MOTIVATIONAL INFLUENCES ON FEEDBACK PROCESSING DURING

LEARNING

by

SAMANTHA DEPASQUE SWANSON

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Professor Elizabeth Tricomi

and approved by

Dr. Mauricio Delgado

Dr. Luis Rivera

Dr. Jennifer Mangels

Dr. Elizabeth Tricomi

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ABSTRACT OF THE DISSERTATION

Motivational Influences on Feedback Processing during Learning

By Samantha DePasque Swanson

Dissertation Director

Elizabeth Tricomi

Feedback is a valuable tool used by educators, clinicians, and others to facilitate learning. However, the extent to which feedback shapes changes in knowledge and behavior may be influenced by the affective salience of the feedback, which can vary depending on one's goals and expectations for learning. Using functional magnetic resonance imaging (fMRI), I conducted three experiments to examine the role of the striatum as a potential neural mediator of such motivational influences on learning. This dissertation unites two disparate lines of research: the cognitive neuroscience of reinforcement learning and the social psychology of achievement motivation, to uncover the neural processes by which achievement goals influence learning. Converging evidence from behavioral and cognitive neuroscience has characterized the striatum as part of a learning system that uses positive and negative consequences to reinforce advantageous behaviors. Its responses to positive and negative outcomes are modulated by factors that increase or decrease the motivational significance of the outcomes, making it a prime candidate for biasing learning on the basis of achievement motivation. My three dissertation studies used behavioral methods inspired by the motivation literature to investigate the motivational effects of expectations, beliefs, and values on the striatal processing of performance-related feedback during learning. I observed that learning can be enhanced or diminished through the manipulation of motivationally relevant expectations, values, and beliefs that either increase or attenuate striatal responses to feedback.

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Chapter One: General Introduction

Educators, prevention specialists, and psychotherapists share a common goal: to teach effective, adaptive ways of thinking and behaving. However, old habits and thoughts can obstruct learning if individuals are not motivated to engage in new behaviors and thinking patterns. Motivation is thus a crucial factor in designing effective pedagogical and therapeutic techniques. The focus of my dissertation work is on achievement motivation, and how personality and contextual factors interact to influence neural and behavioral responses to feedback during learning. This research has focused on feedback-based learning, in which information is learned through trial and error responding, with feedback about performance accuracy after each response.

THE STRIATUM & FEEDBACK-BASED LEARNING

Feedback-based learning is subserved at least in part by the basal ganglia, an evolutionarily ancient brain region that is involved in the control of both learned and unlearned actions (Kirchhoff, Wagner, Maril, & Stern, 2000). As the input region for the basal ganglia, the striatum receives projections from throughout the cortex as well as from midbrain dopaminergic neurons, which produce phasic activation responses to prediction error, or the discrepancy between expected and actual rewards (Schultz, 1998). Human neuroimaging research has revealed that the striatum is sensitive to rewards, with increases in activation following rewards and decreases following punishments (Delgado, 2007). Such reward responses in the striatum have been experimentally linked with dopaminergic activity (e.g., Pessiglione, Seymour, Flandin, Dolan, & Frith, 2006; Schott et al., 2008), and correlate with behavioral evidence of reward-based learning

(Schonberg, Daw, Joel, & O'Doherty, 2007). Lesions or illness that cause damage to the striatum are known to impair feedback- and reward-based learning, indicating that this region plays a critical role in learning to predict and pursue rewarding outcomes (e.g., de Borchgrave, Rawlins, Dickinson, & Balleine, 2002; Shohamy et al., 2004). As a result of its involvement in both reward prediction and action control, the striatum is positioned to play a crucial role in the modulation of behavior by motivation.

While lateral parts of the striatum have been implicated in habitual responding (executing well-learned action plans in response to a cue or triggering stimulus), the medial striatum, which includes the caudate nucleus, is required for goal-directed behaviors that are sensitive to whether the outcome is valued or desirable at a given moment (Balleine & O'Doherty, 2010). The study of goal-directed behavior has typically used primary or secondary reinforcers, such as food or money. However, in humans, goals can be more abstract, and activation in the striatum tracks the valence of performance-related feedback even when it is not accompanied by such extrinsic rewards (e.g., Daniel & Pollmann, 2010; Satterthwaite et al., 2012; Tricomi, Delgado, McCandliss, McClelland, & Fiez, 2006). Learning can be a goal in itself, and individual differences in achievement goals, such as the goal to outperform one's peers, may imbue performance feedback with varying levels of reward value in an achievement context. The goal of these dissertation studies was to investigate the way that variations in achievement goals and contextual variables might interact to influence the striatal responses to performance-related feedback.

ACHIEVEMENT MOTIVATION

Goals channel motivation toward pursuit of a particular objective, and have thus

been defined as cognitive representations of a future state that an organism wants to achieve or avoid (Elliot & Niesta, 2009). The types of goals that individuals adopt can be a function of stable traits or predispositions as well as environmental factors, such as the type of academic setting in which achievement goals are pursued. Goals, as distinct from motives, are viewed as contextually sensitive, situation-specific objectives, while motives are defined as socially or experientially acquired preferences that remain stable over time and across different contexts (Elliot & Niesta, 2009). Since goals are considered the more proximal cause of behavior, much of the achievement motivation literature focuses on patterns of goal pursuit rather than individual differences in underlying motives. Nonetheless, established links between achievement goal orientations and underlying motives allow researchers to explore individual differences in temporally stable patterns of goal pursuit (Elliot & Church, 1997). People who adopt different goals may feel more or less committed to a particular outcome, thus influencing the energy or vigor with which they will expend effort to attain it. This might then affect the value attributed to signals of goal attainment. For example, a student who is motivated to earn higher grades than his classmates might work harder in his classes and find positive feedback from his teacher more rewarding than a student who is merely trying to get passing grades so that she can remain on the track team. The present research focuses on the impact of different types of achievement goals on neural processing reflecting the value which is attributed to positive and negative feedback during learning.

ACHIEVEMENT GOAL SUBTYPES

The achievement goal construct is grounded primarily in the need for competence (Deci & Moller, 2005; Deci & Ryan, 2000). Depending on whether one strives to

demonstrate competence versus improve competence, achievement goals can be subdivided into performance (competence demonstration) versus learning/mastery (competence improvement) goals (Elliott & Dweck, 1988). Performance goals have been associated with poorer outcomes than learning goals, due to responses of helplessness in the face of failure or setbacks (Elliott & Dweck, 1988), although the relation between performance goals and impaired achievement has been inconsistent (Grant & Dweck, 2003; Harackiewicz, Barron, & Elliot, 1998).

Inconsistencies in the effects of performance goals on achievement have been attributed to the way that performance goals are defined: questionnaires assessing performance goals sometimes emphasize performance in relation to other people, or they can emphasize the need to validate or confirm one's abilities. Performance goals can therefore be classified as either normative or ability goals, based on the type of competence that one wishes to demonstrate: people who adopt normative goals strive to perform well relative to other people, while those with ability goals wish to perform well to validate or confirm their abilities. Recent research suggests that normative goals (e.g., "My goal in class is to get a better grade than most of the students") are associated with more positive academic outcomes relative to ability goals (e.g., "In school I am focused on demonstrating my intellectual ability"; (Hulleman, Durik, Schweigert, & Harackiewicz, 2008; Hulleman, Schrager, Bodmann, & Harackiewicz, 2010). Normative goals can be viewed as bestowing a competitive orientation that may buffer individuals against the fear of failure that often accompany ability-oriented performance goals (Grant & Dweck, 2003).

THREAT & AVOIDANCE GOALS

Another way to subdivide achievement goals is with respect to whether one seeks to attain a positively valenced outcome (approach goal) or to avoid a negatively valenced outcome (avoidance goal). Performance goals such as those outlined above can be oriented toward approaching good performance or avoiding poor performance. People who are driven by performance-approach goals often achieve more success than those who are driven by performance-avoidance goals, especially in the face of obstacles (Elliot & Church, 1997). For example, in the classroom, performance-approach goals that are directed towards achieving a high level of performance are linked with increased effort, persistence, and exam performance, while performance-avoidance goals that are directed at avoiding appearing incompetent are associated with decreased depth of processing and poorer exam performance (Elliot, McGregor, & Gable, 1999).

Experimental manipulations can induce cognitive appraisals of a task as threatening (Tomaka, Blascovich, Kibler, & Ernst, 1997), which could increase the tendency to interpret negative feedback as punishment and impede learning (Mangels, Butterfield, Lamb, Good, & Dweck, 2006; Mangels, Good, Whiteman, Maniscalco, & Dweck, 2011). Some motivational theories, such as Higgins's theory of regulatory fit, predict that a match between trait orientations (i.e., promotion/prevention goals, which are conceptually similar to approach/avoidance goals) and situational task demands (e.g., rewarding correct responses versus punishing incorrect responses) would result in the most optimal outcomes (e.g., Higgins, 2000); however, research highlighting the aversive nature of avoidance motivation suggests that a threatening context might exacerbate the maladaptive effects of an avoidance goal orientation (Elliot & Niesta, 2009).

EXPECTATIONS & GOALS

Motivated behavior in achievement settings is affected by goals as well as expectations about the likelihood of success (Wigfield & Eccles, 2000). For example, avoidance goals have been linked with low competence expectancies (Elliot & Church, 1997). Expectations for success can reflect beliefs about one's ability as well as contextual factors, such as the perceived difficulty of the goal (Latham & Locke, 1991). In these dissertation experiments, expectations about the task difficulty (Experiment 1) and beliefs about ability (Experiment 3) were manipulated to explore the way that these two types of experimental contexts might interact with individual differences in achievement goal orientation to affect behavioral and neural responses to performance-related feedback.

NEUROSCIENCE OF ACHIEVEMENT MOTIVATION

The neural mechanisms that mediate situational effects on motivation and learning remain unclear, but are likely to involve the striatum, due to its roles in reward processing and feedback-based learning. It is already known that striatal reward responses are sensitive to contextual influences (e.g., Nieuwenhuis et al., 2005), and that individual differences in temperament and achievement orientations can be reflected in brain activity (e.g., Eddington, Dolcos, Cabeza, KR, & Strauman, 2007; Lee, Reeve, Xue, & Xiong, 2012; Spielberg et al., 2012). These results suggest that a wide network of brain regions may be modulated by achievement motivation and its related constructs. However, prior studies of the effects of goals on the brain have focused in large part on the maintenance of cognitive representations of achievement goals, rather than the downstream valuation processes that should presumably be affected by such goals (e.g., Eddington et al., 2007; Spielberg, Heller, & Miller, 2013). The relationships between

these neural effects and the performance outcomes that have been linked to achievement goals in large-scale behavioral research have yet to be demonstrated. In further exploring the precise effects of these motivational factors on neural processing in the striatum, I set out to investigate the neural mechanisms that are responsible for motivational effects on learning. Observing the factors that interact to manipulate feedback processing during learning can help to shed light on how we might increase the value of a goal itself, without resorting to extrinsic reinforcers, which would have far-reaching pedagogical and clinical implications. The process of education can be difficult if not impossible if we do not encourage students to adopt the goal of learning, and an understanding of the precise mechanisms by which temperamental and situational factors interact to influence the value of the information we provide can ultimately aid in developing strategies to increase the value of an adaptive goal.

The goal of this dissertation research was to use functional magnetic resonance imaging (fMRI) to examine the role of the striatum in motivational influences on learning. The thesis of this dissertation is that the striatum, a brain region that has been implicated in reward learning and motivated behavior, is a key mediator of the effects of motivation on learning. Experiment 1 was designed to test the effects of expected task difficulty on learning and feedback processing for individuals who differ in achievement goal orientations (DePasque Swanson & Tricomi, 2014). The findings from Experiment 1 suggest that expectation related effects in the brain may be due to motivational factors, so to follow up on this idea, Experiment 2 was performed to more directly assess the effects of motivation on learning. In Experiment 2, participants engaged in two independent sessions of a learning task, one before and one after a motivational

manipulation that was designed to enhance motivation to perform well on the task. Experiment 3 was then designed to look at the neural mechanisms underlying the potentially maladaptive effects of avoidance goals on learning. In Experiment 3, I investigated the effects of threat on feedback processing in the striatum for individuals who vary in avoidance goal orientation. In these three distinct experiments manipulating different aspects of motivation, I demonstrated that striatal responses to informative feedback about the accuracy of one's responses can be modulated by the context in which this feedback is received and by individual differences in trait and state achievement goal orientation.

Chapter 2: Experiment 1: Goals and Task Difficulty Expectations Modulate Striatal

Responses to Feedback

Feedback about one's performance is a valuable tool for facilitating learning. It is used by educators, mental health professionals, physicians, and others to teach new skills, encourage adaptive behaviors, and promote healthful lifestyle changes. However, the context in which feedback is received can influence how successfully it motivates learning. For example, negative feedback more effectively facilitates learning when individuals focus on increasing their knowledge rather than on demonstrating their abilities (Cianci, Schaubroeck, & McGill, 2010), but is less effective when individuals are experiencing stereotype threat (fear of confirming a negative stereotype by performing poorly; Mangels, Good, Whiteman, Maniscalco, & Dweck, 2011).

Contextual factors that influence learning may do so through their effects on feedback processing in the striatum. As the input region of the basal ganglia, the striatum has been heavily implicated in reward processing and the motivation of reinforcement-driven behaviors (Balleine, Delgado, & Hikosaka, 2007; Robbins & Everitt, 1996; Shohamy, 2011). Activation in the striatum is greater following rewarding outcomes than negative outcomes and appears to scale with prediction error, which is the discrepancy between expected and received reward (O'Doherty, 2004; Schultz & Dickinson, 2000). During feedback-based learning, in which subjects learn to make appropriate choices through trial and error, performance-related feedback engages the striatum in an analogous manner, even in the absence of extrinsic rewards (e.g., Daniel & Pollmann, 2010; Satterthwaite et al., 2012; Tricomi, Delgado, McCandliss, McClelland, & Fiez, 2006). Striatal responses to positive and negative outcomes are associated with learning to adapt

behavior to maximize rewards (e.g., O'Doherty et al., 2004; Pessiglione, Seymour, Flandin, Dolan, & Frith, 2006; Schönberg, Daw, Joel, & O'Doherty, 2007), and proper functioning in this region is required for feedback- or reward-based learning, as evidenced by lesion studies and neuropsychology research (e.g., de Borchgrave, Rawlins, Dickinson, & Balleine, 2002; Shohamy et al., 2004). Due to its role in processing and learning from rewards, the striatum stands to play a critical role in the effects of motivation on feedback-based learning.

A region that modulates behavior based on motivation should be sensitive to motivational context, and there is evidence for such sensitivity in the striatum. Striatal responses to rewards and punishments are modulated not only by objective stimulus properties, such as reward frequency, predictability, and magnitude, but also by subjective factors, including hunger/satiety, individual preferences, and the social contexts in which these outcomes are received (e.g., Delgado, Frank, & Phelps, 2005; Fliessbach et al., 2007; Hariri et al., 2006; Peters & Buchel, 2010.; Schultz, 2010; Tricomi, Rangel, Camerer, & O'Doherty, 2010). Because reward responses in the striatum are sensitive to such a variety of influences, the responses produced during feedback-based learning might be similarly modulated by an individual's goals and expectations. Thus, the striatum may mediate the effects of achievement motivation on learning.

Goals and expectations for success are known to influence persistence, effort, and performance in achievement settings (Wigfield & Eccles, 2000). Expectations for success depend in part upon the perceived difficulty of the goal (Latham & Locke, 1991). In the present study, we manipulated beliefs about the difficulty of a novel feedback-based learning task, independently of actual task difficulty, to influence expectations for

success. We aimed to explore the effects of these expectations on the motivational salience and instructive efficacy of feedback during learning. We predicted that feedback would engage the striatum and that beliefs about task difficulty would modulate striatal feedback responses during learning.

Because expectations about task difficulty may differentially impact individuals who vary in their goals, we further hypothesized that the effects of expectations on performance might depend critically upon individual differences in achievement goals. Achievement goals can be subdivided into performance versus learning/mastery goals (Elliott & Dweck, 1988), and performance goals can be further classified as either normative or ability goals (Grant & Dweck, 2003). Recent research suggests that those high in normative goals (e.g., "My goal in class is to get a better grade than most of the students") fare better academically than those high in ability goals (e.g., "In school I am focused on demonstrating my intellectual ability"; Hulleman, Durik, Schweigert, & Harackiewicz, 2008; Hulleman, Schrager, Bodmann, & Harackiewicz, 2010).

Highly motivated individuals benefit from adopting competitive goals, and especially so when they are provided with information about the likelihood of performing well (Epstein & Harackiewicz, 1992). Thus, participants who spontaneously adopt normative goals, which are inherently competitive, may similarly benefit when they are provided with information about task difficulty. Individuals who are motivated by normative goals might exhibit enhanced interest and effort when they believe a task to be more difficult, since it would be more diagnostic of the differences between low- and high-performing individuals and would provide a chance for them to demonstrate their superiority. We expected that this might result in enhanced performance and exaggerated striatal

responses to feedback during experimental blocks that are expected to be more difficult.

To investigate our hypotheses about the neural processing of cognitive feedback under varying levels of expected difficulty, we used functional magnetic resonance imaging (fMRI) during a feedback-based learning task. We hypothesized that striatal feedback responses would be stronger when the task instructions suggested a low probability of success ("HARD"-labeled blocks), and that individual differences in normative goals might moderate the relationship between expectations and feedback processing. Due to the relationship between striatal feedback responses and learning, we further hypothesized that striatal modulation by task difficulty expectations would be accompanied by enhanced performance on the learning task.

Method: Experiment 1

Participants

Participants were recruited from the university community, were predominantly university students and staff, and possessed a broad range of demographics. Twenty right-handed adults (12 males), aged 18-35 completed the study. Four additional participants were excluded from analysis due to failure to finish the task (fatigue, $n = 2$, light-headedness, $n = 1$) and ceiling performance, which resulted in too few trials containing negative feedback ($n = 1$). All participants received compensation of $50 for their time spent in the experiment. Our procedures were approved by the institutional review boards of Rutgers University and the University of Medicine & Dentistry of New Jersey (UMDNJ).

Materials and Procedure

Experimental Task. We developed a novel visual categorization learning task with arbitrary block difficulty labels, presented in a mixed block/event-related design (see Figure 1a). Participants learned to categorize figures from eight different "families" of alien-like creatures through trial-and-error responding with feedback (stimulus images courtesy of Michael J. Tarr, Center for the Neural Basis of Cognition and Department of Psychology, Carnegie Mellon University, http://www.tarrlab.org).

Sixteen blocks of trials contained twelve trials each, with twelve distinct stimuli in each block sampled from two of the eight families (Figure 1b). During each trial, a single figure appeared on the screen for four seconds. During stimulus presentation, the participant made a judgment about the family membership of the figure by pressing one of two buttons on an MRI-compatible button box. Each of the twelve figures within a given block belonged to one of two families; six members of one family were associated with one button and members of the other family were associated with the alternate button. Feedback was presented for one second, immediately after the four-second stimulus screen: correct responses resulted in green checkmarks (√√√), incorrect responses resulted in red "X"s (XXX), and no response resulted in three dashes (---). A jittered fixation cross appeared for one to six seconds following the feedback. We did not include jitter between the stimulus screen and feedback, since previous research suggests that delaying feedback by even a few seconds can influence learning strategies and diminish striatal responsiveness to feedback (e.g., Foerde & Shohamy, 2011; Maddox, Ashby, & Bohil, 2003).

Stimuli. The stimuli used in this study ("YUFOs") come from a set of rendered 3D objects used previously in vision research, which are highly visually similar, sharing

the same size, color, and general spatial configuration (Gauthier, James, Curby, & Tarr, 2003; Rossion, Kung, & Tarr, 2004). Subtle differences in shape can be used to distinguish stimuli from different families. Within each family, the stimuli were all variations on the same basic shape, and pilot testing demonstrated that participants were able to learn to discriminate between stimuli from the different families at above-chance levels. Within families, there were "male" and "female" figures with differences in shape that were consistent across families. To create blocks of trials that were objectively easier, we selected stimuli that differed both in family and gender, as opposed to stimuli that differed only in family. Because the differences in shape do not tend to be simple or easily verbalizable, a rule-based strategy is not ideal for performing well on the task.

Manipulation. There were two levels of actual difficulty (high and low), based on the visual similarity of the two families in each block, crossed with two levels of labeled difficulty (labeled "HARD" and labeled "EASY"). Task difficulty labels appeared at the beginning of each new block, for five seconds before the trials began. A four-block training session preceded the sixteen experimental blocks. Instructions emphasized that the participant's goal was to learn which aliens come from which families, and that sometimes the differences between families could be very subtle and therefore harder to tell apart. Participants were informed that the blocks that contained families with very subtle differences would be labeled "HARD" while the others would be labeled "EASY." During training, the labeled difficulty always matched the actual difficulty level, to strengthen the expectation that an "EASY" block would be easier to perform than a "HARD" block. During the sixteen experimental blocks, the difficulty labels were independent of the true difficulty level but were presented to influence task difficulty

expectations. The sixteen experimental blocks were evenly divided across the four conditions (low difficulty, labeled "EASY"; low difficulty, labeled "HARD"; high difficulty, labeled "EASY"; high difficulty, labeled "HARD").

