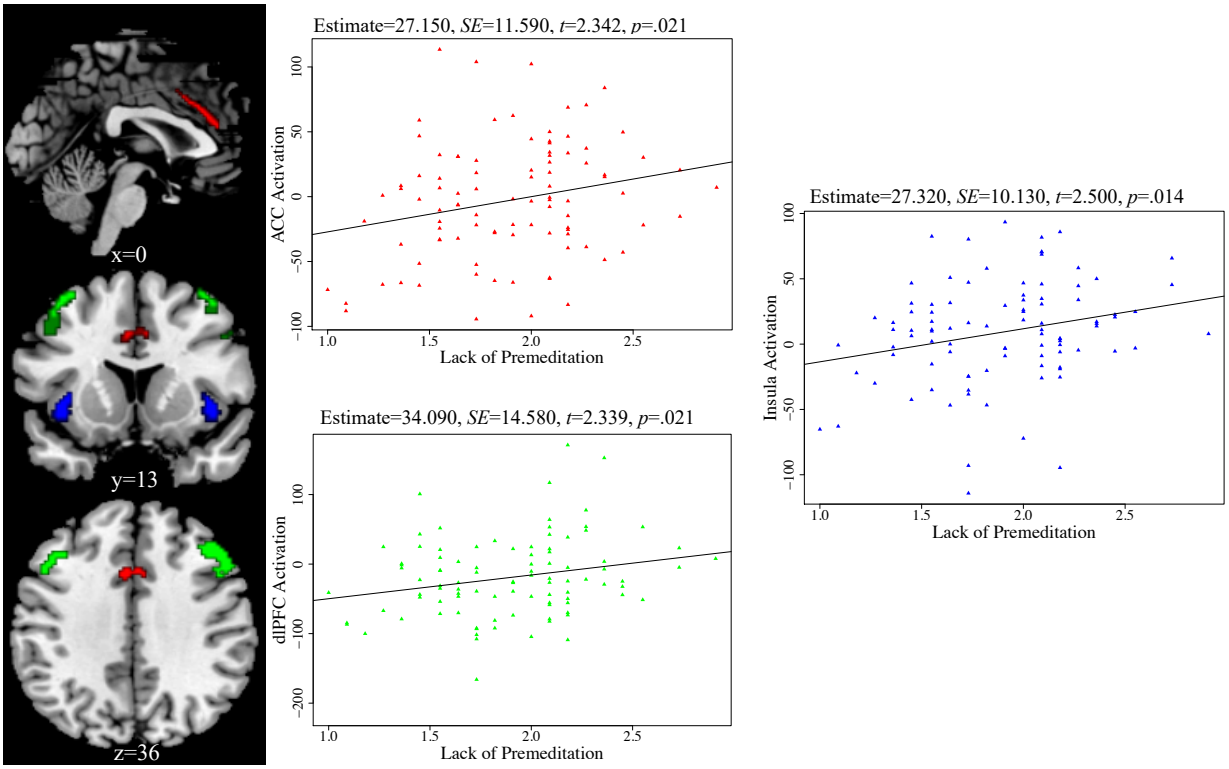


Figure 4.7. Lack of premeditation was positively associated with activation in response to negative versus positive feedback in the anterior cingulate cortex (ACC, red), bilateral insula (blue), and bilateral dorsolateral prefrontal cortex (dlPFC).

Sensation seeking was positively associated with greater activation in the striatum in response to negative versus positive feedback (Figure 4.8): left striatum Estimate=13.438, *SE*=6.776, *t*=1.983, *p*=.050; right striatum Estimate=19.780, *SE*=6.880, *t*=2.875, *p*=.005; bilateral striatum (pictured) Estimate=16.710, *SE*=6.640, *t*=2.516, *p*=.014. The striatum-sensation seeking association held controlling for perseverance but did not interact with perseverance decisions. No associations were significant between sensation seeking and neural response to reward.