Questionnaires. After the training session but before the experimental trials, participants rated their perception of the difference between the (objectively more difficult) "HARD" blocks and the "EASY" blocks, on a scale of 1 (certain there was a difference) to 4 (certain there was no difference). After the conclusion of the fMRI study, each participant completed a post-experiment questionnaire to determine whether they continued to believe in the difficulty labels throughout the task. The open-ended responses were coded according to whether participants expressed suspicion in the accuracy of the labels (1) or not (0). In addition, participants completed the Achievement Goal Inventory (Grant & Dweck, 2003), an eighteen-item questionnaire that distinguishes between normative goals (6 items, $\alpha = .92$, e.g., "My goal in class is to get a better grade than most of the students,") and non-normative ability goals (3 items, $\alpha = .81$, e.g., "In school I am focused on demonstrating my intellectual ability"). Additional subscales include learning goals (6 items, $\alpha = .86$) and outcome goals (3 items, $\alpha = .85$). Agreement with each statement is rated on a Likert scale from 1 ("Strongly Disagree") to 7 ("Strongly Agree"), and responses to individual subscales are averaged to produce a single score for each. Analyses in the current study focus on the normative and ability subscales in particular.

Data Analysis

Behavioral Analysis. Task performance was defined as the percentage of trials with correct responses in each condition. Two within-subjects factors (actual difficulty

and labeled difficulty) were used in a 2 x 2 analysis of variance (ANOVA) to assess the

effect of labeled difficulty on performance, and whether the effect differed depending on

actual difficulty T-tests were used to test significance of the labeled difficulty effect

within each level of actual difficulty. To determine whether normative goals might

modulate the effect of expectations on performance, individual differences in the

magnitude of the expectation effect were calculated by subtracting performance (%

correct) on "EASY" trials from performance on "HARD" trials, separately for low-

difficulty and high-difficulty blocks. For the conditions under which an expectation effect

was observed, the magnitude of the effect was entered into bivariate correlations with

normative goals and ability goals.

fMRI Data Collection and Analysis. Scanning took place at the UMDNJ

Advanced Imaging Center, with a 3 Tesla Siemens Allegra scanner and standard eight-

channel head coil. Stimulus presentation and behavioral data collection were

implemented with E-Prime software (Psychology Software Tools, Pittsburgh, PA). The

fMRI data were preprocessed and analyzed using BrainVoyager software version 2.3.1

(Brain Innovation, Maastricht, The Netherlands). Preprocessing included motion

correction, spatial smoothing (8mm, FWHM), and high-pass temporal filtering.

Preprocessed data were spatially normalized to the Talairach stereotaxic space (Talairach

& Tournoux, 1988). After preprocessing, the Talairach-transformed fMRI data were

analyzed using a random-effects general linear model (GLM) that focused on activation

at the time of feedback presentation. The predictors of interest were modeled as events at

the time of feedback onset and convolved with a canonical hemodynamic response

function. These predictors included positive and negative feedback during each of the

four experimental conditions: low versus high actual difficulty crossed with "EASY" versus "HARD" difficulty label. In addition, the model included the onset of the difficulty labels that occurred at the start of each block. Missed trials and six motion parameters were included in the model as predictors of no interest.

Due to our a priori interest in feedback responses within the striatum, we examined feedback-related activation in three bilateral regions of interest (ROIs), created by drawing five-millimeter spheres centered around coordinates in left and right caudate nucleus (+/-12, 8, 11), putamen (+/-24, 4, 3), and ventral striatum (+/-12, 7, -7) and combining the left and right spheres from each subregion into a single ROI. These coordinates were selected because they represent each of the major subdivisions within the striatum, and were converted to Talairach coordinates from MNI coordinates that have been used in previous literature (e.g., Zink. Pagnoni, Martin, Dhamala, & Berns, 2003). In our data, the overall patterns of activation observed within these ROIs did not differ between the left and right hemispheres, so we report the results from each of the three combined bilateral ROIs. To explore effects of actual difficulty, instructed difficulty, and feedback valence in the striatum, beta estimates from each ROI were subjected to a 2 (actual difficulty) x 2 (labeled difficulty) x 2 (feedback valence) repeated measures ANOVA. We also performed a bivariate correlation for each ROI, between normative goals and the effect of expectations on feedback sensitivity: "HARD" (positive > negative feedback) > "EASY" (positive > negative feedback). To determine whether these regions demonstrated any differential response at the time of label onset, we subjected the parameter estimates from each ROI to a t-test comparing activation during

the onset of the "EASY" labels to activation at the onset of the "HARD" labels. Whole-brain analyses were also conducted as detailed in the Supplemental Methods.

A second random-effects GLM was also used to explore condition-related differences in sustained activation during the entire duration of each block. In this second GLM, the entire duration of each block was modeled as an epoch, from the onset of the first trial to the offset of the last trial. The ROI beta estimates were subjected to a 2 (actual difficulty) x 2 (labeled difficulty) ANOVA to determine whether sustained activation differed as a function of actual difficulty, labeled difficulty, or an interaction between the two factors.

Results: Experiment 1

Behavioral Results

Overall, participants were able to perform above chance on the task (M = 68.75% correct, SD = 9.63%), with a wide range of scores (min = 52.88%, max = 87.50%) suggesting diverse ability levels. Participants exhibited a broad range of scores on both the normative and ability goal subscales of the Achievement Goal Inventory (normative M = 3.625, SD = 1.107, min = 1, max = 5; ability M = 4.367, SD = 1.048, min = 1.333, max = 6). No gender differences were observed in measures of performance or achievement goals. A 2 x 2 repeated measures ANOVA detected no main effects of either labeled difficulty ("EASY" versus "HARD") or actual difficulty (low versus high) on task performance, although a trend emerged toward an interaction of labeled difficulty and actual difficulty ($F = 3.54$, $p = 0.075$). As seen in Figure 2a, there was a significant effect of labeled difficulty for the blocks that were low in actual difficulty, where performance was superior during "HARD"-labeled blocks ($t(19) = 2.17$, $p = 0.043$, two-

tailed). No such difference was observed for the high difficulty blocks ($t(19) < 0.01$, $p =$ 0.997, two-tailed). The performance differences for low-difficulty blocks emerged during the final trials of each block, as depicted in the Figure 2b. T-tests that focused on the percentage of correct responses during trials nine through twelve exhibited the same pattern of results as the original analysis: for low-difficulty blocks, participants performed significantly better on "HARD"- than "EASY"-labeled blocks (t(19) = 2.303, p = 0.033), but for high-difficulty blocks, the same pattern did not hold (t = .570, p = 0.575).

 To assess individual differences in the effects of expectations on learning, an "expectation effect" for low-difficulty blocks was calculated for each participant by subtracting percent correct on the "EASY"-labeled subset of those blocks from percent correct on the "HARD"-labeled subset. Expectation effects ranged from -.10 to .27 ($M =$ 0.05, $SD = 0.10$), with positive values indicating better performance on "HARD"-labeled blocks and negative values indicating better performance on "EASY"-labeled blocks. As displayed in Figure 3, the size of the expectation effect was positively correlated with the normative goals subscale of the achievement goal questionnaire ($r(18) = 0.52$, $p = 0.019$). Participants who expressed higher levels of normative goals showed greater performance benefits from expectations of higher difficulty, specifically for the low-difficulty blocks in which high performance was objectively more attainable. Despite this increased tendency to perform better on "HARD" than "EASY" blocks, normative goals were not correlated with overall task performance ($r(18) = -0.06$, $p = 0.817$), suggesting that the effect of normative goals on performance was related to the effect of expectations rather

than baseline ability levels. In contrast to normative goals, ability goals did not exhibit a relationship with the effect of expectations on performance ($r(18) = -.144$, $p = 0.544$).

After training, the majority of participants reported perceiving the difference in difficulty between "EASY" and "HARD" blocks (n = 15). However, after the conclusion of the experiment, many subjects reported suspecting a possible mismatch between the label and the actual difficulty (n = 15). Among the subjects for whom training questionnaire data were available (data for one participant not logged due to software malfunction), ratings indicating greater perceived difference between "EASY"- and "HARD"-labeled blocks during the practice session (when labels were accurate) were negatively correlated with the tendency to suspect that the labels were false at the end of the study ($r(17) = -.518$, $p = 0.023$). Given that we observed an effect of expectations on performance, it is likely that for many the mismatch did not become apparent until late in the experiment or when filling out the questionnaire.

fMRI Results

The results from the analysis of the three striatal ROIs are reported here. Supplemental Table 1 lists valence-sensitive regions identified by the whole-brain GLM analysis, including peaks within the putamen and ventral striatum. The results of a 2 x 2 x 2 repeated measures ANOVA are reported for each ROI in Table 1. As predicted, feedback valence modulated activation in each of the striatal ROIs. In the caudate, putamen, and ventral striatum, activation at the onset of positive feedback exceeded that for negative feedback across all task conditions (see Figure 4). No other main effects from the event-related GLM reached significance in the three striatal ROIs (see Supplemental Tables 2-4 for regions outside the striatum exhibiting effects of actual

difficulty, labeled difficulty, and the interaction of labeled difficulty and feedback

valence). However, several analyses identified trends that suggest that null findings

should be interpreted with caution. A medium effect size was observed for the main effect

of actual difficulty in the putamen ($F = 2.31$, $p = 0.146$, $\eta^2_p = 0.108$), with greater

feedback-related activation for high-difficulty blocks than for low-difficulty blocks. An

interaction between actual difficulty and feedback valence also exhibited a medium effect

size in the caudate ($F = 2.872$, $p = 0.106$, $\eta^2_p = 0.131$), with greater differentiation

between positive and negative feedback during high- than low-difficulty trials.

Most notably, both caudate and ventral striatum demonstrated medium effect sizes

for the interaction between label and valence, such that the differentiation between

positive and negative feedback was greater during "HARD"-labeled blocks than during

"EASY"-labeled blocks (caudate $F = 1.412$, $p = 0.249$, $\eta^2_p = 0.069$, Fig. 4a; ventral

striatum $F = 1.205$, $p = 0.286$, $\eta^2_p = 0.06$, Fig. 4c). This interaction is most evident in the

caudate, where differentiation between positive and negative feedback is only significant

in "HARD"-labeled blocks (see Fig. 4a). Although these effects were nonsignificant, each

of the trends reported above can be characterized as medium effect sizes according to the

guidelines set forth by Cohen (1988), and may have reached significance in a study with

greater power to detect subtle effects. Supplemental Figure 1 illustrates the broader extent

of activation observed throughout the brain for positive > negative feedback during

"HARD"-labeled blocks relative to "EASY"-labeled blocks, which is again consistent

with the idea that striatal valence sensitivity may be modulated by expectations about

task difficulty.

Normative goals exhibited a significant correlation with the effect of labeled difficulty on feedback valence sensitivity ("HARD" positive vs. negative feedback > "EASY" positive vs. negative feedback) in both the caudate (r = 0.518, p = 0.019; Figure 5a), and the putamen (r = 0.635, p = 0.003; Fig. 5b). These ROI results are corroborated by a whole-brain ANCOVA, which identified a region in the putamen in which normative goals correlated with the effect of expectations on valence sensitivity (see Supplemental Figure 2). This relationship suggests that those individuals who are most motivated to outperform their peers exhibit the strongest effect of expectations on feedback processing in the dorsal striatum.

The behavioral expectation effect (% correct trials in low-difficulty "EASY" versus "HARD" blocks) was not significantly correlated with the effect of expectations on valence sensitivity in the three striatum ROIs (caudate $r(18) = .258$, $p = .272$; putamen $r(18) = .209$, $p = .376$; ventral striatum $r(18) = .052$, $p = .828$). None of the striatal ROIs exhibited differential activation at the time that the difficulty label was displayed to start each block, or any significant differences in sustained activation throughout each block as a function of actual or labeled difficulty. However, a whole-brain analysis identified some regions that exhibited a main effect of actual difficulty on sustained activation, including a cluster in the putamen (Supplemental Table 5).

Discussion: Experiment 1

The goal of this study was to investigate whether feedback-related activation in the striatum is sensitive to subjective expectations and goals. We have shown that task difficulty expectations modulate striatal sensitivity to positive versus negative feedback for individuals with high normative goals. That is, the beneficial effects of increased task

difficulty expectations were most pronounced for these subjects. This suggests that the desire to perform well in comparison with one's peers may influence the affective response to task difficulty expectations, and enhance learning for low-difficulty tasks that are expected to be difficult. The behavioral effect may have been absent for high-difficulty blocks because performance was objectively more difficult to improve. Thus, motivation may have been affected for both low- and high-difficulty blocks, but enhanced task investment may have paid off only in blocks in which the correct categories were more easily discerned.

Achievement goals and feedback sensitivity

The effect of normative goals on task performance was reflected in feedback processing in the striatum. Specifically, in the caudate and putamen, normative goals were positively correlated with a larger effect of expectations on striatal sensitivity to feedback valence. Such striatal differentiation between positive and negative feedback has been previously associated with the ability to learn from trial and error (e.g., O'Doherty et al., 2004; Pessiglione, Seymour, Flandin, Dolan, & Frith, 2006; Schönberg, Daw, Joel, & O'Doherty, 2007). Thus, because the differentiation we observed was greater in "HARD"-labeled blocks than in "EASY"-labeled blocks for subjects who were highest in normative goals, it is fitting that these same participants also showed the greatest performance benefits from being told a low-difficulty block would be "HARD."

Given these results, we suggest that a desire to measure up favorably against other participants may result in a greater commitment to performing well in the "HARD" blocks. Under these circumstances, subjects might value positive feedback more strongly and find negative feedback more aversive, due to the greater affective investment in

performing well. Without subjective ratings of the importance of performing well on "HARD" versus "EASY" blocks, this remains speculative. However, this interpretation is consistent with our finding of a correlation between normative goals and heightened striatal sensitivity to feedback valence during blocks that are expected to be more difficult.

Feedback processing in the striatum

As anticipated, positive feedback resulted in greater activation in the striatum compared to negative feedback. The valence effects we observed in ventral striatum are consistent with previous studies of reward learning and prediction error, where positive outcomes result in greater activation in the nucleus accumbens and ventral putamen (Breiter, Aharon, Kahneman, Dale, & Shizgal, 2001; McClure, Berns, & Montague, 2003; O'Doherty et al., 2004). However, while previous studies have found cognitive feedback responses in the head of the caudate (e.g., Daniel & Pollmann, 2010; Dobryakova & Tricomi, 2013; Tricomi et al., 2006), the current task also produced activation in the putamen. Valence sensitivity has been previously observed in the putamen during reward learning (e.g., Delgado, 2007; Liu et al., 2011; Luking & Barch, 2013), but the key factors that determine which striatal subregions will be activated for a particular task are still being explored (Lopez-Paniagua & Seger, 2011).

One factor influencing putamen activation may involve the visual nature of our task. Studies of visual categorization learning have implicated the more posterior regions of the dorsal striatum, including the body and tail of the caudate and the putamen, in category learning that requires integration across multiple visual stimulus dimensions (information integration; Ashby & Maddox, 2011; Nomura & Reber, 2008). These

posterior striatal regions are associated with the visual corticostriatal loop, while rule-based learning would be more likely to recruit the executive loop involving the caudate head (Cincotta & Seger, 2007). Because our subjects were instructed to attend globally to the whole complex visual stimulus rather than its individual features, performance on our task likely depended upon information-integration learning strategies. Interestingly, we also observed differential activation to positive and negative feedback in the posterior inferotemporal cortex, which has been implicated in object part integration, object recognition, and object discrimination (Brincat & Connor, 2006), and which has been linked anatomically with the ventral putamen, the peak site of feedback activation in our study (Yeterian & Pandya, 1995). Future research will be needed to further clarify the roles of striatal subregions in different types of feedback-based learning tasks.

Relation to prior research

The finding that normative goals enhanced the effect of task difficulty expectations on learning complements the growing body of evidence that performance goals can be beneficial when they are normative in nature, because they can prompt individuals to set higher standards for themselves and help them excel when they perceive those goals as achievable (Hulleman et al., 2008, 2010). Superior exam performance for those high in normative goals has been attributed to increased effort and persistence (Elliot, McGregor, & Gable, 1999), so it is possible that subjects in our study who adopted normative goals may have invested more effort during blocks they expected to be more challenging. The amount of effort exerted during a task can influence striatal sensitivity to rewards and losses (Hernandez Lallement et al., 2014); thus, our finding of enhanced striatal sensitivity during "HARD"-expected blocks for those high in normative

goals may be due to enhanced effort during those blocks. It is also possible, since striatal feedback activation reflects goal satisfaction (Han, Huettel, Raposo, Adcock, & Dobbins, 2010), that the modulation of activation in our task is caused by enhanced motivation affecting the subjective value of performing well during those blocks. This interpretation is consistent with a large body of research that suggests that reward responses in the striatum vary with the subjective value of outcomes (Bartra, McGuire, & Kable, 2013). Furthermore, normative goals are inherently competitive, and social competition has been shown to increase the amount people are willing to pay at auctions (e.g., Goeree, Holt, & Palfrey, 2002; Delgado, Schotter, Ozbay, & Phelps, 2008). If willingness to pay is viewed as a proxy for subjective value, then there is evidence that competitive goals can drive subjective value. Future research will be needed to tease apart the effects of effort per se and the enhanced motivation that may occur for individuals high in normative goals when a task is expected to be more challenging.

Our finding that achievement goals and contextual information can jointly influence striatal sensitivity to feedback during learning fit within the broader picture of research showing modulation of striatal reward responses by individual differences in motivation and goals. For instance, individual differences in reward sensitivity, drive, extrinsic versus intrinsic motivational orientation, and trait approach versus avoidance motivation have been found to influence responses to rewarding and aversive stimuli in the ventral striatum, putamen, and caudate (Beaver, Lawrence, Passamonti, & Calder, 2008; Costumero et al., 2013; Linke et al., 2010; Spielberg et al., 2012). Our results extend this work by demonstrating that striatal processing of cognitive feedback is sensitive to variation in expectations and goals.

Limitations

Our study demonstrated a modulatory effect of normative goals on the influence of task difficulty expectations on both performance and striatal sensitivity to positive versus negative feedback. However, in order to firmly establish the effects of the difficulty labels on participants' expectations, we used training blocks that differed from the experimental task in that they used only veridical task difficulty labels. To avoid confounding effects of actual difficulty with effects of expectations, by necessity half of the blocks in the experimental task contained difficulty labels that were false. It is possible that presenting only accurately labeled blocks during training could have influenced subsequent performance by providing an opportunity for participants to learn subtle differences in strategy that could distinguish low- from high-difficulty blocks and thus reduce their belief in the labels during the experiment. However, pilot testing of the experimental paradigm suggested that participants were more likely to believe in the manipulation if the difficulty levels of the easy and the hard blocks were experienced as noticeably different during training. Data from our fMRI participants are consistent with this view, in that the participants who did not notice a difference in difficulty during training appeared to be the most likely to report suspicion about the difficulty labels after the study concluded. If we had included training blocks with a mix of accurate and inaccurate difficulty labels, participants may have learned even sooner that the difficulty labels did not appear to reflect actual task difficulty, and thus our results may not have been as strong.

An additional limitation of the current study is that it did not demonstrate a direct relationship between striatal sensitivity to feedback valence and performance on the

learning task. One possibility is that this could reflect the declarative nature of the task. Although the striatum is engaged by positive and negative feedback in this task, it is possible that the magnitude of the striatal response is not as directly responsible for declarative learning as it is for nondeclarative learning (e.g., Poldrack et al., 2001). The modulation of feedback responses by normative goals may have more strongly reflected the motivational salience of the feedback than the amount learned from the feedback. Further research will be needed to determine the precise neural mediators of the effects of normative goals on learning.

Conclusion

This study provides novel insight into a potential neural mechanism for the interaction between trait academic achievement motivation and contextual influences on learning. The integration of the psychology of academic achievement motivation and the neuroscience of feedback-based learning allowed us to probe the joint effects of personality and context on the striatal processing of performance-related feedback. Due to the relationship we observed between normative goals, task difficulty expectations, and the magnitude of the striatal response to positive and negative feedback, we suggest that striatal feedback responses are influenced by the affective salience of the feedback. We have demonstrated that striatal processing of cognitive feedback can be affected by goals and expectations, much like the modulation of extrinsic reward responses by subjective value. These results lend support to the notion that the striatum is a key region in the modulation of learning by achievement motivation.

Chapter 3: Experiment 2: Effects of Motivation on Feedback Processing During

Learning.

Performance-related feedback is an important part of effortful learning, as information about correct responses and errors can motivate learners to adapt their behaviors. Such feedback engages the striatum, which is widely regarded as a key region for processing reward-related information, even in the absence of extrinsically rewarding or punishing outcomes (e.g., Daniel & Pollmann, 2010; Satterthwaite et al., 2012; Tricomi et al., 2006). However, the affective experience of performance-related feedback may be more or less salient depending upon one's motivation to successfully complete the task. For example, positive performance feedback may be more reinforcing for a student who values scholastic achievement than for one who sees academics as irrelevant to his or her goals. As a result, it is likely that striatal engagement during feedback processing would be modulated by an individual's motivation to perform well.

The striatum serves a critical role in the reinforcement learning system, receiving input from midbrain dopamine neurons that convey information about unexpected rewards, and using information about rewarding consequences to learn to select adaptive behaviors (O'Doherty, 2004). Feedback-related responses in the striatum are presumed to reflect the affective value of positive and negative feedback in much the same way that reward responses reflect the subjective value of extrinsic rewards such as food or money (Satterthwaite et al., 2012). However, while previous research has established sensitivity to contextual influences in striatal responses to extrinsic rewards (e.g., Brosch et al., 2011; Chein et al., 2011; Delgado et al., 2008; Guitart-Masip et al., 2010; Nieuwenhuis et al., 2005), it is unclear how the learning context might influence the response of the

striatum to positive and negative performance feedback. In particular, motivation to perform well on a task may increase the affective salience of performance feedback, resulting in exaggerated striatal feedback responses.

Striatal reinforcement signals are most often associated with procedural or nondeclarative forms of learning, whereas declarative learning is dependent upon the medial temporal lobes (Squire, 2004). Although reinforcement learning and declarative learning are often viewed as separate processes with distinct neural substrates, performance-related feedback is an important part of effortful learning in academic settings. There is a growing literature exploring the interactions between striatal reward signals and declarative learning processes in the medial temporal lobes, suggesting that the two systems may interact in both competitive and cooperative capacities (e.g., Dickerson, Li, & Delgado, 2011; Poldrack et al., 2001; Shohamy, Myers, Hopkins, Sage, & Gluck, 2009). The present study uses a trial-and-error learning task that has been demonstrated to engage the striatum, yet which also requires declarative learning of paired word associates (Tricomi & Fiez, 2008).

Stable patterns of goal pursuit, assessed by trait measures of achievement goals, have been found to influence motivation and performance in experimental and academic situations (e.g., Grant & Dweck, 2003; Harackiewicz et al., 1997; Harackiewicz et al., 1998). Such traits have been linked with feedback-related activation in the striatum (e.g., DePasque Swanson & Tricomi, 2014); however, the relevance of a particular goal can also vary over time based on situational factors (Covington, 2000). For example, prior experimental work suggests that monetary rewards can enhance learning for boring material (Murayama & Kuhbandner, 2011). It is not always feasible or desirable to

motivate academic performance or health behaviors with payments or other extrinsic rewards, which can potentially undermine intrinsic motivation for the desired behavior (Deci et al., 1999) or result in unintended negative long-term effects on future motivation (Gneezy et al., 2011); consequently, it is important to understand the effects of task-specific motivation on learning from feedback in the absence of extrinsic rewards or punishments. We aimed to increase the value of the learning goal itself, rather than using rewards that are extrinsic to the task in order to increase goal pursuit.

Intrinsic motivation is characterized by a focus on the inherent satisfaction in performing a particular behavior for its own sake, in contrast with extrinsic motivation, in which the focus is on attaining some separable outcome (Ryan & Deci, 2000). Behavioral research suggests that a sense of autonomy, or being in control of one's choices, facilitates intrinsic motivation (Deci & Ryan, 1987). Because we sought to increase our participants' intrinsic motivation for our learning task, we required a manipulation that would support their autonomy at the same time as promoting reflection on the value of the task. Motivational interviewing is a strategy for enhancing motivation to change in substance abuse treatment and other health domains, which uses directive questioning to elicit "change talk," or self-generated statements in favor of pursuing treatment (Miller & Rollnick, 1991). In this regard, motivational interviewing supports autonomy to enhance intrinsic motivation.

Brief interventions based on the principles of motivational interviewing have demonstrated comparable efficacy to longer-term cognitive behavioral therapies for reducing substance abuse (Burke et al., 2003), but specific techniques used within motivational interviewing have rarely been tested experimentally. One notable exception

is an fMRI study that found diminished neural responses to alcohol cues following self-generated change talk in alcohol dependent subjects, suggesting that motivational interviewing can promote the inhibition of maladaptive reward responses (Feldstein Ewing et al., 2011). Rather than diminishing the value of a maladaptive behavior, we aimed to use the principles of motivational interviewing to enhance motivation and performance on our learning task, by encouraging participants to generate statements about the value of the learning task. The aim of the present study was to investigate the effect of enhanced motivation on feedback processing during learning.

Two experiments were performed, first to establish a manipulation that could influence performance via effects on motivation to perform a learning task, and subsequently to investigate the effects of changing motivation on the neural processing of feedback during learning. In both, participants completed two sessions of a feedback-based paired associate learning task, one before and one after a brief motivational interviewing manipulation. Experiment 2a was conducted to observe behavioral effects of the motivational interviewing manipulation in relation to a control condition. Experiment 2b was conducted using fMRI to observe motivation-related changes in the neural processing of feedback before and after the motivational interviewing manipulation.

Method: Experiment 2a

Participants

Fifty adult participants completed the study for course credit. Data from eight were excluded due to prior experience with the learning task (n=6) and failure to complete the entire task (n=2). Forty-two participants remained in the final sample (13 males). The participants were recruited from undergraduate courses offered by the

Rutgers Newark psychology department and received course credit in exchange for their participation. Participants were randomly assigned to either the experimental or control condition using a virtual coin flipper (http://www.random.org/), but were not informed about the manipulation or their condition assignment. The final sample consisted of 21 experimental participants (10 males), who experienced a motivational interviewing manipulation to enhance their motivation, and 21 control participants (3 males), who experienced a quiet rest period in place of the manipulation. The procedures were approved by the Institutional Review Board of Rutgers University, and all participants gave written informed consent.

Materials and Procedure

     Experimental Task. Participants completed two independent sessions of a paired associate word-learning task, adapted from a previous study of feedback processing in the striatum (Tricomi & Fiez, 2008); illustrated in Figure 6. During this feedback-based learning task, participants learned arbitrary word pairs through trial and error. Each trial required participants to associate one main word with one of two other word choices, as in a multiple choice test with two response options. Since the words were semantically unrelated, learning was dependent on the feedback that followed each response.

     Each session (one BEFORE and one AFTER the motivational manipulation/control rest period) contained a distinct set of 80 word pairs to be learned. Within each session, there were two learning phases, presenting two opportunities to learn the correct match for the main word, followed by a test phase, which was identical to the learning phases but without feedback. Each phase of the experiment contained the same 80 trials in random order. During learning phase 1, guesses as to the correct match

for the top word were arbitrary, and therefore feedback about the participant's responses during learning phase 1 was simply informative and did not reflect personal efficacy on the task. During learning phase 2, the 80 word pairs that were shown during phase 1 were repeated, allowing participants a second opportunity to learn the correct answer. Because participants had previously viewed the word pairs, feedback during phase 2 reflected the accuracy of the participants' memory in addition to providing information about the correct response. The word pairs tested BEFORE the Motivational Interviewing (MI) manipulation/quiet rest phase included only those pairs that were learned BEFORE the MI manipulation (or quiet rest period for control subjects), and those tested AFTER included only the 80 new word pairs that were introduced AFTER the MI manipulation/rest period.

Stimulus presentation and behavioral data collection were implemented with E-Prime software (Psychology Software Tools, Pittsburgh, PA). Each trial during the two learning phases began with a jittered fixation point (1-6 seconds), followed by the stimulus screen with the three words displayed (4 seconds), during which participants used a numeric keypad to choose one of the two response options, and finally the feedback screen (2 seconds) which displayed either a green checkmark (√) or a red "x." The test phase was nearly identical to the learning phases but did not include performance feedback or jittered inter-trial intervals.

Word lengths were limited to 1-2 syllables and 4-8 letters, and all words were controlled for Kucera-Francis frequency (20-650 words per million) and imagibility ratings (score of over 400 in the MRC database (Coltheart, 1981). Within each trial, words were matched for length and frequency, and did not rhyme or begin with the same

letter. In addition, words presented within each trial were rated with a Latent Semantic Analysis similarity matrix score below 0.2 to ensure that no preexisting semantic relationships would bias responses toward either option (Landauer, Foltz, & Laham, 1998).

Motivational Manipulation. Twenty-one participants completed the experimental condition, which involved a motivational manipulation adapted from motivational interviewing. Motivational interviewers use a technique known as the "importance ruler" as a prompt to initiate discussion about the importance of changing maladaptive behaviors (Miller & Rollnick, 1991). On a scale of 0 to 10, interviewees rate the importance of changing their behavior and the interviewer follows up by asking them why they indicated the score they did, rather than a lower number. This phrasing prompts the respondents into generating positive statements in favor of change: even if the original importance rating was low, they must explain why they are at least somewhat motivated to perform well on the task. This allows the interviewer to elicit self-generated motivational statements from the participants, which should be more beneficial to intrinsic motivation than externally provided reasons why the participant should care about the task (Deci & Ryan, 1987). Between the first (BEFORE) and second (AFTER) sessions of the learning task, participants completed a brief motivational survey that was based on these techniques from motivational interviewing. On a typed handout, subjects rated their task motivation in response the question: "How important would you say it is for you to perform well on this task?" After indicating their responses on a scale from 0 to 10, participants wrote down at least two reasons why they gave the rating they did,

rather than a lower number. The question was open-ended and therefore allowed subjects to rely on their own values to explain their answers.

Control Condition. The twenty-one control participants did not participate in the motivational manipulation; instead, they sat quietly for approximately five minutes between the first and second sessions of learning to ensure that the spacing between the two learning sessions was comparable to that for the experimental group.

Manipulation Check. After the experiment, participants completed a brief post-experiment questionnaire. They were asked to rate the importance of performing well on the task, on a scale from 0 to 10. For the experimental group, this was the second time they made this rating (the first rating taking place during the motivational interviewing manipulation). In contrast, this was the only rating collected for the control group, since mid-session motivation ratings were not collected to avoid any potential influence of such ratings on their motivation. To more directly assess whether participants in both groups felt their motivation had changed between sessions, all participants completed a *motivation change rating,* in which they reported whether they felt more, less, or equally motivated during the second half of the test as compared with the first half, on a scale of 1 ("a lot less motivated") to 5 ("a lot more motivated"). Participants were also asked to indicate at what point during the study they became bored or sleepy, on a scale from 1 ("right away") to 7 ("never").

Behavioral Analysis. Performance on the task was defined as the percentage of trials with correct responses in each phase BEFORE and AFTER the manipulation. Again, the word pairs presented in the second session of learning did not duplicate those presented before the manipulation; any gains in performance reflect more efficient

learning of the new word associations and cannot be attributed to memory from the previous learning session. To test the effect of the motivational manipulation on performance, we examined within-subject changes in test accuracy (BEFORE vs AFTER) and learning phase 2 accuracy (BEFORE vs AFTER), using two-tailed paired t-tests in both the experimental and control groups.

In addition, phase 2 and test phase *difference scores* were calculated by subtracting the percent correct BEFORE the manipulation from the percent correct AFTER the manipulation for the learning phase 2 and test phases. Two-tailed independent samples t-tests were used to assess between-groups differences in the change in performance after the motivational interviewing manipulation/rest period. Furthermore, the *difference scores* were also used to explore individual differences in performance changes after the manipulation. We were particularly interested in the relationship between increasing task motivation and task performance, so we conducted bivariate correlations between the *motivation change rating* from the post-experiment manipulation check and the performance *difference scores* from Learning Phase 2 and Test Phase.

Results: Experiment 2a

Behavioral Results

Motivation Ratings. *Experimental Group:* At the time of the mid-session motivation manipulation, the experimental group rated their motivation slightly above the midpoint of the importance ruler rating scale, with all subjects reporting motivation levels above zero (M = 6.50, SD = 2.259, min =1). End ratings for the experimental group were similar (M = 6.63, SD = 2.314, min = 1), and were highly correlated with mid-session

ratings ($r(16) = 0.917$, $p < 0.001$), suggesting that motivation ratings were relatively consistent. When asked to compare their motivation for the second session ("AFTER" the manipulation) versus the first, approximately half of participants reported increased motivation (n = 10) in contrast to six who reported no change in motivation, and three who reported decreases in motivation after the manipulation. The most common response chosen by the experimental group was a slight increase in motivation (n=7).

Control Group: To avoid influencing their motivation for the task, mid-session motivation ratings were not collected for the control group. End ratings were near the midpoint of the rating scale (M=5.33, SD=2.614, min=0). Although the motivation ratings at the end of the experiment did not significantly differ from the experimental group, there was a nonsignificant trend for lower ratings in the control group $t(38)=1.656$, $p=.106$. Motivation change ratings also did not differ significantly from the experimental group, $t(38)=.975$, $p=.336$; however, the majority of participants in the control group either declined in motivation (n=8) or exhibited no change (n=5), and the most common response chosen by the control participants was a slight decrease in motivation (n=6).

Task Performance. Performance on the learning task is displayed in Figure 7 for both the experimental and control groups across all sessions of the learning task.

Experimental Group: The motivational manipulation affected performance mainly on the test phase, which represented associations acquired through both sessions of trial-and-error learning. Experimental participants performed marginally better on Phase 2 and significantly better on the Test Phase AFTER the manipulation ($t(20) = 1.884$, $p = 0.074$ and $t(20)=2.455$, $p=0.023$, respectively). In contrast, Phase 1 performance, which was

necessarily at chance both BEFORE and AFTER the manipulation, did not differ

BEFORE versus AFTER the manipulation ($t(20) = 1.252$, $p = 0.225$).

Relation of motivation to performance in experimental group: Experimental

participants varied in the extent to which both their Phase 2 and Test Phase performance

differed after the manipulation (% correct AFTER - % correct BEFORE), with an average

Phase 2 *difference score* of +4.25% (SD = 10.33%) and an average Test Phase *difference*

score of +7.37% (SD = 13.76%). Most importantly, individual differences in *motivation*

change ratings were significantly correlated with the change in Phase 2 performance

($r(18) = 0.612$, $p = 0.005$) and Test performance ($r(18) = 0.528$, $p = 0.020$) from

BEFORE to AFTER the manipulation (see Fig. 8). Individuals who experienced the

greatest increases in motivation also evinced greater gains in performance from the

BEFORE to AFTER sessions. Thus, improved learning performance appears to depend

upon the extent to which motivation increased after the manipulation.

Control Group: Control participants performed significantly better on Phase 2

AFTER the manipulation ($t(20) = 2.575$, $p = 0.018$). However, unlike the experimental

group, their Test Phase performance did not differ significantly between the BEFORE

versus AFTER learning sessions ($t(20) = -.617$, $p=.545$). Phase 1 performance, in which

participants made random guesses about the correct answer, also did not ($t(20) = .384$, p

$= 0.705$). In other words, the control group appeared to improve in their ability to learn

from the initial feedback phase from BEFORE to AFTER the manipulation, which may

reflect a practice effect, but this improvement did not carry over to the test phase.

Comparison of Experimental & Control Groups' Performance Changes: Two-

tailed independent samples t-tests revealed that the experimental and control groups did

not differ in their Phase 2 difference scores ($t(40)$=-.236, p=.815), but the experimental group exhibited significantly greater increases in their Test Phase scores from the BEFORE to AFTER sessions ($t(40)$=2.234, p=.031). In other words, the motivational interviewing manipulation produced greater gains in learning performance than the control condition.

Relation of motivation to performance across groups: All participants varied in the extent to which both their Phase 2 and Test Phase performance differed after the motivational interview manipulation/quiet rest period (% correct AFTER - % correct BEFORE), with an average Phase 2 *difference score* of +4.59% (SD = 9.49%) and an average Test Phase *difference score* of +2.85% (SD = 13.75%). Most importantly, individual differences in *motivation change ratings* were significantly correlated with the change in Phase 2 performance ($r(40) = 0.471$, $p = 0.002$) and Test performance ($r(40) = 0.574$, $p < 0.001$) from BEFORE to AFTER the manipulation/rest period. Individuals who experienced the greatest increases in motivation also evinced greater gains in performance from the BEFORE to AFTER sessions. Thus, improved learning performance appears to depend upon the extent to which motivation increased during the learning of the second set of word pairs.

Discussion: Experiment 2a

The administration of a motivational interviewing manipulation resulted in a greater tendency for participants to report slight increases in their motivation across two sessions of a lengthy learning task, as opposed to the slight decreases reported by the control group. The motivation change experienced by participants correlated positively with gains in task performance, suggesting that individual differences in the extent to

which motivation was maintained or enhanced for the second learning session influenced performance. These results provided a validation of the use of the motivational interviewing manipulation, which we next used during an fMRI study to explore the effects of motivation changes on feedback processing in the brain.

Method: Experiment 2b

Participants

Twenty-six right-handed adult participants (11 males) were recruited from the university community to participate in the study. One participant failed to complete the task due to illness. Twenty-five participants (10 males) remained in the final sample, which consisted of predominantly university students and staff with a broad range of demographics. All participants who completed the study received compensation of $50 for their time. Our procedures were approved by the Institutional Review Board of Rutgers University, and all participants gave written informed consent.

Materials and Procedure

Experimental Task. Participants completed two independent sessions of the same paired associate word-learning task used in Experiment 2a. As in the prior experiment, During this feedback-based learning task, participants learned through trial and error to associate one main word with one of two other word choices, as in a multiple choice test with two response options. Since the words were semantically unrelated, learning was dependent on the feedback that followed each response.

Within each session (one BEFORE and one AFTER the motivational manipulation), there were two learning phases, presenting two opportunities to learn the correct match for the main word, followed by a test phase, which was identical to the

learning phases but without feedback or time limits. Each phase of the experiment contained the same 80 trials in random order. During learning phase 1, guesses as to the correct match for the top word were arbitrary, and therefore feedback about the participant's responses during learning phase 1 was simply informative and did not reflect personal efficacy. During learning phase 2, the 80 word pairs that were shown during round 1 were repeated, allowing participants a second opportunity to learn the correct answer. Because participants had previously viewed the word pairs, feedback during phase 2 reflected the accuracy of the participants' memory in addition to providing information about the correct response. The word pairs tested BEFORE the Motivational Interviewing (MI) manipulation included only those pairs that were learned BEFORE the MI manipulation, and those tested AFTER included only the 80 new word pairs that were introduced AFTER the MI manipulation.

Stimulus presentation and behavioral data collection were implemented with E-Prime software (Psychology Software Tools, Pittsburgh, PA). Each trial during the two learning phases began with a jittered fixation point (1-6 seconds), followed by the stimulus screen with the three words displayed (4 seconds), during which participants used an MRI-compatible button box to choose one of the two response options, and finally the feedback screen (2 seconds) which displayed either a green checkmark (√) or a red "x." The test phase was self-paced and did not include performance feedback or jittered inter-trial intervals.

Motivational Manipulation. The same motivational interviewing manipulation used in Experiment 2a was administered to all participants while they lay in the scanner after completing the first session of learning. Still inside the scanner, subjects rated their

task motivation in response the question: "How important would you say it is for you to perform well on this task?" After using the button box to indicate their responses on a sliding scale from 0 to 10, participants were verbally prompted to state at least two reasons why they gave the rating they did, rather than a lower number. The experimenter instructed the subject to think about their answer until ready, and to state it out loud over the intercom. The question was open-ended and therefore allowed subjects to rely on their own values to explain their answers. The results of Experiment 2a suggested that this manipulation was effective at increasing motivation and task performance relative to a control condition without the manipulation, and that individual differences in motivation influenced changes in task performance. Focusing on individual differences within the experimental group allowed us to explore the relationship between changing motivation, feedback processing, and task performance.

Manipulation Check. After the scan, participants completed a brief post-experiment questionnaire. They were asked a second time to rate the importance of performing well on the task, on a sliding scale from 0 to 10. In addition, to more directly assess whether participants felt their motivation had changed between sessions, they also were asked to complete a *motivation change rating,* in which they reported whether they felt more, less, or equally motivated during the second half of the test as compared with the first half, on a scale of 1 ("a lot less motivated") to 5 ("a lot more motivated"). In addition to the motivation related questions, participants were also asked to indicate at what point during the study they became bored or sleepy, on a scale from 1 ("right away") to 7 ("never").

Behavioral Analysis. Performance on the task was defined as the percentage of trials with correct responses in each phase BEFORE and AFTER the manipulation. Again, the word pairs presented in the second session of learning did not duplicate those presented before the manipulation; any gains in performance reflect more efficient learning of the new word associations and cannot be attributed to memory from the previous learning session. To test the effect of the motivational manipulation on performance, we examined within-subject changes in test accuracy (BEFORE vs AFTER) and learning phase 2 accuracy (BEFORE vs AFTER), using two-tailed paired t-tests. In addition, to explore individual differences in performance changes after the manipulation, phase 2 and test *difference scores* were calculated by subtracting the percent correct BEFORE the manipulation from the percent correct AFTER the manipulation for the learning phase 2 and test phases. We were particularly interested in the relationship between increasing task motivation and task performance, so we conducted bivariate correlations between the *motivation change rating* from the post-experiment manipulation check and the performance *difference scores* from Learning Phase 2 and Test Phase.

fMRI Analysis. Scanning took place at the Rutgers University Brain Imaging Center (RUBIC), with a 3 Tesla Siemens Trio scanner and 12-channel head coil. The fMRI data were preprocessed and analyzed using BrainVoyager software version 2.3.1 (Brain Innovation, Maastricht, The Netherlands). Preprocessing included motion correction, spatial smoothing, and high-pass temporal filtering. Preprocessed data were spatially normalized to the Talairach stereotaxic space (Talairach & Tournoux, 1988). A general linear model (GLM) was used to identify voxels that differentiated between

feedback presented during the two learning phases BEFORE the manipulation and the subsequent two learning phases AFTER the manipulation.