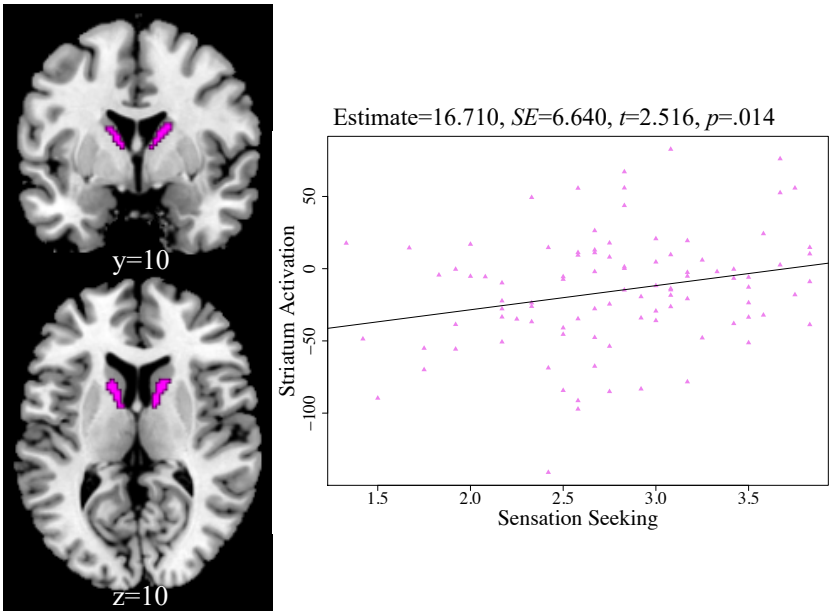


Figure 4.8. Sensation seeking was positively associated with activation in response to negative versus positive feedback in the bilateral striatum (violet).

Positive urgency was positively associated with response to negative versus positive feedback in the mPFC (Figure 4.9a), Estimate=30.490, *SE*=14.400, *t*=2.118, *p*=.037. The mPFC-positive urgency association held controlling for perseverance but did not interact with perseverance decisions. Positive urgency was negatively associated with right insula response to

positive feedback versus monetary reward (Figure 4.9b), Estimate=-61.090, *SE*=28.110, *t*=-2.173, *p*=.032.