After preprocessing, the fMRI data were analyzed using a random-effects GLM to identify voxels throughout the brain that differentiated between the experimental conditions at the time of feedback presentation. The predictors of interest included activation at the time of positive and negative feedback during each of the four learning phases: learning phase 1 BEFORE, learning phase 2 BEFORE, learning phase 1 AFTER, and learning phase 2 AFTER. Imaging data from the self-paced test phases were not analyzed, as this phase lacked jittered inter-trial intervals and did not include feedback presentation. Six motion parameters were also included in the model as predictors of no interest. Clusters of voxels identified by the GLM analysis at an uncorrected statistical threshold of $p < 0.005$ were subjected to a cluster threshold estimator in Brain Voyager, resulting in a corrected threshold of $p < 0.05$. Whole-brain contrasts were used to detect differences in brain responses to positive and negative feedback during different learning sessions.

Motivation and feedback processing. To identify regions in which feedback processing was modulated by motivation, a whole-brain analysis of covariance (ANCOVA) was performed, with self-reported changes in motivation from BEFORE to AFTER as a covariate for the contrast representing the change in feedback valence sensitivity: AFTER (positive > negative) > BEFORE (positive > negative).

Task performance. To identify regions in which changes in feedback processing related to gains in task performance, a whole-brain ANCOVA was performed with the test phase performance *difference score* as a covariate for the same contrast of AFTER

(positive > negative) > BEFORE (positive > negative). Furthermore, because task

performance might be supported by regions beyond those involved in feedback

processing, a subsequent memory analysis was used to identify regions where activation

during learning trials predicted subsequent test performance. To explore subsequent

memory effects, a new GLM analysis was performed on the activation during the entire

trial, from cue onset to feedback offset, during Learning Phase 1, with two predictors of

interest: trials which were subsequently answered correctly during Learning Phase 2 and

trials which were incorrect during Learning Phase 2. Trials without responses for both

Learning Phase 1 and Learning phase 2 were coded as missed trials and included in the

GLM as predictors of no interest.

Effective Connectivity. To illuminate the neural mechanisms by which

motivation affects the learning efficacy of feedback, five regions implicated in feedback

processing, motivation, and learning were submitted to an effective connectivity analysis.

The five regions were functionally defined, based on the results of the GLM analyses.

They were located in the bilateral ventral striatum (the peak site of feedback-related

activation from the positive > negative feedback contrast), the left superior temporal

sulcus (STS) and parahippocampal gyrus (where changes in valence-sensitive feedback

responses AFTER the manipulation were modulated by motivation change ratings), the

left prefrontal cortex (PFC) including the inferior and middle frontal gyrus (IFG/MFG),

and the middle temporal gyrus (identified in the subsequent memory analysis).

Within each of the five ROIs, the raw BOLD activity following initial (learning

phase 1) feedback presentation, starting at the time of feedback onset and including two

2.5-second TRs following feedback onset was used in the analysis (three acquisitions

(TRs) starting with feedback onset were included for each trial). The analysis was performed separately for positive and negative feedback, since different cognitive process may be required for learning from positive as opposed to negative feedback. We initially limited the connectivity analysis to Phase 1 of learning, because the proportion of correct to incorrect feedback was approximately equal during this phase, and because it is during initial learning that the feedback is most informative. Phase 2 connectivity is also displayed.

Patterns of effective connectivity were analyzed graphically using Independent Multi-sample Greedy Equivalence Search (IMaGES; Ramsey et al., 2010) and Linear non-Gaussian Orientation, Fixed Structure (LOFS; Ramsey, Hanson, & Glymour, 2011), modules available in the Tetrad IV statistical modeling program (http://www.phil.cmu.edu/projects/tetrad/). IMaGES performs a Bayesian search for causal connectivity structure over sets of directed acyclic graphs where connections are added after estimating conditional independence relations between the ROIs. LOFS directs the connections that are left undirected after IMaGES processing by selecting the model with most non-Gaussian residuals (see Ramsey et al., 2011 for description of the underlying assumptions). A combination of IMaGES and LOFS has been validated as a measure of effective connectivity on 28 simulated datasets with accuracy of connectivity structure ranging from 80 percent for directed connections to above 90 percent for detection of undirected connections (Ramsey et al., 2011).

Results: Experiment 2b

Behavioral Results

Motivation Ratings. At the time of the mid-session motivation manipulation, motivation ratings were already high as indicated on the importance ruler, with all subjects reporting motivation levels at or above the mid-point of the rating scale (M = 8.00, SD = 1.384, min =5). End ratings were similarly high (M = 8.00, SD = 1.708, min = 4), and were positively correlated with mid-session ratings ($r(23) = 0.775$, $p < 0.001$). When asked to compare their motivation for the second session versus the first, approximately half of participants reported increased motivation (n = 13) in contrast to eight who reported decreased motivation, with four reporting no motivation change after the manipulation. This variability in the effect of the manipulation on motivation levels allowed us to focus our analyses on individual differences in motivation.

Task Performance. Figure 9a shows the percentage of correct responses during each learning and test phase both BEFORE and AFTER the manipulation. Participants performed significantly better on Phase 2 AFTER the manipulation ($t(24) = 2.234$, $p = 0.035$). In contrast, neither Phase 1 performance, which was necessarily at chance both BEFORE and AFTER the manipulation, nor Test Phase performance, which reflected accurate recall of 75.28% of the word pairs, differed significantly BEFORE versus AFTER the manipulation ($t(24) = 0.653$, $p = 0.520$; $t(24) = 1.219$, $p = 0.235$, respectively). In other words, the motivational manipulation affected performance mainly on learning phase 2, which represents the first opportunity for participants to demonstrate the amount they learned from the study phase.

Participants varied in the extent to which both their Phase 2 and Test Phase performance differed after the manipulation (% correct AFTER - % correct BEFORE), with an average Phase 2 *difference score* of +4.89% (SD = 10.93%) and an average Test

Phase *difference score* of +2.65% (SD = 10.87%). Most importantly, individual

differences in *motivation change ratings* were significantly correlated with the change in

Phase 2 performance ($r(23) = 0.601$, $p = 0.001$; Fig. 9b) and Test performance ($r(23) =$

0.435, $p = 0.030$) from BEFORE to AFTER the manipulation. Individuals who

experienced the greatest increases in motivation also evinced greater gains in

performance from the BEFORE to AFTER sessions. Thus, improved learning

performance appears to depend upon the extent to which motivation increased after the

manipulation.

fMRI Results

     Feedback Sensitivity. Regions involved in feedback processing were identified

using a whole-brain contrast of activation at the onset of positive versus negative

feedback during the learning phases of both sessions of the task, illustrated in Figure 10.

During both learning phases, positive feedback elicited higher activation than negative

feedback in many regions that have previously been implicated in reward and feedback

processing, including the bilateral ventral striatum, right amygdala, ventromedial

prefrontal cortex, and posterior cingulate cortex (Table 2). In addition, the inferior

temporal gyrus, middle temporal gyrus, fusiform gyrus, parahippocampal gyrus, inferior

parietal lobule, thalamus, middle frontal gyrus, and posterior cerebellum also exhibited

stronger BOLD responses at the onset of positive relative to negative feedback. Despite

previous findings that the dorsal striatum is more responsive to feedback during the

second phase of learning, when feedback reflects the accuracy of one's memory (Tricomi

& Fiez, 2008), no striatal regions exhibited significantly greater sensitivity to feedback

valence during phase 2 compared with phase 1, although this pattern was observed in the paracentral lobule and parahippocampal gyrus (Table 3).

Changes across sessions. When comparing across sessions, we used intra-session contrasts of positive > negative feedback to control for potential effects of time or separate scanning sessions on the BOLD signal for individual conditions. To examine differences in feedback sensitivity BEFORE and AFTER the manipulation, we compared feedback sensitivity (positive > negative) BEFORE versus AFTER the manipulation using the contrast AFTER (positive > negative feedback) > BEFORE (positive > negative feedback). Valence sensitivity declined after the manipulation in the ventral striatum, as well as parts of the occipital cortex and cerebellum (Fig. 11a; Table 4), which is consistent with decreases in task engagement that were reported by the subjects (see section below).

Relationship between feedback sensitivity and motivation. Within the ventral striatum ROI identified above, the decline in valence sensitivity was negatively correlated with the raw motivation ratings from the manipulation between the two learning sessions ($r(23) = 0.466$, $p = 0.019$; Fig. 11b) and the end of the study ($r(23) = 0.461$, $p = 0.020$). In other words, the most motivated subjects showed the smallest decline in valence sensitivity over the course of the experiment. This pattern suggests that more motivated subjects may maintain focus and remain responsive to feedback later during the experiment, bucking the trend of becoming less attentive due to sleepiness or boredom that often occurs later in the experiment. Because the learning task takes over an hour to complete, it is normal for participants to lose focus later during the experiment, and in

fact 21 out of 25 reported becoming bored or sleepy either halfway through the experiment (n=10) or during the second experimental session (n=11).

The whole-brain ANCOVA using *motivation change rating* as a covariate identified regions in which BEFORE to AFTER changes in valence sensitivity correlated with changes in motivation from BEFORE to AFTER the manipulation. Two regions in the left temporal lobe exhibited a positive relationship between increasing motivation and increasing valence sensitivity, including a medial temporal region peaking in the left anterior parahippocampal gyrus (peak x, y, z = -22, -20, -24; $r(23) = 0.692$, $p < 0.05$ corrected; Fig. 12a) and the middle STS (peak x, y, z = -40, -23, -12; $r(23) = 0.622$, $p < 0.05$ corrected; Fig 12b). In the parahippocampal gyrus and the STS, differential activation for positive > negative feedback increased AFTER the manipulation for participants who also reported increases in motivation AFTER the manipulation. These regions have been implicated in associative learning, strength of associations during retrieval (parahippocampal gyrus; Achim et al., 2002; Spaniol et al., 2009), and speech processing (middle STS; Hein & Knight, 2008), so this pattern of activation may represent task-related activation that is enhanced when motivation is high.

Relationship between feedback sensitivity and test phase performance. A whole-brain ANCOVA using the *test phase difference score* as a covariate identified bilateral posterior cingulate regions in which BEFORE to AFTER changes in valence sensitivity correlated with changes in test phase performance from BEFORE to AFTER the manipulation (Fig. 13). Additional regions that demonstrated an inverse correlation between test phase performance changes and changing valence sensitivity are included in Table 5, which lists all of the regions identified in this analysis.

Subsequent memory analysis. A subsequent memory analysis identified large

regions, including a wide area of left PFC, spanning the IFG and parts of MFG and

precentral gyrus (peak in IFG, x, y, z = -40, 7, 24; $t(24) = 5.050$, $p < 0.05$ corrected), as

well as the left middle temporal gyrus (peak x, y, z = -61, -47, -9; $t(24) = 5.426$, $p < 0.05$

corrected), where activation during the first learning phase predicted accuracy during the

second learning phase (Fig. 14). All regions showing a subsequent memory effect are

listed in Table 6.

Effective connectivity. We conducted an exploration of effective connectivity to

shed light on possible relationships between feedback processing, motivationally

modulated task activation, and subsequent memory effects that were observed during the

learning task. Patterns of effective connectivity are displayed in Figure 15 for five

functional ROIs that were implicated in feedback processing (ventral striatum),

motivationally sensitive task activation (the middle STS and anterior parahippocampal

gyrus), and subsequent memory performance (the peak PFC region in left IFG and the

posterior middle temporal gyrus). The clusters were functionally defined based on the

analyses described in the Methods, and clusters that spread across multiple brain areas

(IFG/MFG and middle temporal gyrus) were bounded by 8mm spherical masks centered

on their peak coordinates. Left and right ventral striatum ROIs were combined into a

single bilateral ROI. Connectivity was estimated separately for positive and negative

feedback occurring during Phase 1 and Phase 2 of learning. During phase 1, the ventral

striatum influenced activation in the broader performance network by way of the STS, the

area where sensitivity to feedback valence was modulated by motivation in our study.

The STS in turn influenced activation in regions that showed a subsequent memory effect

in our study. This pattern of activation suggests that during Phase 1, feedback processing in the reward network has downstream effects on motivationally sensitive task processing in the temporal lobe, which in turn appears to influence processing in the regions implicated in successful learning.

Patterns of connectivity were broadly similar across both positive and negative feedback within each learning phase, but varied across phases. During Phase 2, activation in the performance network appears to affect activation in the ventral striatum. This difference from Phase 1 may reflect the change in task demands, as during Phase 2, retrieval of existing associations can precede feedback responses and generate expectations about whether a response is likely to be correct or incorrect.

Discussion: Experiment 2b

In experiment 2b, participants completed a learning task before and after the motivational intervention, which had been validated in Experiment 2a as a means to improve task performance via changes in motivation from BEFORE to AFTER the manipulation. Performance increases after the manipulation were associated with increasing motivation, suggesting that the instructive efficacy of feedback is enhanced when motivation is increased. Motivation appeared to sustain feedback processing in the striatum across the duration of the lengthy task, and increases in motivation following the manipulation were associated with heightened sensitivity to positive versus negative feedback in the left STS and parahippocampal gyrus. These results suggest that neural processing of feedback valence is dependent upon motivation to perform well on the task. Since the STS is associated with the processing of verbal information and the parahippocampal gyrus with associative memory, the observed effects may relate to

enhanced task processing during periods of high motivation (e.g., Hein & Knight, 2008; Achim, Bertrand, Montoya, Malla, & Lepage, 2007).

Motivational Effects on Feedback Processing

In the ventral striatum, differentiation between positive and negative feedback weakened after the manipulation. Participants reported that they became bored or sleepy approximately halfway through the study, and this loss of focus may have contributed to the decline in feedback sensitivity later in the experiment. However, task-specific motivation attenuated the general trend for feedback sensitivity to decline across the two sessions of the learning task, suggesting that the more motivated participants may have remained more attuned to the feedback in spite of their weariness. The ventral striatum has been previously implicated in reward processing and learning to predict positive outcomes, so its involvement during feedback-based learning has been interpreted as evidence that positive feedback is viewed as a rewarding outcome (Satterthwaite et al., 2012). Highly motivated subjects may be the most likely to replenish their declining interest and maintain their valuation of the feedback, thus explaining the modulating influence of motivation on this decline in feedback sensitivity.

The regions that were most affected by changes in motivation were in the left temporal lobe. The left anterior parahippocampal gyrus exhibited increasing valence sensitivity after the manipulation for those subjects who reported increases in motivation after the motivational interview. The parahippocampal gyrus has been implicated in associative encoding of arbitrary pairs of objects (Achim et al, 2007), emotional memory encoding (Murty, Ritchey, Adcock, & LaBar, 2010), and memory retrieval, including activation during recognition tests that is highest for items that are remembered with the

highest confidence (Spaniol et al., 2009). During Experiment 2b, this parahippocampal region was thus likely involved in the learning and recall of the arbitrary word pairs. The differential activation to positive versus negative feedback, which increased with increasing motivation, may reflect differences in success or confidence between correct and incorrect word pairs. When motivation increases, participants may be more successful at remembering the correct responses with high confidence, which have been associated with greater activation in the parahippocampal gyrus. The motivational modulation of the parahippocampal gyrus in this study is consistent with evidence that dopaminergic projections from the midbrain to the MTL communicate information about the motivational significance of information (Shohamy & Adcock, 2010).

The more lateral temporal region near the middle STS may have been recruited due to the role of this region in speech processing (Hein & Knight, 2002), which could be engaged when the previously learned word pairs are being recalled and/or rehearsed. Greater activation for positive than negative feedback when motivation is higher might indicate more successful retrieval and maintenance of relevant verbal information. It is plausible that task-specific motivation would enhance processing in regions relevant to the processing of words (e.g., the STS) and the formation of associative memories (e.g., the parahippocampal gyrus) during our paired associate word learning task, since previous research has shown motivation-related increases in task-relevant processing in cognitive control and visual networks (e.g., Pessoa, 2009).

Neural processing supporting task performance

While it is important to demonstrate that motivation can influence feedback processing, we were also interested in exploring other brain regions that supported the

learning of declarative associations. The first analysis we used to identify performance-relevant regions was to seek out brain areas where increases in feedback sensitivity AFTER the manipulation would correlate with gains in test performance. The posterior cingulate cortex, which had already been identified in the positive > negative feedback contrast, showed this pattern. Positive > Negative activation during learning increased the most after the manipulation for those subjects who showed the largest performance increase on the AFTER posttest . Although the PCC is considered to be a part of the default network, it has also shown sensitivity to reward prediction error during reinforcement learning (Cohen, 2007), and it has anatomical connections to areas involved in reward, memory, and attention (Pearson et al., 2011). Because it has been implicated in salience processing, reward value, and attentional shifts (Leech et al., 2011), its sensitivity to feedback valence in our task may represent a reward or salience reaction that is translated into shifts in attention and enhanced task performance. A subsequent memory analysis revealed left prefrontal and lateral temporal regions where greater activation during the initial trial + feedback presentation predicted subsequent memory for the correct answer during the second learning phase. Such prefrontal and lateral temporal regions have been previously implicated in encoding and subsequent memory (H. Kim, 2011; Kirchhoff et al., 2000); however, previous studies have also found activation in the medial temporal lobes (e.g., Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998; Wagner, 1998). It is possible that the absence of significant subsequent memory effects in MTL may be due to the comparatively greater reliance on language-related lateral temporal areas resulting from the semantic nature of the task, compared with the more complex associations that are frequently involved in studies that implicate

the MTL (Eichenbaum, 2000). However, null results should be interpreted with caution.

The left PFC region that was heavily recruited during our task has exhibited subsequent memory effects in a previous study involving the same learning task (Tricomi & Fiez, 2008), and activation in this region may reflect greater depth of processing, control over semantic retrieval, and verbal elaboration (Vannest et al., 2012). These functions are relevant to the declarative paired associate task, as a popular strategy for remembering the word pairs involved using associations to connect the two words in a meaningful way. It is likely that the greater engagement of the left PFC during successful elaboration of the word pairs is what contributed to subsequent memory success.

Effective connectivity between motivationally modulated and performance-related areas

To explore the neural processes linking motivation to performance gains, we conducted an effective connectivity analysis, in which interactions were observed between the feedback-sensitive ventral striatum, the motivationally modulated temporal regions, and the prefrontal and temporal areas where activation predicted subsequent memory. Effective connectivity analyses revealed significant interactions among the distinct brain regions that were implicated in feedback processing, motivationally modulated task processing, and subsequent memory during feedback processing. During the initial learning of the word pairs in Phase 1, striatal feedback processing appears to influence activation in a network of regions involved in performance of the task. During Phase 2, when participants have already been exposed to the correct word pairs, the direction of influence appears to reverse, with the performance network regulating activation in the ventral striatum.

Connectivity During Learning Phase 1. During Phase 1 (i.e., the initial exposure to the word pairs), the ventral striatum (the peak site of feedback related activation in this study) exerted an influence over the motivationally modulated task-related activation in the STS. This relationship represents a potential avenue for information about feedback valence to influence the strength of processing in the temporal lobe that is strongest at the times that people felt most motivated to perform well on the task, possibly by way of their mutual anatomical connections to the medial temporal lobe (e.g., Haber & Knutson, 2010; Seltzer & Pandya, 1994; Turken & Dronkers, 2011). This could indicate that, during initial learning, information about feedback valence produces motivationally relevant increases in task activation related to phonological processing of the word pairs which would occur during active maintenance of the words in verbal working memory (*speculative but based on relation to speech processing described in* Hein & Knight, 2002).

Activation in the motivationally sensitive STS in turn affected activity in the IFG during both positive and negative feedback trials, thus potentially influencing which trials might be successfully recalled during the subsequent learning phase. IFG activation has been associated with attention to semantic associations in verbal working memory (e.g., McDermott, Petersen, Watson, & Ojemann, 2003), so this relationship may suggest that motivationally enhanced retrieval in the STS strengthens IFG-driven attentional processes required to successfully remember the word pairs.

Connectivity During Learning Phase 2. During Phase 2, performance-related regions including the IFG and the parahippocampal gyrus influenced activation in the ventral striatum. This could suggest that while feedback valence drives processing during

initial learning, cognitive control regions and those involved in the processing the verbal information take over and regulate responses to feedback during later learning.

Overall, these patterns of connectivity indicate that enhanced task processing during periods of increased motivation may influence activation in areas that support learning, particularly during the initial stages of feedback-based learning when the correct answer is unknown. These findings help to demonstrate a link between the motivational effects on feedback processing and the effects of motivation on learning and imply that the effects may result from interactions between brain networks involved in feedback processing and those involved in doing the work of learning.

General Discussion: Study 2

The present study was designed to test the notion that neural responses to feedback during learning reflect the motivational value of the feedback. We engaged participants in a feedback-based learning task both before and after a motivational manipulation, to determine whether feedback responses in the brain would be affected by motivation to perform well on the task.

Limitations

Because the BEFORE and AFTER sessions of learning took place during separate runs that were spaced apart in time, it was necessary to control for a potential order effect confound. Experiment 2a demonstrated test phase improvements for participants who experienced the manipulation and not the control group, suggesting that performance improvements cannot merely be attributed to the prior exposure to the experimental paradigm. Additionally, to address this confound within the fMRI sample, individual conditions were never contrasted between sessions, but rather within-session contrasts

(e.g., positive > negative feedback) were compared across the two sessions. Because we were not able to directly compare individual conditions, our results are limited to regions where motivation or task performance were related to differential processing of positive versus negative feedback. The second-order contrasts make interpretation difficult in brain areas that are not typically associated with effects of feedback valence, such as the temporal lobes and lateral prefrontal cortex, but are a necessary compromise to rule out global differences in signal that may occur across experimental sessions.

The motivation change ratings that we used to determine whether motivation increased from BEFORE to AFTER the motivational interview were collected at the end of the experiment. Retrospective reporting on whether motivation increased, decreased, or remained the same across the two sessions of learning may have been biased by awareness that the motivational interview was meant to increase motivation. However, because motivation change was correlated with task performance even for control participants who did not complete the motivational interview, these results do not appear to have been biased by awareness of the purpose of the interview.

One additional limitation is the discrepancy between the findings in Experiment 2 and those from previous implementations of this task. Previous research on striatal engagement during learning has demonstrated that feedback is only differentially processed in the caudate when that feedback reflects successful goal attainment – not when it informs about the accuracy of arbitrary responses (Tricomi & Fiez, 2008). Experiment 2 did not replicate this pattern. In the Experiment 2, during the very first learning phase, responses were meant to be completely arbitrary as the participants had no way of deducing which option was correct. However, it is possible that the

participants in this sample may have experienced a "gambler's fallacy," or a belief that they had the power to choose the "correct" option during the very first learning phase, in spite of the instructions emphasizing the arbitrary nature of the associations. Although there are no data to speak to this hypothesis, anecdotally there were a handful of participants who reported one session or another seeming "easier" in spite of the words being paired at random, due to perceived differences in the ease with which they formed associations between the correct pairs. It is known that striatal responses are heavily context dependent, and that even the illusion of agency can result in stronger engagement of the caudate during reward processing (Tricomi, Delgado, & Fiez, 2004). Thus, it is possible that due to subtle differences either in the task instructions or the demographics of the present sample, participants may have felt a stronger sense of control over their responses during the first learning phase.

Conclusions

This study provides evidence that striatal processing of performance-related feedback is modulated by motivation, with more motivated subjects maintaining a greater differentiation between positive and negative feedback during the second half of the study (after the point that the majority of subjects begin to feel bored or sleepy). Furthermore, other brain areas involved in language processing, including the left medial and lateral temporal lobe, showed valence sensitivity that was modulated by increasing motivation. These regions functionally interact with the prefrontal and temporal cortical areas from the subsequent memory analysis, suggesting that motivational influences on learning may involve a wider network than merely the reinforcement learning system that is based in the striatum. The reward system appears to interact with brain regions

implicated in declarative memory, semantic processing, and executive functioning, to

jointly influence subjective experience and successful learning.

Chapter 4: Study 3: Effects of avoidance goals on striatal responses to feedback following a competence threat

Not all forms of motivation are conducive to learning. When motivation is channeled towards goals that emphasize positive strivings, as in Study 2, performance can benefit. However, there are times when motivation is directed towards avoidance of negative states. A great deal of behavioral research has yielded support for a distinction between performance-approach goals, which are oriented towards attaining positive outcomes, and performance-avoidance goals, which are geared towards avoiding failure (e.g., Elliot & Thrash, 2010). Performance-avoidance goals have been associated with adverse impacts on motivation and performance in academic settings (e.g., Elliot, McGregor, & Gable, 1999), and laboratory research has shown that the threat of punishment can impair declarative learning when compared with reward-based learning (e.g., Murty, LaBar, Hamilton, & Adcock, 2011).

Performance discrepancies due to approach versus avoidance motivational biases can be viewed in terms of stress and coping. When confronted with the same stressor, a person who feels capable of success might perceive a difficult task as an exciting challenge, while another might perceive it as a threat and become anxious about the possibility of failure. Which response a person will exhibit — threat or challenge — depends upon cognitive appraisals about the demands of the situation, as well as one's perceived ability to cope with those demands (Folkman, Lazarus, Dunkel-Schetter, DeLongis, & Gruen, 1986). Threat appraisals are associated with diminished academic performance (Seery, Weisbuch, Hetenyi, & Blascovich, 2010), much like performance-

avoidance goals, which have been linked with decreased depth of processing and poorer exam performance (Elliot, McGregor, & Gable, 1999).

Achievement goals are founded in the desire to pursue and display competence (Deci & Moller, 2005). A threat to one's competence could be expected to induce a motive to restore that sense of competence that has been lost (Laws & Rivera, 2012), which might take the form of either approach- or avoidance-oriented achievement goals. Within a threatening context, individual variations in task-specific avoidance goals might increase the tendency to interpret negative feedback as punishment, which could consequently impede learning (Mangels, Butterfield, Lamb, Good, & Dweck, 2006; Mangels, Good, Whiteman, Maniscalco, & Dweck, 2011).

Prior research suggests that punishment-motivated declarative learning can rely on the amygdala (Murty, Labar, & Adcock, 2012); however, it remains unclear what effect avoidance-oriented achievement goals might have on the feedback-based learning system, which involves the striatum (Shohamy et al., 2004). Neural evidence suggests that both approach and avoidance learning can recruit similar corticostriatal circuitry (Schlund, Magee, & Hudgins, 2011). Striatal responses to rewards and punishments have been well-characterized (e.g., Delgado, Nystrom, Fissell, Noll, & Fiez, 2000), with similar patterns of responding for positive and negative performance feedback in the absence of extrinsic rewards and punishments (e.g., Daniel & Pollmann, 2010; Tricomi & Fiez, 2008). Because reward and feedback responses in the striatum have been shown to be context dependent (e.g., DePasque Swanson & Tricomi, 2014; S. Kim, Lee, Chung, & Bong, 2010; Nieuwenhuis et al., 2005; Tricomi, Delgado, & Fiez, 2004), it is likely that the modulation of reward- and punishment- related responses in this region may play a

role in the modulation of learning based on approach and avoidance goals.

While Study 2 can be viewed as an exploration of the positive effects of motivation on feedback-based learning, Study 3 was designed to shed light on the neural mechanisms underlying the often detrimental effects of avoidance goals on performance. Because neural responses to negative feedback are highly sensitive to the context in which it is received (e.g., Mixed Fb study, Katya's study), we wanted to create a context in which negative feedback would be more likely to be perceived as a punishment. To this end, we posed a threat to participants' competence, which enabled us to investigate the potential negative effects of threat and avoidance goals on the processing of negative feedback during learning. In experiment 3a, we validated this threat manipulation behaviorally, and in experiment 3b we examined the neural correlates of feedback processing within a group exposed to the threat manipulation. This study provides the first experimental evidence for threat-related effects of avoidance goals on negative feedback processing in the striatum.

General Methods: Study 3

Threat Manipulation. Before engaging in the learning task, participants completed a bogus, but believable, computerized intelligence test, consisting of fifteen questions ostensibly related to verbal and reasoning abilities, within a twenty-minute time limit. The test and instructions were in accordance with the procedures described by Laws and Rivera (2012). This test was completed immediately prior to the scan and was described as a separate study on "cognitive factors" that was being conducted in collaboration with another researcher. On-screen instructions described the test as a new and accurate form of intelligence test that assesses both verbal and reasoning abilities.

Upon completing the test, participants received a test score with a low percentile rank (47th percentile), which presents a threat by undermining subjects' perceived competence (Laws & Rivera, 2012).

Experimental Task. The paired-associate word learning task used in Study 2 was modified for this study (Fig. 16). In the present study, all 180 trials were presented in a single learning session that took place after the threat manipulation, rather than being divided into separate "BEFORE" and "AFTER" sessions. The second modification involved a change to the first learning phase.

Due to our interest in affective reactions to negative feedback, it was important that the first experience of performance feedback should reflect goal achievement rather than the result of an arbitrary choice, which might be interpreted as purely informational and reduce the affective impact of negative feedback (Tricomi & Fiez, 2008). To this end, the original learning phase 1 was eliminated and replaced with a study phase, during which the correct answer was highlighted in green (illustrated in Figure 14). During the study phase, all 180 trials were presented in random order, with the same trial durations used in Study 2. The word pairs were displayed, as in Study 2, but with the correct option highlighted in green. Subjects were instructed to memorize the word pairs so they could choose the correct option during the subsequent learning phase.

The study phase was followed by a single feedback-learning phase, in which all 180 trials were shown again in random order, this time without the correct answer highlighted. The same response options and trial timing were used: a 4-second trial screen, during which participants could select either the first or the second option using two buttons on an MRI-compatible button box; followed immediately by 1.5-second

feedback screen; and a fixation point between trials (1-6 seconds jitter). After completing

the feedback phase, participants began the self-paced test phase, during which they

entered their final response and rated their confidence in their answer on a sliding scale

from 1 (completely guessing) to 7 (completely certain).

Although the addition of a study phase introduces an observational learning

component to the task, a previous experiment using the same paradigm demonstrated that

further learning took place during the feedback learning phase, even when it followed an

opportunity to study the word pairs (Dobryakova & Tricomi, 2013). Consistent with these

prior findings, the Study 3 participants exhibited significant gains in accuracy between

the feedback learning phase and the test phase (see Results).

Method: Experiment 3a

Experiment 3a was designed to validate the manipulation as a means to influence

the subjective experience of feedback during learning. To this end, this behavioral study

included a threat group and a control group.

Participants. Fifty-two undergraduate psychology students completed

Experiment 3a in exchange for course credit. Participants were randomly assigned to

either the experimental group (n=27) or the control group (n=25). The procedures were

approved by the Institutional Review Board of Rutgers University, and all participants

gave written informed consent.

Threat Manipulation/Control Procedure. The experiment was programmed to

randomly assign each participant to either the threat or the control group at the start of the

experiment. Both groups completed the timed intelligence test; however, the control

group received test instructions that explained they would not receive a test score at the

end of the test. Consistent with the instructions, they did not receive any percentile score. In contrast, the experimental group subjects received a test score with a low percentile rank (47th percentile) after they completed the test, which has been established as sufficiently low to pose a threat to perceived competence (Laws & Rivera, 2012).

Questionnaires. At the conclusion of the study, both threat and control participants reported their feelings about the intelligence test, both in an open-ended ("Please describe how you felt after completing the intelligence test/receiving your score"), and a Likert scale response format ("Please indicate how you felt after completing the intelligence test," on a scale from 1/negative to 7/positive). The post-experiment questionnaire also included questions about how rewarding and punishing subjects found positive and negative feedback and how concerned they were with performing well on the learning task, all rated on the same scale from 1 to 7.

After the study, participants also completed the Achievement Goal Questionnaire (Elliot & Church, 1997) to assess general trait achievement goal orientations. The questionnaire contains 18 items, with 6 each for three subscales: performance-approach goals, performance-avoidance goals, and mastery goals. Each item contained a statement with respect to a university-level college course (e.g., "I am motivated by the thought of outperforming my peers in this class"), and participants were instructed to think about their current psychology class (if applicable) or a specific alternate class of their choice when rating their agreement with the statement. Each question was rated on a scale from 1(not at all true of me) to 7 (very true of me).

Behavioral Analysis. Performance on the paired associate learning task was defined based on the percentage of trials with correct responses in the feedback learning

phase as well as the test phase. Between-group differences in test accuracy and phase 2 accuracy were tested using two-tailed, independent samples t-tests, as were between-group differences in average confidence scores as reported during the test phase. To determine whether avoidance goals influenced affective responses to the intelligence test, we examined correlations between participants' feelings after the manipulation and their avoidance goals. In addition, we examined correlations between performance and individual differences in avoidance goals, reward value of positive feedback, and aversion to negative feedback.

Results: Experiment 3a

Behavioral Results. Among the pilot subjects, those in the threat group ($n = 27$) rated their feelings after the bogus intelligence test on the "negative" end of the rating scale (mean = 3.22, neutral = 4), and these ratings were significantly lower (i.e., more negative) than control subjects ($n = 25$; CONTROL mean = 4.38; $t(51) = 3.12, p < 0.01$). These ratings indicate that receiving a score in the 47th percentile was indeed perceived as a negative experience. There were no preexisting differences in IQ test accuracy between the threat and control groups, $t(51) = 0.17, p = 0.87$, so these differences cannot be attributed to differences in actual performance on the bogus test. Despite the bias in participants' affective responses, the manipulation did not exert a significant influence on overall task performance, $t(51) = 0.66, p = 0.52$, or on average confidence during the test phase, $t(51) = 1.01, p = 0.32$. However, within the threat group, avoidance goals were negatively correlated with test phase performance, $r(25) = -.0389, p < 0.045$. This relationship was not observed in the control group, $r(24) = 0.01, p = 0.98$, suggesting that individual differences in the adoption of avoidance goals during learning may predict

whether or not a threat to one's competence will have a detrimental effect on performance.

Across all subjects, performance-avoidance goals were also correlated with how negatively subjects rated their feelings about receiving negative feedback, $r(51)= .290, p = .035$. This relationship was not significant in the control or experimental groups alone, although there was a marginal trend, in the threat group, $r(25)=.352, p=0.072$. Together these results suggested that avoidance goals in conjunction with a competence threat may interfere with performance and increase the sense of punishment caused by negative feedback.

Discussion: Experiment 3a

Although the bogus intelligence test scores influenced affective ratings after the manipulation, a direct effect of the manipulation on performance was not observed. Rather, the effects appeared to be modulated by predisposing factors, specifically performance-avoidance goals, which predicted diminished task performance and increased aversion to negative feedback after a competence threat. Taken together, these findings suggest that the psychological impact of a competence threat may be influenced by the level of avoidance motivation reported at the time of the experiment.

This enhancement of the effects of the threat on performance by avoidance goals is consistent with previous research, which has suggested that outcomes may be influenced via interactions between trait achievement goals and state-induced goals (e.g., Capa, Audiffren, & Ragot, 2008; Cianci, Schaubroeck, & McGill, 2010; Pulfrey, Buchs, & Butera, 2011; Yeo, Loft, Xiao, & Kiewitz, 2009). Experiment 3a yielded hints that trait differences in performance avoidance goals correlate with affective responses to the IQ

test, indicating that the poor evaluation has a stronger effect on people who are predisposed toward avoidance goals. For that reason, Experiment 3b was designed to probe individual differences in performance avoidance goals that might correlate with neural responses to feedback under conditions of threat.

Method: Experiment 3b

Due to the findings of Experiment 3a, which indicated that individual differences in avoidance goals exhibit stronger relationships with performance and subjective feedback responses after a competence threat, we conducted the fMRI experiment within a threat sample to better understand the neural processing underlying these individual differences. All participants experienced the threat manipulation prior to the learning task, and neural responses to feedback were examined with respect to individual differences in avoidance goals and in task performance.

Participants. Twenty-nine right-handed adult participants (12 males) were recruited from the university community to participate in the study. Imaging data from one participant were excluded due to a software logging error, leaving data from twenty-eight participants (11 males) in the final fMRI analyses as opposed to the twenty-nine that were included in behavioral analyses. As in the previous studies, the sample consisted of predominantly university students and staff with a broad range of demographics. Participants were pre-screened to ensure that they had never taken part in a prior study involving either the word-learning task or the competence threat manipulation. All participants who completed the study received compensation of $50 for their time. The procedures were approved by the Institutional Review Board of Rutgers University, and all participants gave written informed consent.

Questionnaires. *Prescreen:* Prior to scheduling an appointment, all fMRI

participants completed a prescreening survey, which consisted mainly of MRI safety

related questions, but which also included the Achievement Goal Questionnaire (Elliot &

Church, 1997) to assess general trait achievement goal orientations. The questionnaire

contains 18 items, with 6 each for three subscales: performance-approach goals,

performance-avoidance goals, and mastery goals. Each item contained a statement with

respect to a university-level college course (e.g., "I am motivated by the thought of

outperforming my peers in this class"), and participants were instructed to think about

their current psychology class (if applicable) or a specific alternate class of their choice

when rating their agreement with the statement. Each question was rated on a scale from

1(not at all true of me) to 7 (very true of me). Because the three subscales can be

correlated (people who are highly motivated by approach goals can also be motivated to

avoid negative outcomes as well), and because of our interest in the specific effects of

avoidance goals rather than overall motivation levels, an *avoidance goal bias* was

calculated by subtracting the average rating for the performance-approach subscale from

the average rating from the performance-avoidance subscale of the questionnaire. As a

result, *avoidance goal bias* can vary from positive (relatively more avoidance-motivated)

to negative (relatively more approach-motivated), with higher scores for individuals for

whom avoidance goals loom larger. The use of a bias score also helped to circumvent

potential gender effects: on the prescreening survey, there was a trend for females to

score slightly higher than males on both the avoidance and approach achievement goal

subscales of the original Achievement Goal Questionnaire, but there was no gender

difference in avoidance goal bias (see results).

Post-questionnaire: After completing the experimental task, participants completed a post-experiment questionnaire, during which they rated how rewarding and punishing they found positive and negative feedback, on a scale of 1 (not at all) to 7 (extremely), and how important it was to them to perform well on the learning task on a scale from 0 (not at all important) to 10 (extremely important). Because post-experiment ratings of achievement goals might be sensitive to the threat manipulation, participants also completed a modified version of the Achievement Goal Questionnaire (Elliot & Church, 1997), in which the text was changed to reflect goals specific to the experimental task (e.g., instead of "I am motivated by the thought of outperforming my peers *in this class*," the wording would be changed to "I was motivated by the thought of outperforming my peers *during this task*"). As with the prescreening survey, a task-specific avoidance goal bias (*"task avoidance bias"*) was calculated by subtracting the average subscale score for performance-approach goals from the score for performance-avoidance goals. The responses on this task-specific measure of achievement goals were used to investigate the effects of avoidance goals on feedback processing in the brain.

Behavioral Analysis. As in Experiment 3a, performance was defined based on the percentage of trials with correct responses in both the feedback learning phase and the test phase. To examine the effects of avoidance goals on feedback processing under threat, correlations were performed between *task avoidance bias* and performance on the learning and test phases. In addition, to determine the effects of avoidance goals on the perception of feedback during learning, *task avoidance bias* was also subjected to correlations with the subjective ratings of how rewarding and punishing the participants found positive and negative feedback, respectively. In addition, to assess the stability of

approach versus avoidance goals, we also conducted correlations between the trait achievement goal scores obtained in the prescreen and the state ratings provided during the post-experiment questionnaire.

fMRI Analysis. After preprocessing, the fMRI data were analyzed using a random-effects GLM to identify voxels throughout the brain that differentiate between positive and negative feedback at the time of feedback presentation. The predictors of interest include positive and negative feedback during the Learning Phase, in which feedback is presented after each response. Six motion parameters were also included in the model as predictors of no interest. Clusters of voxels were identified by the GLM analysis at an uncorrected statistical threshold of $p < 0.005$, and the resulting map was subjected to a cluster threshold estimator, resulting in a corrected threshold of $p < 0.05$. Because the activation observed was extensive, with continuous regions of activation that spread from prefrontal cortex through the posterior cingulate, the threshold was increased to disambiguate the separate regions involved in the contrast. The data are visualized in Figure 4 and described in Table 7 at the more conservative threshold of $p<0.0001$, cluster corrected to $p<0.05$, so that separate peaks could be reported for each of the brain regions contained within the mass of activation.

Because caudate activation has been previously associated with subsequent confidence in one's responses (Tricomi & Fiez, 2012), we also conducted a whole-brain GLM in which learning phase trials were grouped according to whether the participant subsequently rated their confidence that they accurately remembered the word pair during the test phase. High subsequent confidence trials (test phase ratings between 5-7) were contrasted against low subsequent confidence trials (test phase ratings between 1-3),

clusters of voxels were identified at a threshold of p<0.005, and the resulting map was subjected to cluster threshold correction, resulting in a corrected threshold of p<0.05.

Whole-brain ANCOVAs. To identify brain regions where feedback processing was modulated by threat-related avoidance goals, whole-brain analyses were performed using *task avoidance bias* as a covariate. Of primary interest was the analysis that focused on negative feedback, in which *task avoidance bias* was entered as a covariate for the contrast between baseline and negative feedback. Since baseline estimates reflect average activation across all time points during the scan that are not accounted for in the GLM, this estimate includes fixation time as well as time spent during the stimulus/response periods. This method of calculating baseline does not include a true "rest" period but rather posits an average level of activation during all of the non-feedback time points during the scan. A separate ANCOVA included *task avoidance bias* as a covariate and used the contrast of Positive Feedback > Baseline to examine regions where positive feedback responses were correlated with the threat-related avoidance goals. Finally, a third ANCOVA was performed to identify regions where the sensitivity to feedback valence (Positive > Negative Feedback) correlated with *task avoidance bias*. Clusters of voxels were identified by the whole-brain ANCOVA at an uncorrected statistical threshold of p < 0.005, and again the resulting map was subjected to a whole-brain cluster threshold estimator, resulting in a corrected threshold of p < 0.05.