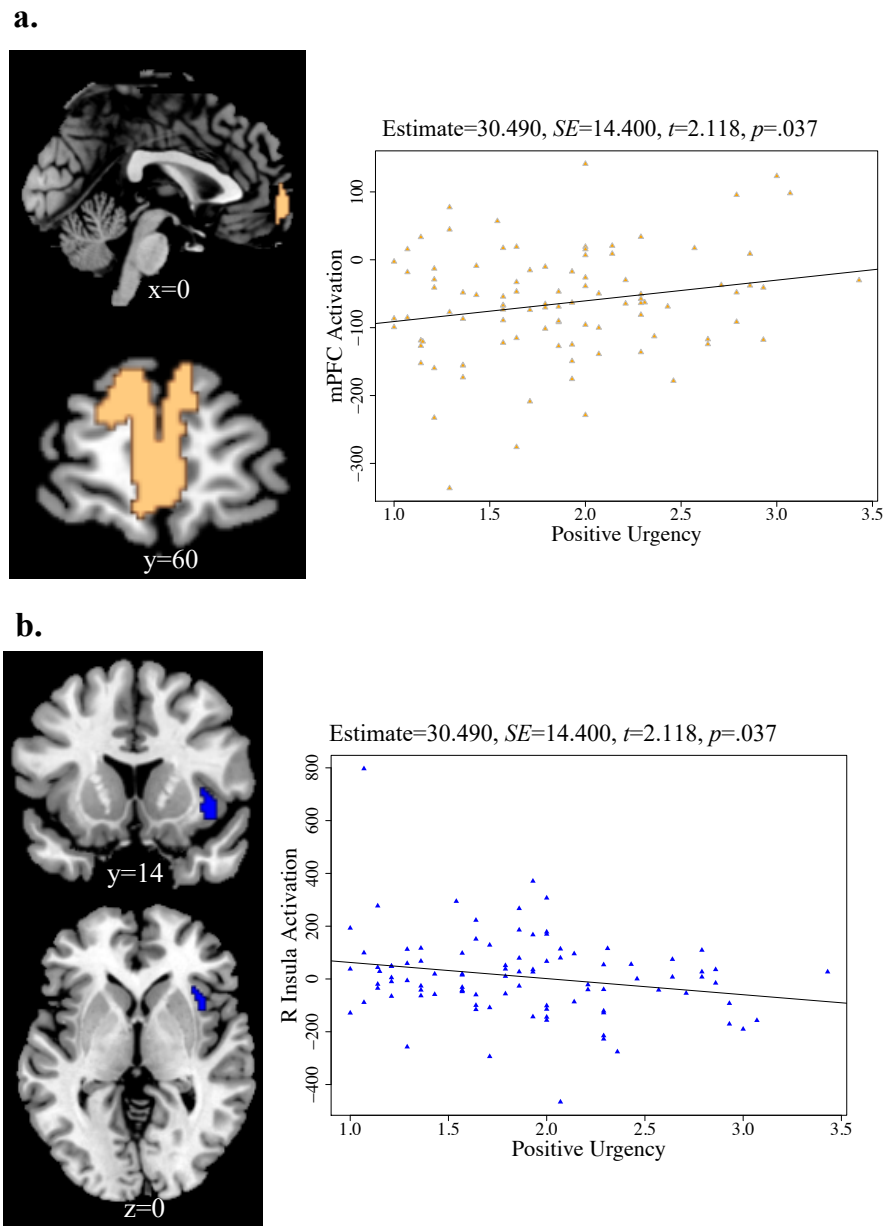


Figure 4.9. Positive urgency was **(a)** positively associated with activation in response to negative versus positive feedback in the medial prefrontal cortex (mPFC; orange); and **(b)** negatively associated with activation in response to positive feedback versus monetary reward receipt in the right insula (R insula; blue).

Lack of perseverance and negative urgency were not significantly associated with neural response to feedback or reward.

Discussion

This study examined several individual differences hypothesized to relate to perseverance as well as neural response to feedback and reward. Male sex, higher IL-6, and more deliberative thinking (decreased lack of premeditation) were associated with perseverance. Associations with neural activation lend insight into facets of the Perseverance Task that can inform future research and enrich understanding of how individual difference manifest at the neural level.

Intriguingly, higher concentrations of IL-6, a pro-inflammatory cytokine, were associated with perseverance as opposed to quitting. Reduced insula activation in response to negative versus positive feedback was also associated with higher IL-6. Stress exposure can stimulate a neuroendocrine response that increases inflammation and affects perception of threat and reward cues in the environment (Hollon et al., 2015; Steptoe et al., 2007). Extensive work links inflammation with depression and dysregulation of neural systems responsive to reward (Dantzer et al., 2008; Felger et al., 2016; Miller & Raison, 2016). Administration of cytokine inducers (including endotoxins) also results in blunted reward sensitivity in humans (Eisenberger et al., 2010). However, recent work using the Effort Expenditure for Rewards Task, a task that indexes willingness to exert physical effort for higher monetary reward, demonstrates stress-induced increases in IL-6 are associated with increased selection of high effort trials, particularly those with low reward probability (Boyle et al., 2020). During intrinsically motivated decision-making, no extrinsic reward is provided, more closely approximating a low reward probability context. Additionally, hedonic reward-sensitivity was not the main mechanism that motivated perseverance in the Perseverance Task. Thus, the relation between inflammation and reward

motivation may be more complex than prior work suggests, particularly for intrinsic motivation. Additionally, a key purpose of immune response is to protect an organism from environmental threats, including socioemotional stressors like threats to an individual's self-esteem (for a review, Allen et al., 2014). Negative feedback may act as such a threat, and may interact with factors like social support and identity not assessed in this work (Destin, 2019). At a neural level, recent work using randomized placebo and endotoxin administration resulted in the endotoxin group exhibiting overall reduced activity in the anterior insula in response to negative, positive, and neutral feedback compared with placebo participants (Muscatell et al., 2016). In that study, endotoxin administration increased responsivity in the ACC and amygdala to negative feedback versus neutral feedback, suggesting functioning of threat circuitry in response to inflammation is not uniform across regions. In this study, IL-6 was negatively associated with insula activation and IL-8 was positively associated with ACC activation in response to negative feedback. IL-8 is also a proinflammatory cytokine, but has a stronger link to adolescent psychopathology than IL-6 (Gariup et al., 2015). The role of IL-8 in psychopathology may account for its positive association with ACC activation in this study, but limitations with sample size and lack of psychiatric assessment caution against strong conclusions. Notably, inflammation in this study was not tested in response to the Perseverance Task but rather prior to any study tasks reflecting baseline circulating levels. Chronic levels of arousal from repeated or extended exposure to stress can reprogram elements of the immune system resulting in higher levels of proinflammatory cytokines, including IL-6 (Miller et al., 2009). It is possible that adolescents who chose to persevere engage with challenge more regularly in everyday life than those who quit. Thus, these findings likely reflect pre-existing inflammatory and neural profiles developed in response to challenge-related stressors.