ROI Analysis. Due to the a priori interest in the striatum, two striatal regions of interest were created on the basis of prior data, one in dorsal striatum and one in ventral striatum, to further explore correlations between feedback responses and *task avoidance bias*. Because the learning tasks completed in Experiments 2 and 3 were highly similar,

the striatal clusters were chosen based on the peak coordinates from the positive >

negative contrast in Experiment 2. To define the ROIs, 6 mm spheres were created,

centered on the Experiment 2 peak coordinates within the caudate nucleus (x, y, z = 11,

10, -1) the right ventral striatum (x, y, z = 14, 1, -9), and the left ventral striatum (x, y, z =

-16, 1, -12). The left and right ventral striatum regions were then combined into a single

bilateral ROI. Correlations were performed between *task avoidance bias* and responses to

feedback within each ROI.

In addition, to build on the findings from Experiment 1, correlations were

performed between normative goals and feedback activation in the a priori ROIs. For the

present study, normative goals were defined using the average scores on the five

normatively-oriented performance-approach items from the modified task-specific

Achievement Goal Questionnaire (e.g., "It is important to me to do well compared to

others in this task").

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Results: Experiment 3b

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Behavioral Results.

Score on Bogus Intelligence Test. Actual performance (% correct responses) on

the bogus intelligence test was 60.72% correct (min=33.00%, max=87.00%, SD=.149).

Performance on this test was marginally correlated with *task avoidance bias* (r(27)=-

.359, *p*=.056), indicating the *task avoidance bias* was most pronounced for people who

performed poorly. However, performance on the intelligence task did not correlate with

task performance during either the learning phase or test phase of the experimental task

(r(27)=.174, .273, p = .368, .152, respectively). This suggests that although poor

performance during the bogus intelligence test may have enhanced the effects of the

threat manipulation on avoidance motivation, it did not reflect any underlying differences in ability to perform well on the learning task.

Task Performance. Performance on the learning task is displayed in Figure 17. The percentage of correct responses made during the learning phase (after completion of the study phase) was above chance (mean=.672, SD=.123; t(28)=7.536, p<0.001). Response accuracy at test phase significantly improved over the learning phase (mean= .743, t(28)=6.062, p<.001), indicating that learning occurred both during the study phase, when the correct answer was highlighted, and during the feedback learning phase.

Subjective Feedback Ratings. On a scale from 1 (not at all rewarding) to 7 (extremely rewarding), participants rated positive feedback as a relatively rewarding experience (mean=5.759, SD=1.156). On an analogous scale from 1 (not at all negative) to 7 (extremely negative), negative feelings about negative feedback were significantly less intense than the rewarding experience of positive feedback (mean=3.828, SD=1.338; t(28)=6.013, p<0.001). This could be due to the informative nature of the negative feedback.

Avoidance Goals. As noted above, the prescreen questionnaire revealed a trend for females to score slightly higher than males on both the performance-avoidance and performance-approach achievement goal subscales (*t*(27)=1.777, 2.535; *p*=0.087, 0.017, respectively) of the original Achievement Goal Questionnaire. No gender difference was observed in *avoidance goal bias* (*t*(27)=0.512, *p*=0.613), calculated by subtracting the performance-approach subscale average from the performance-avoidance subscale average. Consequently, bias scores were used in all further analyses to avoid the necessity of splitting the sample by gender, which would result in small and uneven groups. The

average prescreen *avoidance goal bias* was close to neutral, mean=-.822, SD=1.232, with scores ranging from -3.83 (bias toward approach goals) to 1 (bias toward avoidance goals). The majority of participants (*n*=19) fell on the approach end of the bias scale, indicating that in general people are more likely to endorse higher approach goals than avoidance goals, at least within the university and surrounding community from which our sample was recruited.

Task avoidance bias scores were calculated based on the post-experiment achievement goal questionnaire, and represented task-specific goals that were adopted during the experiment. These task-specific avoidance bias scores ranged from -2.83 (bias toward approach goals), to 2.33 (bias toward avoidance goals). The average *task avoidance bias* score was again close to neutral (mean=-.3908, SD=1.288), and correlated significantly with *avoidance goal bias* from the prescreen, *r*(27)=.369, *p*=.049. This correlation, while significant, represents only a medium effect size (Cohen, 1988), suggesting that task-specific avoidance goals may be affected by factors other than one's general trait achievement goal orientation (possibly including the threat manipulation). As with the prescreen questionnaire, there were no gender differences in *task avoidance bias*, *t*(27)=.233, p=.817, so analyses focused on the group as a whole. Because task-specific goals should relate more directly to motivation and behavior after the intelligence threat, the following analyses focus on the relation of *task avoidance bias* to neural activation and subjective experiences of feedback during learning.

Relationships between Avoidance Bias Subjective Ratings, and Task Performance.

Individuals who experienced higher levels of *task avoidance bias* found positive feedback subjectively more rewarding, as evidenced by a positive correlation between

task avoidance bias and subjective reward ratings for positive feedback, ($r(27)=.486$, $p=.008$; Figure 18a), which remained significant even when controlling for performance on the bogus intelligence test ($r(26)=.374$, p=.050). However, no such relationship was observed between *task avoidance bias* and the subjective ratings of negative feedback, $r(27)=-.127$, $p=.512$. Although these results might indicate that avoidance goal bias affects the reward processing of positive feedback more than the negative affective responses to negative feedback, it is also possible that self-report about how negatively the participants felt about negative feedback might not accurately reflect the true range of affective responses at the time of feedback.

Task avoidance bias scores did not correlate with task performance, either for the learning phase ($r(27)=-.052$, p=.790) or the test phase ($r(27)=.052$, p=.790. As a result, the observed relationships between *task avoidance bias* and neural activation during feedback processing are not confounded with performance differences. Similarly, no relationship was observed between positive feedback ratings and performance during either the learning ($r(27)= -.076$, p=.694) or test phase ($r(27)= .008$, p=.966). However, subjective ratings of negative feedback were significantly correlated with performance during both the feedback phase of the learning task, $r(27)=.406$, $p=.029$, and on the test phase, $r(27)=.393$, $p=.035$, indicating that the feedback was perceived as most aversive by those who were performing the best at the task (Figure 18b). Due to the relationship between negative feedback ratings and task performance, it is possible that recollections about the subjective experience of negative feedback might be biased based on the frequency at which negative feedback was received. This may reflect a true difference in the immediate affective responses to feedback, but it is also possible that affective

responses during the negative feedback trials were simply easier to recall for better performers because they stood out in contrast with the higher number of positive feedback trials.

To investigate whether normatively focused achievement goals, similar to those measured in Experiment 1, related differently to task performance under conditions of threat, a correlation was performed between task performance and the average score on performance-approach items on the Achievement Goal Questionnaire that reflected normative goals. A nonsignificant but trending negative relationship was observed: learning phase $r(29)=-.299$, $p=.115$; test score $r(29)=-.312$, $p=.099$. Participants who were high in normative goals tended to perform slightly worse on the task.

fMRI Results

Neural sensitivity to feedback valence. The network of brain regions involved in feedback processing during this experiment closely resembled that from Experiment 2. As illustrated in Figure 19, positive feedback elicited higher activation than negative feedback in areas including the caudate, putamen, and ventral striatum, vmPFC, medial temporal lobes, and posterior cingulate cortex. For a complete list of these regions and their statistics, see Table 7.

Subsequent confidence effects. Table 8 displays regions throughout the brain that were identified in the whole-brain subsequent confidence analysis. Notably, the body of the caudate exhibited greater activation during learning for trials that were subsequently remembered with high confidence.

Avoidance goals in the brain. To explore the effects of threat-induced avoidance goals on striatal of feedback, correlations were conducted between *task avoidance bias*

and neural activity, both throughout the brain and in two a priori ROIs. Regions identified in the whole-brain correlational analyses are listed in Table 9, and the striatal ROI analyses are reported in Table 10. *Task avoidance bias* correlated significantly with the contrast of Negative Feedback < Baseline in a wide extent of subcortical areas, including the caudate nucleus, ventral striatum, and midbrain (Figure 20a). ROI analyses revealed a similar pattern: in both the a priori caudate and ventral striatum ROIs, there was a significant negative correlation between task avoidance bias and signal at the time of negative feedback (Figures 20b, 20c). That is, higher bias toward avoidance goals was associated with lower striatal activation in response to negative feedback. In addition, *task avoidance bias* correlated significantly with the contrast of Positive > Negative feedback in the head of the caudate nucleus (Figure 21). For positive feedback processing, no regions of the striatum were modulated by *task avoidance bias*. A median split was used to plot of the time course of each of these ROIs separately for those who were highest and lowest in *task avoidance* bias. This plot, displayed in Figure 22, illustrates how individuals who were more avoidance-biased show a larger dip in striatal activation following negative feedback – a response that has sometimes been referred to as a "punishment response" (Delgado, Locke, Stenger, & Fiez, 2003).

To build on the findings from Experiment 1, the performance-approach items that reflected normative goals were also investigated with respect to activation in the a priori striatal ROIs. In the caudate, but not the ventral striatum, normative goals were positively correlated with signal at the onset of both positive and negative feedback (Caudate positive/negative: $r(26)=.394/.427$, $p=.0386/.023$; Ventral Striatum positive/negative: $r(26)=.146/.194$, $p=.458/.324$, respectively). A plot of the time course for individuals high

versus low in normative goals (based on a median split) illustrates that individuals who are higher in normative goals exhibit a slower but more sustained increase in activation for positive feedback relative to the earlier rise exhibited by those lower in normative goals. The high normative goals group also exhibits a slightly attenuated "punishment" response to negative feedback (Figure 23).

Discussion: Experiment 3b

The aim of Experiment 3b was to investigate the relationship between individual differences in task-specific avoidance goals and the neural processing of feedback during learning, particularly within the striatum. A threat manipulation was used to create a context in which avoidance goals might influence affective responses to negative feedback. A bias toward avoidance goals was associated with greater differentiation between positive and negative feedback in the dorsal striatum, and with exaggerated decreases below baseline in response to negative feedback in the ventral striatum.

Subjective Experience of Feedback

In accord with the hypothesis that achievement goals might influence the motivational salience of feedback, bias toward avoidance goals was associated with a greater sense of reward from positive feedback. This could indicate a sense of relief, since it is a signal that failure has been successfully avoided (Higgins, Shah, & Friedman, 1997). Avoidance bias was not associated with exaggerated negative feelings toward negative feedback as hypothesized; however, since it was linked with heightened neural sensitivity to negative feedback it is possible that the self-report ratings were not sensitive to the true affective responses experienced by the participants. Interestingly, the negative feedback ratings were significantly correlated with performance on the learning task. This

relationship may indicate that participants who were performing better on the task found negative feedback more aversive because of its relative rarity, or because of elevated expectations for success, which could have made it more surprising due to their superior performance.

Achievement Goals in the Striatum

In the dorsal and ventral striatum, as well as in the midbrain, a bias toward avoidance goals during the task was associated with a larger dip below baseline after receiving negative feedback. Positive feedback responses did not elicit a stronger reward response, suggesting that the experience of negative feedback was most closely linked to this avoidance goal bias, at least in the neural circuitry associated with learning from feedback and rewards. This may help to explain why task avoidance bias did not correlate with task performance. If the neural repercussions of threat and avoidance goals affected striatal processing of negative feedback more than positive feedback, then it is possible that it would not affect learning that was dependent upon responses to positive feedback. This would be consistent with evidence that the dorsal striatum supports learning from positive reinforcement, whereas other regions such as the amygdala, anterior cingulate, and lateral orbitofrontal cortex promote learning from punishments (Murty et al., 2012; Wrase et al., 2007). The task used in Experiment 3 has been previously associated with striatal processing and therefore may be more strongly driven by neural responses to positive feedback than negative feedback.

The absence of a performance effect may alternatively suggest that, in the context of this task, avoidance bias may not be a maladaptive trait. Performance-avoidance goals may particularly impede performance on tasks where there is an expectation or fear that

one might perform poorly (Brodish & Devine, 2009), but if success on the task is perceived as easily accomplished, then even those individuals who were more biased toward avoidance goals may have felt that successful attainment of those goals was likely. In other words, the aim to avoid doing poorly may not be maladaptive when expectations for success are high. Thus, it will be important for future research to disentangle the effects of performance-avoidance goals and expectations for success.

In addition to the results regarding avoidance motivation, activation in the striatum was also modulated by normative performance-approach goals. Task-specific normative goals were correlated with heightened signal for both positive and negative feedback in the caudate, and plots of the time course suggest that this is due to a lower-magnitude but more prolonged rise above baseline for positive feedback and attenuated dip below baseline for negative feedback. This finding is intriguing in light of the results of Experiment 1, which also demonstrated an effect of normative goals on feedback processing in the caudate (DePasque Swanson & Tricomi, 2014). Unlike the findings from Experiment 1, in which normative goals were associated with a differentiation between positive and negative feedback that was most exaggerated during blocks that were expected to be more difficult, the present study revealed no difference in positive > negative feedback differentiation but rather a more sustained positive feedback response and attenuated punishment response. Furthermore, in the present study, there was a trend for normative goals to be associated with poorer learning performance. The different role of normative goals in the two experiments could be due to the contextual differences, including the threat manipulation in Experiment 3, as well as due to the different nature of the analyses (in Experiment 1, we correlated normative goals with the effects of a

within-subjects manipulation, whereas here we are looking at individual differences in the processing during a single condition). The relation of these findings will be further discussed in Chapter 5.

General Discussion: Study 3

Experiment 3a established that a competence threat manipulation could influence affect and increase the relevance of avoidance goals in shaping the subjective experience of feedback during learning. Because the perception of negative feedback can be biased toward the punishing aspects or the more informative aspects depending upon the context in which it is received (e.g., Tricomi, Delgado, & Fiez, 2004), it was important to create a context that would bias participants toward viewing negative feedback as a punishment in order to better understand the relationship between striatal activation and the punishing aspects of negative feedback during learning. Experiment 3b demonstrated sensitivity of this relationship to the goals endorsed by the participants; specifically that people for whom avoidance goals loomed larger during learning showed exaggerated decreases in striatal activation following negative feedback. These results support the hypothesis that the striatum is responsible for encoding not only the motivational value of positive feedback but also the degree to which negative feedback provides an aversive motivational signal during learning.

Relation to prior research

Approach and avoidance goals have been theorized to reflect distinct underlying behavioral systems, instantiated in different patterns of neural processing (Corr & McNaughton, 2012). Some researchers have suggested that the maintenance of approach versus avoidance goals is carried out within the PFC (e.g., Berkman & Lieberman, 2010;

Eddington et al., 2007). In the present study, rather than attempting to localize the source of the goal representations guiding behavior, I aimed to investigate the evaluative processes that occur after performance-related feedback, since this feedback indicates whether one's goal was achieved on a given trial and might be sensitive to the type of goals participants hold during learning. Declarative learning that is motivated by punishment has been linked to interactions between the amygdala and the medial temporal lobes, suggesting that the experience of aversive consequences modulates learning by engaging a punishment related system rather than the reward-driven basal ganglia (Murty et al., 2012). Increased arousal due to the threat of punishment has been associated with detrimental effects of on declarative learning, suggesting that the anxious anticipation of a punishment is a less effective means of motivating learning than the pursuit of reward (Murty et al., 2011). However, while this previous research relied on manipulation of aversive versus appetitive stimuli or reinforcers to induce approach or avoidance goals, the present study was designed to investigate individual differences in aversive responses to negative performance-related feedback without manipulating the stimulus itself.

The present study is unique in that it used a competence threat to create a context in which avoidance goals would be relevant, and analyses focused on individual differences in the processing of identical stimuli (i.e., green checkmark for positive performance-related feedback and red X for negative performance-related feedback). Avoidance goals appeared to bias responding to these outcomes in the striatum, particularly with respect to negative feedback. These results suggest that the extent to which an individual seeks to avoid poor performance can modulate the subjective

"punishment response" in the striatal system that is integral for feedback-based learning. These findings parallel neural evidence that arousal-related activation in the dorsal striatum is moderated by avoidance temperament (Spielberg et al., 2012), but add to the literature by linking task-specific goals with modulation of feedback-related responses during learning.

Limitations

The aim of Study 3 was to explore individual differences in the processing of negative feedback that might reflect exaggerated punishment signals for those who were more motivated by avoidance goals. Although an effect of *task avoidance* bias was observed in striatal responses to negative feedback, self-report did not corroborate the view of this exaggerated striatal dip as reflecting subjective affective responses to the feedback. This discrepancy could be interpreted in several ways: First, we could assume that the self-report is accurate and look to change our view of what the striatum is coding during negative feedback. It is possible that the negative feedback may be considered more relevant to one's goals if one's goal is to avoid negative feedback. Perhaps it is the relevance to their goals, rather than the punishing nature of the feedback, that causes this exaggerated dip in activation.

A second way to interpret this discrepancy is in questioning the accuracy of self-reported affective reactions to negative feedback. After the study concluded, participants might have a chance to reflect on the informative nature of the feedback and forget their initial aversive reactions. This would be consistent with a previous study, which showed that negative feedback was processed more similarly to positive feedback after a delay (Dobryakova & Tricomi, 2013). Reflecting on negative feedback outside the moment of

the initial response, one might no longer think of the feedback as punishing, and may report feeling less negatively about it than if they had been asked at the time of their initial response. The behavioral pilot group did exhibit a relationship between their ratings of negative feedback and their avoidance goals, which may be due to the fact that they made their ratings at the same computer at which they completed the learning task. The fMRI group took the post-experiment questionnaire after exiting the scanner, which introduced a slightly longer time period between the task and the questionnaire as well as a change in setting. These factors could help to explain why the subjective experience of negative feedback was more strongly linked with avoidance goals in the behavioral group than in the fMRI group.

Finally, it is possible that both approach- and avoidance-oriented individuals would perceive negative feedback as being equally "negative," but in different ways that could be reflected differently in neural feedback responses. The strength of a person's goals may influence the emotional intensity associated with goal attainment, but the goal content could be expected to influence the type of emotion experienced (Higgins, Shah, & Friedman, 1997). It is possible that a difference in the nature of the aversive reaction to negative feedback for individuals biased toward avoidance versus approach goals would not be captured by the phrasing of the question, which merely inquired how "negative" it felt to receive negative feedback. Feeling very disappointed could be described as very negative by individuals pursuing approach goals, but the greater tension or unease experienced by the avoidance motivated participants could be associated with a stronger striatal punishment response, even if given the same rating for general "negativity."

A related concern is the possibility that the self-reported task avoidance goals at the end of the study might reflect a hindsight bias, and reflect the individual's interpretation of their goals at the end of the study rather than the goals they were experiencing during learning. Such a rating might be biased by the prominence of negative feedback experienced over the course of the task, rather than goals that the participant had adopted prior to learning. However, the lack of a relationship between task avoidance bias and performance within the fMRI sample provides some evidence that avoidance goals were not simply effects of how much negative feedback a person had received. This supports the idea that the avoidance goals rated by the participants reflected an experience that was general to the learning session and not necessarily a product of the type of feedback received. It is also possible that the ratings may have been affected by an awareness that the manipulation was meant to induce avoidance goals. Individual differences in task avoidance bias might then reflect differences in the degree to which participants were aware of the expected link between avoidance goals and the threat manipulation, or the degree to which they wished to cooperate with the purposes of the study. Yet, the relationship between these ratings and the negative responses to negative feedback during learning suggest that the motives of the individual, whether purely driven by task specific avoidance goals or a concern with being a "good research subject," result in exaggerated responses to negative feedback during learning. This interpretation is still consistent with a role for motivation and goals in driving striatal responses to feedback.

Conclusion

It is important to understand the role that the striatum plays in processing the affective value of negative feedback during learning. Study 3 provides support for the hypothesis that, under a threat to one's competence, goals oriented toward avoiding failure can result in an exaggerated punishment response to negative performance-related feedback in the striatum. These results are exciting because they suggest that responses to negative feedback in the caudate and ventral striatum reflect the subjective experience of negative feedback in a way that is influenced by achievement goals. As a result, it is plausible that in cases where avoidance goals do have an effect on learning, the striatum may play a role. Because avoidance goals were not associated with significantly poorer outcomes in the present study, it is possible that the exaggerated negative feedback signals observed do not harm performance, at least not in all cases. Considering the positive relationship between the subjective aversive ratings of negative feedback and superior performance, it is even possible that, given the right circumstances, exaggerated affective responses to negative feedback might result in enhanced learning. These findings illustrate the complex role that feedback can play during learning, serving a motivational role in addition to its instructive function. A greater understanding of the motivational factors that influence striatal responses to feedback can help to shed light on the precise role of the striatum in learning from negative feedback, as well as illuminating the factors that can increase or decrease the motivational salience of negative performance-related feedback.