Greater lack of premeditation, the tendency to act rashly without deliberative thinking, was associated with quitting. Self-report revealed 25% of participants who quit reported reflecting on their decisions with regret (Chapter 2, Table 2.3). Offering participants multiple opportunities to reconsider their decisions may help boost perseverance behavior for participants high in the tendency to act rashly. Older participants reported more deliberative thinking and were also more likely to persevere. Lack of premeditation was associated with increased response in the insula, ACC, and dlPFC to negative versus positive feedback. Emotionally salient content like negative feedback can capture attention and influence task performance. For individuals high in the tendency to act without consideration of the consequences of one's behavior, increased activation in these regions may reflect compensatory recruitment of control-related neural regions in response to negative stimuli (van Holst et al., 2012). Lack of premeditation significantly mediated age – insula associations. Thus, age-related improvements in deliberative thinking abilities accounted for age-related neural differences in response to negative feedback, representing a potential mechanism worthy of further exploration. Future tasks including facets of impulsive and deliberative decision-making will help elucidate how trait impulsivity contributes to neural functioning and perseverance in different contexts.

Males were more likely to persevere than females. Males also reported higher positive urgency on the UPPS-P, indexing impulsive action under extreme positive emotion, but lower striatal response to monetary reward versus positive feedback. Prior work also identifies increased positive urgency among males (Cyders, 2011), but no significant sex differences in reward sensitivity (Cross et al., 2011). Striatal response to monetary reward in this study may reflect motivation disparities, which have been shown to mediate sex-related differences in neural response to reward (Alarcón et al., 2017). All trials on the monetary reward game resulted

in reward, with relatively higher and lower reward trials randomly interspersed. Additionally, this study did not include an index of impulsive reward seeking, which shows more reliable sex differences (Cross et al., 2011), but rather a calculated decision to continue engagement despite challenge.

TNF-α was associated with reduced activation in the dlPFC and mPFC in response to positive feedback versus monetary reward. Perseverance decisions moderated the TNF-α – mPFC association such that only participants who persevered showed a negative association. Like IL-6, TNF-α is a pro-inflammatory cytokine and rodent work identifies increased TNF-α in the mPFC as a potential contributor to anhedonia susceptibility (Fang et al., 2019). mPFC functioning, including increased connectivity with the striatum, relates to self-attribution and can represent problematic integration of negative information into one's motivational states after processing feedback, contributing to depression and internalizing symptoms (Hanson et al., 2018; Marchetti et al., 2012). In the present study, it is possible that reductions in mPFC activation after positive feedback for perseverers high in TNF-α contributed to perseverance by dampening the impact of positive reinforcement and encouraging participants to seek additional positive feedback on the mental rotation task.

Several limitations should be noted. Inflammation measures were only collected in adolescents, preventing conclusions about developmental differences. Smaller sample size also tempers the ability to make broad conclusions about associations between inflammation and neural functioning and behavior. How inflammation and neural functioning relate during development is a topic of increasing interest. However, little is known about longitudinal implications of circulating cytokines in adolescence, and the associations observed in this study may not hold in a broader age-range. Although impulsivity was hypothesized to have relevance

for perseverance, surprisingly few subscales related to perseverance decisions. The focus on intrinsic motivation may have reduced the associations identified in this study. Lack of mediation effects limit identification of individual difference mechanisms facilitating perseverance using these measures.

Male sex, higher IL-6, and deliberative thinking were associated with perseverance. Increased IL-6 and more deliberative thinking were both associated with reduced insula activation to negative versus positive feedback. Deliberative thinking abilities accounted for age-related declines in insula response to negative feedback. These findings point to insular functioning as an important contributor to perseverance. The brain is responsive to environmental input and future work should seek to elucidate additional factors that aid in regulating insula response to potentially aversive stimuli like negative feedback. This study identifies inflammatory and neural profiles that have likely developed over time in response to engaging with and overcoming the stress of performance challenges, making an important contribution to understanding factors that motivate some individuals to persevere.

Chapter 5

General Discussion

Significance and contributions

Across all ages, challenge is a normative part of daily life. How one chooses to engage with challenge has significant implications for developmental outcomes and can lead to adaptive and maladaptive behavior. When a genuine threat is present, for example in the presence of danger, avoidance can be adaptive. However, when threat is absent or uncertain, avoiding challenge can prevent learning and amplify anxiety about unknown consequences whereas engaging with challenge can promote feelings of self-efficacy and increase effort (Barlow, 2002; Locke & Latham, 2002). Intrinsic motivation is a critical facet of engaging with challenge in daily life. Even when future external benefits may be possible, reward contingencies are not always readily discernible, thus requiring intrinsic motivation to propel action. Despite the rapid increase in neuroscientific investigations of goal-oriented behavior, the study of intrinsic motivation remains relatively sparse. This dissertation elucidated neural, behavioral, and biological substrates of intrinsically motivated perseverance. Study 1 established that individuals who persevere engage neural systems that track stimulus value, and adjust behavior and recruitment of neural resources on trials after receiving negative feedback to a greater extent than those who quit. Study 2 revealed perseverance differences between adolescents and adults, an effect associated with younger participants requiring greater dlPFC regulation of fronto-insular regions in response to negative feedback to persevere. Study 3 suggests psychophysiological stress systems may be altered in individuals who engage in perseverance, identifying inflammation differences by perseverance decision. Study 3 also points to deliberative thinking as a facilitator of perseverance and identifies several neural systems that are differentially evoked in response to performance feedback as a function of premeditative thinking.

Returning to the conceptual model from Chapter 1 (Figure 1.1), this dissertation adds to prior work indicating situational factors like performance feedback influence motivation calculations that result in perseverance decisions. Converging neural and self-report evidence support the proposition that motivation to achieve success facilitated perseverance in some whereas motivation to avoid continued failure led other participants to quit. Demographic, biological, and personality factors also related to perseverance, but added additional potential pathways to the model: person-level factors were directly linked to functioning of neural systems implicated in evaluation of performance feedback. The present studies were not designed to assess whether person-level factors affected neural encoding of situational factors indirectly via motivation calculations or whether they were directly linked, but data support the model assumption that perseverance behavior reflects a motivational balance between success attainment and failure avoidance. Study 1 revealed the importance of valuing feedback for behavior modification and perseverance. The theoretical model in Chapter 1 proposed feedback would modify goal value and attainment expectancy, but it is possible that these motivational components influenced perception of feedback or that bidirectional pathways exist. Future work more directly manipulating these features of the Perseverance Task would be instrumental in illuminating the causal pathways through which these components function.

Utilizing fMRI, this dissertation brings to light processes that underlie intrinsic motivation. The Perseverance Task was designed to identify neural differences between individuals who persevered and those who quit in response to two situational factors thought to influence motivation: performance feedback and reward. Accuracy and feedback received did not differ by perseverance decision nor did they differ by age. Thus, external factors did not signal to participants who quit that the task was less achievable than as indicated to those who

persevered. Unattainable challenges have been shown to increase perceived stress, and quitting in the face of an insurmountable challenge may be adaptive (Wrosch et al., 2003). In the present work, there was nothing to indicate the challenge was insurmountable, eliminating speculation that quitting was adaptive. Rather, differential activation of the mPFC by participants who persevered suggests appraisal of the motivational value of feedback is a key contributor to perseverance in the face of cognitive challenge.