Chapter 5: General Discussion: The modulatory effects of achievement goals and task motivation on striatal feedback responses

Summary

These dissertation experiments were conducted to explore the effects of motivation-relevant expectations and goals on striatal activation during feedback-based learning. Activity within the striatum was modulated by achievement goal orientation (Experiments 1 and 3) and by the level of motivation expressed toward the learning task (Experiment 2), suggesting that such activation reflects the motivational salience of performance-related feedback, rather than merely signaling whether or not performance was accurate. When task difficulty expectations were high, individuals with competitively oriented goals showed enhanced task performance and exaggerated responses to feedback in the dorsal striatum. During a lengthy task, high motivation levels served to attenuate the reduction in feedback sensitivity in the ventral striatum later in the task, as participants grew fatigued. And when competence was threatened, the extent to which participants oriented towards avoidance goals correlated with the strength of the "punishment response" to negative feedback in both the dorsal and ventral striatum. Together, these studies demonstrate that the direction and strength of an individual's motivation during learning, as assessed by measures of achievement goal orientation and task importance ratings, can influence striatal responses to performance-related feedback. These findings suggest that subjective feedback responses in the striatum are modulated by the motivational salience of the information, relating to the relevance of the feedback to one's goals during learning.

Achievement Goals in Dorsal Striatum

Achievement goals direct motivation toward a particular type of outcome (e.g., achieving higher scores than one's peers or proving that one is not incompetent), and as a result they might be expected to influence the motivational value of positive and negative performance-related feedback during learning. In Experiment 1, the effect of experimentally manipulated task difficulty expectations was enhanced for those who expressed high levels of normative goals, which are goals to outperform one's peers. For the individuals who were most motivated by normative goals, the characteristic difference in striatal signal for positive versus negative feedback trials was exaggerated in blocks that were expected to be hard. Furthermore, in Experiment 3, *task avoidance bias* was linked with exaggerated sensitivity to feedback valence in the caudate.

Notably, effects of normative goals on feedback processing were observed in the dorsal (caudate and putamen) but not the ventral striatum. The localization of these effects, as well as the effect of *task avoidance bias* on positive > negative feedback sensitivity in the dorsal striatum, may relate to the differential roles of these striatal subregions in reward processing and behavioral control. The dorsal/ventral distinction within the striatum has been widely studied, and it is believed that the dorsal striatum is engaged in instrumental learning while the ventral striatum is involved in reward anticipation and prediction (O'Doherty et al., 2004). More specifically, within the dorsal striatum, reward and feedback related signals are believed to reinforce particular actions, rather than merely signaling the presence of unexpected rewards. The ventral striatum has been described as a part of an emotional system that engages general affective and behavioral reactions (e.g., Pavlovian approach or avoid responses) based on stimulus valence, while the dorsal striatum is believed to be more involved in the control of

specific behavioral responses (Gruber & McDonald, 2012). Effects of achievement goals on feedback sensitivity in the dorsal striatum may therefore reflect enhanced relevance of the feedback to one's goals. This fits with previous findings that activation in the caudate is linked with successful achievement of specific goals (Han, Huettel, Raposo, Adcock, & Dobbins, 2010).

Motivation within the Ventral Striatum

Because the provision of extrinsic incentives can reduce the amount of time spent performing a task once those incentives are removed, extrinsic reinforcement is believed to have an undermining effect on the motivation to engage in a task for its own sake (Deci, Koestner, & Ryan, 1999). Evidence for such an undermining effect has been linked with diminished activation in the striatum (Murayama, Matsumoto, Izuma, & Matsumoto, 2010). While it is useful to understand the potential dangers of motivating performance through extrinsic incentives, it is also important to understand how the motivation to perform a task might be enhanced without undermining its intrinsic value. Experiment 2 was designed to enhance the subjective value of a task without resorting to the use of rewards to entice performance. The motivational strategy used in Experiment 2 was adapted from motivational interviewing to encourage reflection on the intrinsic value of the task (Miller & Rollnick, 1991). Subjective motivation to perform well on the task helped to maintain activation in the ventral striatum, which is consistent with a role for this region in the general energization of behavior (Gruber & McDonald, 2012). The ventral striatum has been associated with reward prediction and the representation of reward value (e.g., Diekhof, Kaps, Falkai, & Gruber, 2012; Knutson & Cooper, 2005), as well as the energization of effortful behavior (Salamone, Correa, Farrar, & Mingote,

2007). Therefore, effects of motivation within this part of striatum would likely relate to increased valuation of the feedback and willingness to expend effort to perform well on the learning task.

The ventral striatum also exhibited a relationship with *task avoidance bias* in Experiment 3, with increased bias toward avoidance goals correlating with an exaggerated dip below baseline for negative feedback. This relationship might be suggestive of a more fundamental divide between approach and avoidance motivation, which might bias attention toward signals of positive goal attainment in the case of approach goals, or signals of failure, in the case of avoidance goals. Regulatory Focus Theory describes the distinction as between promotion goals, which are akin to approach goals in their emphasis on attaining ideal outcomes, versus prevention goals, which resemble avoidance goals in their emphasis on avoiding losses (e.g., Shah, Higgins, & Friedman, 1998). Shah and colleagues found that the adoption of promotion-related goals increased motivation to gain points, while the pursuit of prevention goals increased motivation to avoid losing points. In other words, the emphasis of a person's goals can influence the degree to which effort is invested toward attaining positive feedback versus avoiding negative feedback. The presence of avoidance goal bias during Experiment 3 may have resulted in a heightened focus on negative feedback due to the mindset that one is striving to avoid failure. For this effect to be found in the ventral striatum may suggest that avoidance goals create a more fundamental change in the affective value of negative feedback, and is consistent with the role of the ventral striatum in general responses to outcome valence and basic appetitive versus aversive responding (e.g., Gruber & McDonald, 2012).

Interactions between declarative and non-declarative learning systems

Experiments 2 and 3 made use of a task that is known to recruit both the striatum, due to its trial and error structure, and the learning systems involved in declarative memory. Importantly, although achievement goals influenced performance as well as striatal feedback responses during Experiment 1, no achievement goals were less directly linked with performance in Experiments 2 and 3. This lack of a connection between affective responses to feedback and task performance may reflect the complex interplay between these two memory systems: the feedback learning system, which is grounded in the striatum and is responsible for gradual learning of stimulus- or action-outcome contingencies, and the declarative memory system, which is based in the medial temporal lobes and supports the learning of declarative associations (e.g., Squire & Zola, 1996). Neuropsychological research have produced evidence for a double dissociation between the functions of these two systems; however, they may interact in ways that, depending on context, can be either competitive or cooperative (e.g., Delgado & Dickerson, 2012; Hartley & Burgess, 2005). The paired-associate learning task used in Experiments 2 and 3 is known to engage both systems (Tricomi & Fiez, 2008), yet it is not entirely clear to what extent both contribute to performance. The findings from Experiment 2 suggest that in the context of declarative memory, striatal and temporal regions may interact to support the processing of motivationally salient feedback, thus enhancing the executive processing needed to improve performance on the task. However, since the present studies focused mainly on the processing of feedback valence and thus emphasized the role of the striatum; future investigations that emphasize the interactions between the

striatum and the temporal lobes may paint a fuller picture of how motivation might influence this form of learning.

Subsequent Memory

Subsequent memory analyses in Experiment 2 and a prior study using the same task implicated the left inferior frontal gyrus as well as the middle temporal gyrus in activation that give rise to later memory success (Tricomi & Fiez, 2012). The same prior study also demonstrated that caudate activation in response to positive feedback predicts subsequent confidence at test phase, suggesting that the dorsal striatum plays a role in the strengthening of the declarative memory associations. The effective connectivity analysis in Experiment 2 yielded some evidence for an interaction between the striatum and those regions that were involved in successful memory, specifically by way of the STS; however, the motivational influences on activation in the medial temporal lobe region (peaking in parahippocampal gyrus) appeared to result from a cascade of influence that arrives by way of the middle temporal gyrus. These results suggest that the dynamics of learning declarative information through trial and error may be more complex than typical, non-declarative feedback-based learning. A subjective sense of reward may influence memory indirectly by way of interactions between the striatum, or directly by way of projections from the dopaminergic midbrain into the medial temporal lobes (Shohamy & Adcock, 2010); thus, further research will be needed to tease apart their distinct roles in this task, which relies on both.

Declarative influences on striatal learning

In Experiment 1 the presentation of task difficulty information played a role in shaping striatal responses to performance-related feedback, at least for those who were

higher in normative goals. The striatum therefore appeared to be sensitive to declarative knowledge about the task, which is consistent with earlier findings that prior declarative knowledge can shape reward responses in the striatum during learning (e.g., Delgado, Frank, & Phelps, 2005; Li, Delgado, & Phelps, 2011). Experiment 1 demonstrated that preexisting goal orientations can modulate declarative influences on striatal feedback processing, likely by altering the affective impact of such information.

Performance and the posterior cingulate

In experiment 2, brain activations associated with task performance were found in the posterior cingulate, inferior frontal gyrus, and the middle temporal gyrus. Effective connectivity revealed indirect interactions between these regions (specifically the inferior frontal gyrus and middle temporal gyrus) and the ventral striatum, by way of the motivationally modulated STS, suggesting that the successful implementation of semantic retrieval and verbal working memory required for the task are influenced by, but not necessarily reliant on, striatal feedback processing.

The role of the posterior cingulate in this task is intriguing because prior research has primarily implicated it in the default network (e.g., Mason et al, 2007). Yet during both the second and third experiments, it appeared to be engaged in the processing of positive and negative performance-related feedback. This pattern of engagement is not unheard of, as the posterior cingulate has exhibited sensitivity to performance-related feedback, including during a learning task that required the learning of simple stimulus-action associations (Marco-Pallares, Muller, & Munte, 2007). The posterior cingulate is also hypothesized to contribute to the feedback-related negativity (FRN), which is an electrophysiological response that is thought to reflect feedback valence, probability, and

possibly magnitude, and which has been modulated by personality traits much like

striatal responses to rewards (Cohen, Wilmes, & van de Vijver, 2011). It has been

proposed that the posterior cingulate, as part of the default network, may play a role in

"basic cognitive processes typically suppressed during performance of well-learned tasks,

including memory retrieval, internal monitoring, and the global balance of internal versus

external information processing" (Pearson, Heilbronner, Barack, Hayden, & Platt, 2011,

p. 149).

To the extent that the posterior cingulate was differentially engaged by positive

greater than negative feedback during Experiment 2, participants performed better on the

learning task. Thus, it is possible that in monitoring the valence of performance-related

feedback, the posterior cingulate plays a role in learning the novel word pairs presented

in our tasks, which require exploratory cognition in that the associations must be newly

formed rather than accessing well-learned response patterns.

Bridging the gap between feedback and learning

In experiment 1, although normative goals predicted greater effects of task

difficulty expectations on both performance and striatal responses to feedback, the striatal

activations alone did not appear to play a mediating role. Performance effects were

observed only within the objectively less difficult blocks of trials, yet differences in

feedback processing were observed across both sets of trials. It seems that enhancing

striatal responses to feedback is not in itself enough to promote improved learning, at

least in Experiment 1 when performance required identification of successful

categorization strategies. It is possible that learning was more directly supported by

regions outside of the striatum, or that complex interactions between the striatum and

other areas, such as those involved in object recognition, might better capture the neural differences that give rise to learning. Limitations of experiment 1: because of the relatively short time (12 trials each) allowed for the learning of the distinctions between each pair of categories, it is possible that the effects of enhanced feedback processing did not have time to cumulatively affect performance. Had the blocks been lengthened and included repeats of some of the same trials, perhaps we would have seen a more direct link between striatal processing and learning success. Striatal functioning has been linked with relatively more gradual, procedural forms of learning, so the regions that facilitate rapid learning of category distinctions may lie elsewhere (Squire, 2004).

Given the absence of a direct link between feedback responses in the striatum and learning outcomes for Experiments 2 and 3, it is possible striatal engagement during feedback supports learning in a less direct manner than the regions that support the formation of the declarative associations. Future research should take a network connectivity approach and study tasks in which repetition throughout many trials gives the striatal system a time frame in which it stands to influence performance.

Achievement Goals: Why Context Matters

Although normative goals seemed to have a positive effect on performance and subjective responses to feedback in Experiment 1, it is likely that normative goals may have exerted a less beneficial effect if the participants had felt they were unlikely to succeed. Performance goals in general, of which normative goals are an example, have proved to be vulnerable to a steep drop-off in expectations for success when faced with difficulty (Grant & Dweck, 2003). Performance goals have also been linked with exaggerated affective responses to negative feedback, which were also accompanied by

reductions in effortful processing needed to learn new material (Mangels et al., 2006). While normative goals may have bolstered performance in Experiment 1, Experiment 3 presented a threat to participants' competence. In this more challenging setting, participants may have felt less confident in their ability to succeed, and normative goals appeared to be a hindrance to performance on the task.

The Neuroscience of Achievement Goals: Bridging the past and the present

These experiments provided novel evidence that contextual factors and individual differences can modulate the subjective reactions to positive and negative performance-related feedback as processed within the striatum. These findings fit with the notion that reward processing in the striatum is sensitive to the affective significance of the rewards. Previous research has linked individual differences in striatal reward responses to a diversity of traits such as self-interest, extraversion, propensity for exploration, and need for power (e.g., Brosch, Coppin, Scherer, Schwartz, & Sander, 2011; Cohen, Schoene-Bake, Elger, & Weber, 2009; Frank, Doll, Oas-Terpstra, & Moreno, 2009; Schultheiss & Schiepe-Tiska, 2013). Striatal reward processing has also been linked specifically with motivation-related characteristics, such as BIS/BAS (behavioral inhibition/activation systems, which have been framed as reflecting avoidance and approach motivation; Simon et al., 2010), and with intrinsic versus extrinsic motivation (e.g., Linke et al., 2010). This evidence is suggestive of a subjective system that is tuned to the relevance of the rewards in the environment. Whereas these prior studies focused on individual differences in the processing of rewards, the present research aimed to characterize responses in the striatum for informative performance-related feedback, in the absence of extrinsic rewards or punishments. Moreover, these studies helped to integrate what we

know of the striatal reinforcement learning system with the existing constructs from the achievement motivation literature.

My findings complement the limited body of research that has explored the relationship between achievement goals and neural responses during learning. A few prior studies have revealed hints that neural feedback responses may be modulated by such goals. For instance, in the absence of monetary incentives, the strength of subjective motivation appears to increase feedback-related motor preparation in the putamen during a working memory task (Mizuno et al, 2008). Individuals who are high versus low in performance-approach goals differ with respect to which type of feedback (norm-referenced, which compares performance to others, versus criterion-referenced, which compares performance to a set standard) more strongly engages regions putatively linked with negative affect, such as the insula and anterior cingulate (Kim et al., 2010). An undermining effect of rewards on subsequent non-rewarded feedback processing found a significant decline in activation within the striatum (in the head of the caudate, rather than in the ventral striatum), which was associated with declining intrinsic motivation to perform the task (Murayama, Matsumoto, Izuma, & Matsumoto, 2010). This effect could similarly reflect the extent to which the participants' goals were being achieved – on the one hand, the goal to earn money, and on the other hand, the goal to enjoy the task. Furthermore, a recent morphology study found gray matter density in the right putamen to be linked with a measure of competitive achievement motivation (as well as the insula and precuneus; Takeuchi et al., 2014). Together, these findings suggest that individual differences as well as moment-to-moment changes in one's priorities can influence the sensitivity of the reinforcement learning system to performance-related feedback.

Conclusion

Because feedback can be an important motivator of learning, it is important to better understand the conditions that can influence the affective salience of the feedback. These three experiments examined the neural underpinnings of reinforcement learning under varying conditions, to help illuminate the role of achievement motivation in shaping the learning signals produced in response to performance-related feedback. The results suggested that learning can be enhanced or diminished through the manipulation of motivationally relevant expectations, values, and beliefs; and that such factors can either increase or attenuate striatal responses to feedback. These findings have implications for the use of feedback in educational as well as clinical settings: a better understanding of the ways that individual goals, beliefs, and values can influence the motivational impact of our teaching strategies, both neurally and behaviorally, can help to inform more specific interventions to channel motivation toward adaptive outcomes.

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Study 1.

Table 1. Experiment 1: Results of the 2x2x2 repeated measures ANOVA in three a priori striatal ROIs.

Region of Interest	Direction of Effect	F value	p value	η^2_p	Effect Size
Main Effects:					
Actual Difficulty					
Caudate Nucleus	High > Low	0.77	0.391	0.039	Small
Putamen	High > Low	2.31	0.146	0.108	Medium
Ventral Striatum	Low > High	0.265	0.613	0.014	Small
Labeled Difficulty					
Caudate Nucleus	--	0.032	0.859	0.002	--
Putamen	--	0.109	0.744	0.006	--
Ventral Striatum	--	0.057	0.814	0.003	--
Valence					
Caudate Nucleus	Positive > Negative	7.56*	0.013	0.285	Large
Putamen	Positive > Negative	46.743*	0.000	0.711	Large
Ventral Striatum	Positive > Negative	19.695*	0.000	0.509	Large
Interactions:					
Actual Difficulty x Labeled Difficulty					
Caudate Nucleus	--	0.009	0.925	0.000	--
Putamen	--	0.001	0.978	0.000	--
Ventral Striatum	Congruent label > Incongruent Label	0.353	0.559	0.018	Small
Actual Difficulty x Valence					
Caudate Nucleus	High (pos > neg) > Low (pos > neg)	2.872	0.106	0.131	Medium
Putamen	--	0.079	0.781	0.004	--
Ventral Striatum	High (pos > neg) > Low (pos > neg)	0.651	0.43	0.033	Small
Label x Valence					
Caudate Nucleus	"HARD" (pos > neg) > "EASY" (pos > neg)	1.412	0.249	0.069	Medium
Putamen	"HARD" (pos > neg) > "EASY" (pos > neg)	0.583	0.455	0.03	Small
Ventral Striatum	"HARD" (pos > neg) > "EASY" (pos > neg)	1.205	0.286	0.06	Small

Study 2.

Table 2. Experiment 2b: Regions that distinguished between positive and negative

feedback during both learning phases.

Region of Activation	BA	Size (# voxels)	Peak Talairach Coordinates (x, y, z)			T	p
Conjunction of Ph1 & Ph2							
Positive feedback > Negative Feedback							
Middle Temporal Gyrus	21	804	53	-2	-15	4.602542	0.000114
Inferior Parietal Lobule	40	1640	50	-41	42	4.168089	0.000344
Posterior Temporal/Occipital Cortex	37	11331					
Middle Temporal Gyrus	*37*		*44*	*-56*	*-3*	*5.17903*	*0.000026*
Lingual Gyrus	*18*		*35*	*-68*	*-3*	*4.651729*	*0.000101*
Cerebellum (Tuber)		2937	35	-68	-30	4.897619	0.000054
Putamen/Insula		776	26	1	15	3.775207	0.000928
Cerebellum (Tonsil)		701	29	-35	-36	4.587294	0.000119
Medial Temporal Lobe		1312					
Hippocampus			*29*	*-26*	*-12*	*4.273731*	*0.000263*
Parahippocampal Gyrus			*29*	*-38*	*-9*	*3.714557*	*0.00108*
Striatum (R)	34	5132					
Ventral striatum			*14*	*1*	*-9*	*5.601601*	*0.000009*
Caudate head			*11*	*10*	*-1*	*4.037283*	*0.00048*
Posterior Cingulate	29	24138	5	-47	12	5.019207	0.00004
Thalamus		388	23	-20	3	3.79853	0.000875
Anterior Cingulate	32	9893	-7	40	3	5.057983	0.000036
Ventral Striatum (L)	34	5009	-16	1	-12	5.856353	0.000005
Inferior Occipital Gyrus	17	16265	-16	-89	-6	5.426193	0.000014
Parahippocampal Gyrus	36	802	-34	-35	-9	3.943556	0.000608
Insula	13	501	-34	-8	18	4.068482	0.000443

Negative feedback > Positive feedback
no regions were more active during negative than positive feedback across both sessions of the task

BA, Brodmann Area.
To better identify the separate brain areas encompassed within the larger clusters, the threshold was increased until the larger clusters separated into smaller ones and those peaks are also reported.

Study 2.

Table 3. Experiment 2b: Regions that exhibited an effect of learning round on feedback valence sensitivity.

Region of Activation	BA	Size (# voxels)	Peak Talairach Coordinates (x, y, z)			T	p
Comparing learning round 1 (arbitrary choices) to learning round 2 (feedback reflects accuracy of memory)							
Ph 1 (pos > neg) > Ph 2 (pos > neg)							
Insula	13	409	41	19	6	3.834732	0.000799
Cerebellum (Anterior lobe)		192	-4	-44	-30	4.107541	0.000401
Ph 2 (pos > neg) > Ph 2 (pos > neg)							
Paracentral Lobule	5	177	17	-38	51	3.326293	0.002825
Parahippocampal Gyrus		239	11	-8	-15	3.966055	0.000574

BA, Brodmann Area.

Study 2.

Table 4. Experiment 2b: Regions that exhibited an effect of session (BEFORE vs. AFTER

the manipulation) on feedback valence sensitivity.