For participants who persevered, the ventromedial PFC (vmPFC) was activated in response to positive feedback versus monetary reward and in response to positive versus negative feedback. These findings further strengthen the conclusion that intrinsically motivated perseverance is supported by stronger value signals in response to informative reward (i.e., positive performance-related feedback). These value signals in turn likely facilitate projection of future potential for success. According to the somatic marker hypothesis, decision-making is influenced by bioregulatory processes including emotional processing. A key tenant of this hypothesis is that the inability to make advantageous decisions is attributed to a defect in emotion signaling conveying action-consequence contingencies (Bechara & Damasio, 2005). Patients with vmPFC damage are characterized by disadvantageous decision-making guided primarily by immediate consequences rather than projecting possible future consequences (e.g., Bechara et al., 2000). The vmPFC triggers somatic signals associated with affective states generated by hypothetical or recalled events. In the context of the Perseverance Task, activation of the vmPFC in response to positive feedback may reflect a better ability to project the emotional state of future task success on the part of perseverers.

Theories of motivation assert that extrinsic motivation is generated through environmental contingencies and intrinsic motivation is generated through inherent processes

like need for autonomy (Ryan & Deci, 2000). However, this dissertation demonstrates neural perception of environmental stimuli also underpin intrinsic motivation. Internal signals generated in response to environmental stimuli serve to guide future behavior by marking a given stimulus with an emotional tag that links the stimulus to a previously encountered state indicative of punishment or reward. These signals act to warn the individual against previously encountered disadvantageous actions (Damasio et al., 1991). As seen in self-report results from Study 1, participants who quit had aversive emotional responses to negative feedback. Participants who quit also evinced greater insula activation in response to negative feedback, and the insula is a key brain structure for processing emotion and interoceptive information (Gasquoine, 2014). Thus, intrinsically motivated behavior on the Perseverance Task was differentiated by emotional and neural response to situational factors signaling to those who quit that continued engagement might result in additional punishment.

The brain and body are responsive to the environment and as such engaging with challenge may set the stage for motivating future perseverance. Study 2 demonstrated perseverance was different across adolescents and adults and that older participants reported enjoying challenge more than younger participants. This may be due to older participants having more experience with challenge and more diverse challenge experiences over time. Alternatively, as individuals transition out of adolescence, they may less frequently engage with challenge in a "testing" context, resulting in older participants viewing the Perseverance Task as an enjoyable game rather than an evaluative stressor. In Study 3, older participants also reported greater deliberative thinking, which mediated the negative age association with insula activation in response to negative feedback. Heightened insular response in younger participants likely reflects a more emotion-driven response to negative stimuli. In line with this interpretation,

younger participants required more dlPFC regulation of fronto-insular regions to persevere, suggesting younger participants required regulatory resources that may not be as established to engage with challenge. Study 3 also established that adolescents who persevered had higher levels of the pro-inflammatory cytokine IL-6. Arousal from repeated exposure to psychosocial stressors like challenge can condition the immune system resulting in the inflammatory profiles observed in this work. Together, these findings support a biological basis of perseverance and call for future work to determine whether and to what extent perseverance is malleable.

Limitations and future directions

According to the biopsychosocial model of challenge and threat, the evaluation of personal resources and situational demands is critical in determining whether individuals perceive a situation as a challenge or a threat. Performance feedback during the Perseverance Task could be perceived as a challenge or a threat, and self-report reveals that those who chose to persevere did so with motivation to pursue challenge. However, this Task was not designed to test other possible situational factors that may influence intrinsic motivation. For example, fatigue or cognitive load may play a role in assessment of personal resources available for continued effort expenditure. Additionally, resource availability and task demand change across development. This dissertation included participants ranging in age from 14 to 30, but an investigation including younger children and pre-adolescents may reveal different developmental trajectories of perseverance. For example, younger children could demonstrate a further reduction in perseverance suggesting a linear trend across development. However, non-linear trends may also be observable and attributable to different factors than those observed in this work like age-related positivity bias or non-linear neural maturation. The Perseverance Task was designed to reduce performance disparities among participants in order to disaggregate

competency from perseverance. However, predictions of future success are relevant for motivation as are estimations of future effort needed to achieve success (e.g., Sullivan-Toole et al., 2017). Additional work is needed to determine whether the neural systems tracking feedback are also processing competency estimations and whether affective response to feedback fluctuates with task demands. Although the inflammation findings are intriguing and a novel step in understanding brain-body-behavior associations, the inflammatory assays in this study were collected at the start of the study and do not reflect response to acute task manipulations. It would be fruitful to further probe how existing inflammatory profiles change with stress induction and how that change relates to behavior. Lastly, group analyses in this dissertation are based on a single decision to persevere or quit. This design choice was made to approximate real-world decisions like dropping a challenging course in college or quitting a job after a negative evaluation, where consequences shift the individual's future trajectory. However, this precludes conclusions about decision-making stability and whether there was unobserved heterogeneity in decision-making among participants in this study. Offering an "opt-in" opportunity in future work may elucidate an additional profile of behavior such that some individuals initially quit but subsequently re-engage.

A critical avenue for future inquiry involves social context. Individuals may perceive difference situations as a threat versus challenge depending on the context, even if the same motivated behavior is required. Social comparison is particularly salient during adolescence and has previously been linked to alterations in motivated behavior. Additionally, early life experiences influence the development of neural systems that underpin threat perception. Thus, social factors, both in the immediate context and during earlier development, are likely relevant for perseverance. Prior social experiences are also likely pertinent for understanding the

development of perseverance behavior. Neural circuitry important for processing and regulating emotional response to threat demonstrates altered functioning in individuals as a function of early caregiving experiences. Thus, early adversity is an important target for elucidating individual differences in perseverance. Additionally, perseverance is a potentially malleable mechanism underlying adversity-related achievement gaps. Future modifications to the present paradigm can further elucidate antecedents and outcomes of perseverance. First, motivation for social feedback may differ from performance feedback with respect to a cognitive challenge as examined in the present work. Second, social challenges like persevering to make new friends may be viewed differently from cognitive challenges. Lastly, social support may buffer against and social evaluation may enhance the salience of negative feedback, contributing to within-person differences in perseverance. Although no single study can assess all elements of human decision making due to its vast complexity, the current dissertation provides a valuable initial step and strong foundation for future work.

Conclusions

Adolescents and young adults face a myriad of novel situations every day. Some of these situations pose challenges. Persevering through challenge can lead to an expansion of experiences that aids personal and professional growth. Engaging with challenge can also lay the foundation for future perseverance by instantiating biological and neural responses that help mount a motivated response to difficulty. Results of this dissertation indicate several factors influence whether an individual perseveres including encoding of performance feedback at the neural level, sensitivity to non-monetary reward, how responsive biological systems are to psychosocial stressors, and developmental factors like age and deliberative thinking. These

findings identify several access points through which intrinsic motivation may be enhanced to facilitate perseverance in the face of failure.

Appendix A

Perseverance Task Questionnaire

PP#: _____

1. In the **mental rotation task**, which path did you choose?

   PATH A (more mental rotation): **YES** **NO**

   PATH B (NO mental rotation): **YES** **NO**

2. Why did you choose that path?

   _____

   _____

   _____

3. Did you choose that path because it was **MORE** or **LESS** difficult? (circle one)

4. Which types of mental rotations were more enjoyable? (circle one)

   THE ONES I GOT CORRECT or **THE ONES THAT WERE CHALLENGING**

5. Did you choose the path because you thought it was the "right" thing to do or because of the experimenter? **YES** **NO**

   a. If yes, please explain

   _____

   _____

   _____

6. If you chose PATH A did you switch paths at any point? **YES** **NO**

   a. If yes, why did you switch paths?

   _____

   _____

   _____

7. Which was more enjoyable (circle one)

   EARNING MONEY or **DOING MENTAL ROTATIONS**

PP#: _____

8. What was the most enjoyable part of the **mental rotation and cups** task?

9. What was the least enjoyable part of the **mental rotation and cups** task?

10. How did you feel when you got a mental rotation answer correct?

11. How did you feel when you got a mental rotation answer incorrect?

12. How did you feel earning money during the cups game?

13. How did you feel when you selected your path?

THANK YOU!!!!!

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