Region of Activation	BA	Size (# voxels)	Peak Talairach Coordinates (x, y, z)			T	p
Comparing learning sessions BEFORE and AFTER manipulation							
BEFORE (pos > neg) > AFTER (pos > neg)							
Cerebellum (Tuber)		2746	20	-89	-27	4.442522	0.000171
Cuneus	19	2991	-1	-77	36	5.056337	0.000036
Ventral Striatum		789	14	7	0	3.871036	0.000729
Cerebellum (Pyramis)		10530	-43	-74	-33	5.003771	0.000041
Cuneus	19	485	-4	-95	25	3.554545	0.001609
AFTER (pos > neg) > BEFORE (pos > neg)							
no regions showed greater valence sensitivity AFTER than BEFORE							
the manipulation							

BA, Brodmann Area.

Study 2.

Table 5. Experiment 2b: Regions in which changes in test phase performance correlate

with changes in valence sensitivity.

Region of Activation	BA	Size (# voxels)	Peak Talairach Coordinates (x, y, z)			R	p
AFTER (Test % correct) - BEFORE (Test % correct) correlates with AFTER (pos > neg) - BEFORE (pos > neg)							
Change in Test accuracy correlates with change in valence sensitivity							
Positive Correlation							
Posterior Cingulate	30	358	11	-50	15	0.638177	0.000598
Posterior Cingulate	30	757	-19	-50	15	0.713669	0.000509
Negative Correlation							
Superior Frontal Gyrus	10	2642	-25	46	3	-0.691127	0.000131
Precentral Gyrus	6	562	-49	1	33	-0.644324	0.000509
AFTER (Ph2 % correct) - BEFORE (Ph2 % correct) correlates with AFTER (pos > neg) - BEFORE (pos > neg)							
Change in Ph2 accuracy correlates with change in valence sensitivity							
Positive Correlation							
Posterior Cingulate	30	622	-19	-50	12	0.650333	0.000433
Negative Correlation							
n/a							

BA, Brodmann Area.

Study 2.

Table 6. Experiment 2b: Regions in which activation during learning predicts subsequent

memory for individual word pairs.

Region of Activation	BA	Size (# voxels)	Peak Talairach Coordinates (x, y, z)			T	p
SUBSEQUENT MEMORY (activation during Ph1; classified based on Ph2 accuracy)							
Subsequent Correct > Subsequent Incorrect							
Inferior Frontal Gyrus/Middle Frontal Gyrus	9	13511	-43	10	24	5.128897	0.00003
Middle Temporal Gyrus	37	5540	-61	-47	-9	5.411851	0.000015
Subsequent Incorrect > Subsequent Correct							
Precentral Gyrus	4	363	59	-2	21	3.562004	0.00158
Superior Frontal Gyrus	6	939	17	25	54	3.809677	0.000851
Anterior Cingulate	24	464	-1	28	15	3.991459	0.000538
Precuneus	7	662	-4	-53	48	3.762967	0.000957

BA, Brodmann Area.

Study 3.

Table 7. Experiment 3b: Regions that distinguished between positive and negative

feedback during learning.

Region of Activation	BA	Size (# voxels)	Peak Talairach Coordinates (x, y, z)			t	p
Positive feedback > Negative Feedback							
Postcentral Gyrus	2	2843	50	-26	36	7.37881	< 0.000001
Ventral Striatum/Amygdala/MTL		34318					
Putamen (left)			26	-11	6	9.14752	< 0.000001
Ventral Striatum			2	4	-3	7.950954	< 0.000001
vmPFC	10		2	55	9	7.883241	< 0.000001
Caudate Head (right)			5	19	3	7.153072	< 0.000001
Hippocampus (right)			35	-26	-12	6.613299	< 0.000001
Medial Frontal Gyrus	6		5	-20	54	6.327015	0.000001
Amygdala			-28	-11	-12	6.16225	0.000001
Amygdala			26	-8	-12	5.765695	0.000004
Hippocampus (left)			-34	-32	-6	5.658756	0.000005
Inferior Frontal Gyrus	46	517	41	37	6	8.17132	< 0.000001
Middle Occipital Gyrus	19	641	35	-65	6	5.376344	0.000011
Superior Temporal Gyrus	22	657	29	-53	18	5.848066	0.000003
Cerebellum (Uvula)		2326	29	-74	-24	6.533498	0.000001
Middle Occipital Gyrus	18	623	26	-80	0	5.551549	0.000007
Precentral Gyrus	4	858	23	-23	51	6.080144	0.000002
Medial Frontal Gyrus	6	2572	5	-20	54	6.327015	0.000001
Caudate Body/PCC		13056					
Caudate Body			-19	7	18	6.749528	< 0.000001
Posterior Cingulate Cortex	31		-16	-44	24	6.577629	< 0.000001
Cingulate Gyrus	24	398	11	-8	39	7.051751	< 0.000001
Cerebellum (Uvula)		1930	-28	-83	-24	6.191888	0.000001
Superior Frontal Gyrus	8	976	-22	25	48	5.994591	0.000002
Cerebellum (Tonsil)		313	-28	-32	-42	5.561452	0.000007
Inferior Occipital Gyrus	19	1640	-37	-71	0	5.710361	0.000005
Negative feedback > Positive Feedback							
Insula	13	415	-31	19	9	-5.23713	0.000016

BA, Brodmann Area.

*To identify separable peaks within the larger clusters, the threshold was increased. Statistics are reported for the peaks within separate subregions below the heading for the larger cluster.
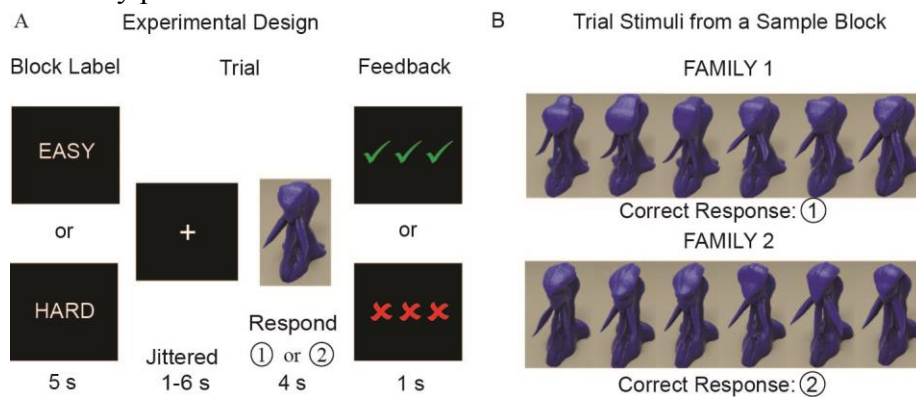
Study 3

Table 8. Experiment 3b: Regions that are modulated by subsequent confidence.

Region of Activation	BA	Size (# voxels)	Peak Talairach Coordinates (x, y, z)			t	p
Subsequent High Confidence > Subsequent Low Confidence							
Cerebellum		1560	17	-71	-24	3.751	0.001
Superior Frontal Gyrus	9	729	-13	37	36	4.483	<0.001
Caudate		815	-19	-8	24	4.559	<0.001
Superior Frontal Gyrus	6	1343	-19	16	51	4.357	<0.001
White Matter near ACC	32	661	-25	37	12	4.209	<0.001
Middle Temporal Gyrus/STS	21	6115	-58	-26	-9	4.955	<0.001
Parahippocampul Gyrus		*36*	*-37*	*-32*	*-9*		
Inferior Frontal Gyrus	47	322	-40	25	-15	4.027	<0.001
Inferior Frontal Gyrus	46	4040	-46	43	6	5.688	<0.001
Fusiform Gyrus	20	608	-46	-11	-24	4.327	<0.001
Subsequent Low Confidence > Subsequent High Confidence							
Inferior Frontal Gyrus	9	1247	53	4	30	-4.618	<0.001
Insula	13	338	38	13	12	-4.187	<0.001
Middle Occipital Gyrus	19	468	32	-86	12	-3.760	0.001
Middle Frontal Gyrus	6	625	20	1	60	-3.725	0.001
Thalamus		469	5	-14	6	-4.120	<0.001
Medial Frontal Gyrus	6	234	-4	-5	48	-3.485	0.002
Middle Occipital Gyrus	19	260	13	-37	-86	-4.078	<0.001

BA, Brodmann Area.

*To identify separable peaks within the larger clusters, the threshold was increased. Peak coordinates are reported for the separate subregions below the heading for the larger cluster.

Study 3.

Table 9. Experiment 3b: Regions in which feedback-related activation correlated with

task avoidance bias.

Region of Activation	BA	Size (# of voxels)	Peak Talairach Coordinates (x, y, z)			r	p
Correlation of Task Avoidance Bias with Negative Feedback < Baseline							
Insula	13	405	38	13	6	0.618832	0.000447
Cerebellum		842	14	-35	-33	0.68398	0.00006
Thalamus/Ventral Striatum		6790					
Thalamus			2	-11	6	0.703655	0.000029
Ventral Striatum			5	1	-3	0.656461	0.000148
Midbrain		572	8	-17	-12	0.731795	0.00001
Cerebellum		1972	-22	-44	-30	0.676253	0.000078
Cerebellum		337	-10	-59	-27	0.649308	0.000185
Caudate nucleus		642	-16	10	15	0.631231	0.000316
Precentral Gyrus	6	569	-25	-11	64	0.615489	0.00049
Middle Frontal Gyrus	6	734	-31	1	51	0.683695	0.000061
Correlation of Task Avoidance Bias with Positive Feedback > Baseline							
Parahippocampal Gyrus	30	542	29	-47	9	0.639264	0.00025
Superior Frontal Gyrus	9	349	-19	61	30	0.661886	0.000125
Superior Frontal Gyrus	8	554	-19	46	46	0.747253	0.000005
Middle Frontal Gyrus	6	332	-31	-2	51	-0.65533	0.000154
Correlation of Task Avoidance Bias with Positive feedback > Negative Feedback							
Insula	13	294	32	-41	21	0.613259	0.00052
Middle Occipital Gyrus		493	32	-71	12	0.557563	0.002052
Cingulate Gyrus	24	330	17	-11	36	0.600283	0.000733
Posterior Cingulate		1125	14	-29	27	0.701753	0.000032
Superior Frontal Gyrus	9	2553	-10	58	33	0.769644	0.000002
Cerebellum		260	-13	-53	-33	0.617686	0.000462
Caudate nucleus		248	-16	16	9	0.64267	0.000226
Occipital Lobe - Lingual Gyrus		655	-19	-77	3	0.665717	0.000111
Superior Frontal Gyrus	8	473	-25	31	55	0.674751	0.000082
Precuneus	7	730	-22	-59	27	0.636191	0.000274
Precentral Gyrus	6	589	-34	-11	33	0.722655	0.000014
Middle Temporal Gyrus	21	269	-52	-2	-12	0.622775	0.000401

BA, Brodmann Area.

*To identify separable peaks within the larger clusters, the threshold was increased. Statistics are reported for the peaks within separate subregions below the heading for the larger cluster.

Study 3

Table 10. Experiment 3b: Results from ROI correlation analyses.

Correlation	Region of Interest	Condition	R value	p value	Effect Size
Task Avoidance Bias & Contrast: Positive Fb > Negative Fb					
	Ventral Striatum	Positive > Negative	0.268	0.169	Small
*	Caudate Head	Positive > Negative	0.378	0.047	Medium
Task Avoidance Bias & Negative Feedback					
*	Ventral Striatum	Negative Feedback	-0.401	0.034	Medium
**	Caudate Head	Negative Feedback	-0.518	0.005	Large
Task Avoidance Bias & Positive Feedback					
	Ventral Striatum	Positive Feedback	-0.233	0.232	Small
	Caudate Head	Positive Feedback	-0.322	0.094	Medium

Study 1

Figure 1. Experiment 1: Experimental design. A. Sixteen blocks of trials were each preceded by an arbitrary task difficulty label, presented to influence expectations about task difficulty. Twelve trials per block included a jittered fixation (1-6 s), stimulus presentation/response period (4 s), and immediate presentation of positive or negative feedback (1 s). B. Within each block of trials, twelve distinct figures from two different families would appear in random order. Members of one family were associated with the first button on the button box, while members of the second family were associated with the second button. During the next block, members from two new families would be randomly presented.

Study 1

Figure 2. Experiment 1: Behavioral results. A. For low-difficulty blocks, performance was significantly better for "HARD"-labeled than "EASY"-labeled blocks. B. Percent correct responses are plotted for early trials (trials 1-4), middle trials (5-8), and late trials within each block (9-12), to visualize the time course over which expectations influenced learning. Expectation-related performance differences emerged during the late trials for low-difficulty blocks.
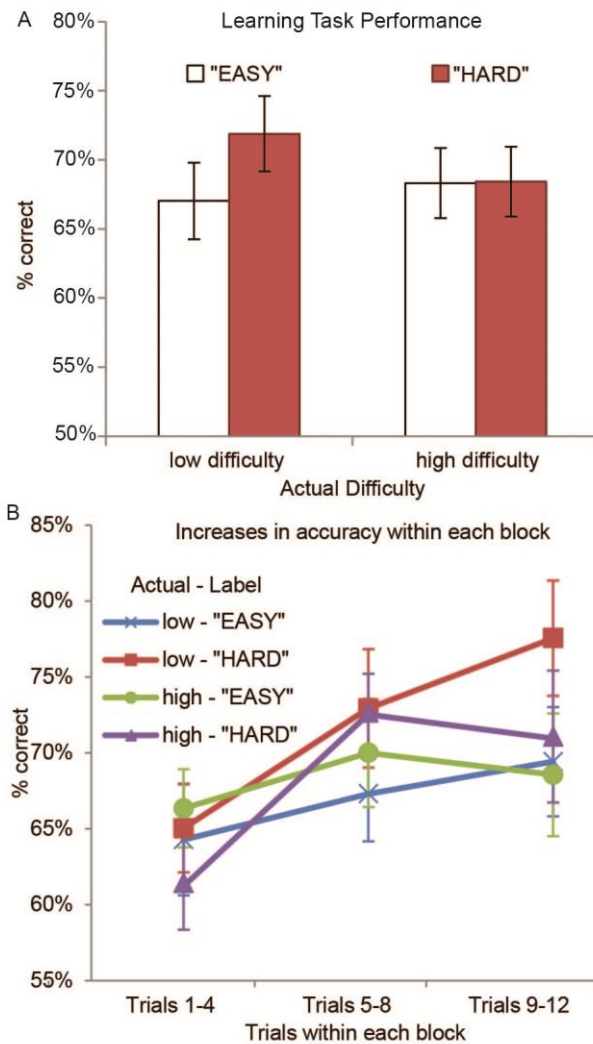
Study 1

Figure 3. Experiment 1: Correlation between normative goals and expectation effect. Average scores from the normative goals subscale of the Achievement Goal Inventory were positively correlated with the effect of expectations on task performance for low difficulty blocks ($r(18) = 0.52$, $p = 0.019$). Expectation effect is defined as the difference in proportion of correct responses on the "HARD"-labeled blocks versus "EASY"-labeled blocks (proportion correct "HARD" – proportion correct "EASY").
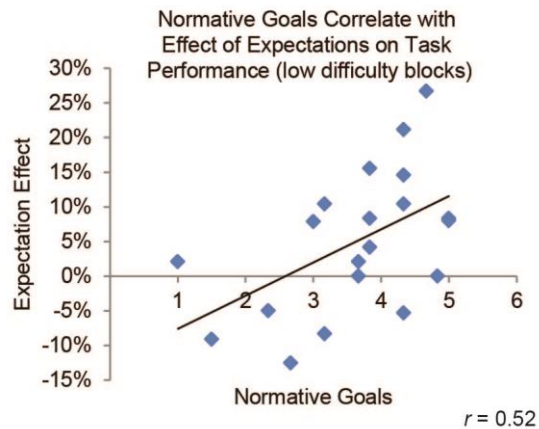
Study 1

Figure 4. Experiment 1: Valence sensitivity in "EASY"- and "HARD"-labeled blocks. Positive feedback elicited greater activation than negative feedback in each of the striatal ROIs. A. The caudate ROI reliably distinguishes between positive and negative feedback during "HARD"-labeled blocks ($t(19) = 2.618$, $p = 0.017$), but not during "EASY"-labeled blocks ($t(19) = 1.465$, $p = 0.159$). B. Feedback activation in the putamen. C. Feedback activation in the ventral striatum.
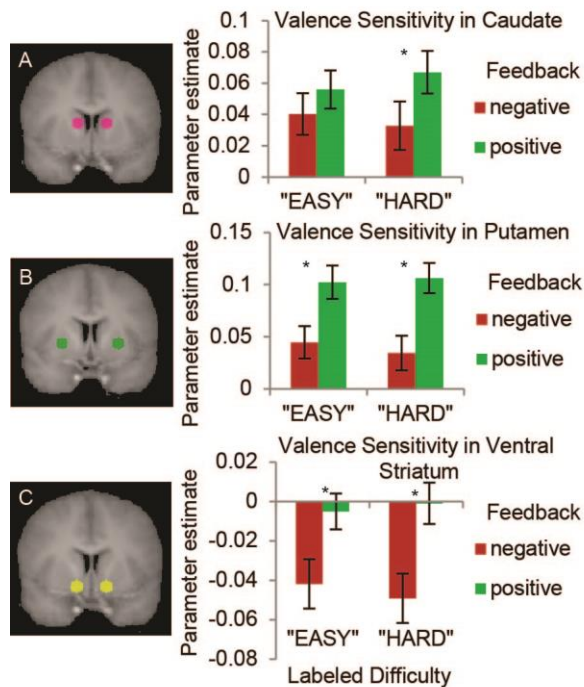
Study 1

Figure 5. Experiment 1: Correlations between normative goals and expectation by valence interaction. In the caudate (A) and putamen (B), normative goals were significantly positively correlated with the difference in "HARD" positive > negative feedback processing versus "EASY" positive > negative feedback processing.
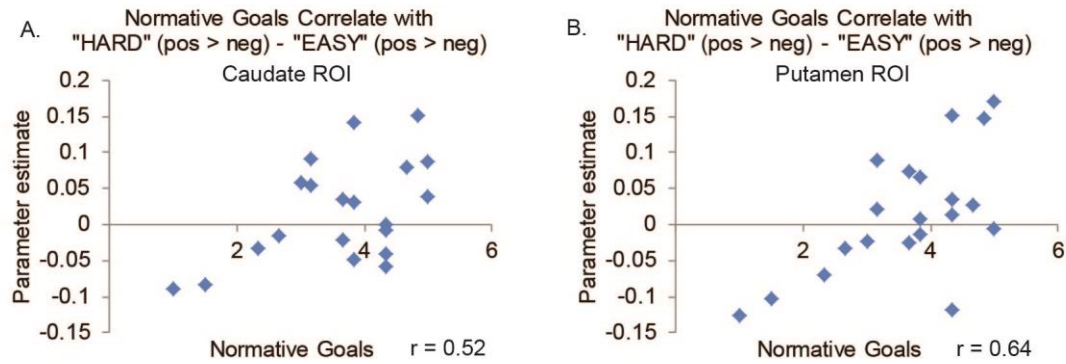
Study 2

Figure 6. Experiment 2: Experimental Design. Each participant completed a BEFORE and an AFTER learning session. Each session contained 80 unique word pairs. Each trial required subjects to learn a word pair, with two opportunities to learn each word pair (Learning Phase 1 and Learning Phase 2) followed by a test phase. The test phase for each learning session probed recall for only the word pairs that were learned during that session.

	BEFORE SESSION	AFTER SESSION
Learning Phase 1	(80 trials)	(80 **new** trials)
Learning Phase 2	(80 trials repeated)	(These 80 trials repeated)
Test	(Test on 80 word pairs)	(Test on these new word pairs)
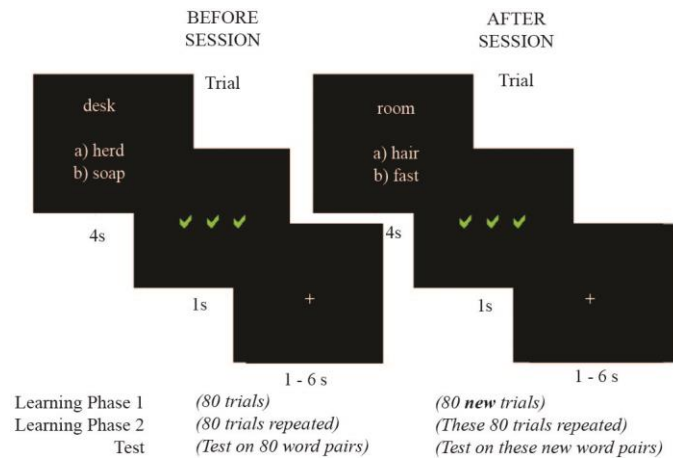
Study 2

Figure 7. Experiment 2a: Task Performance. The percentage of correct responses for each learning phase is plotted separately for each group (control and MI) BEFORE and AFTER the mid-session manipulation/control rest period.

Performance of the Control & Motivation Groups during each phase of learning

Control Group: n=21
MI Group: n=21
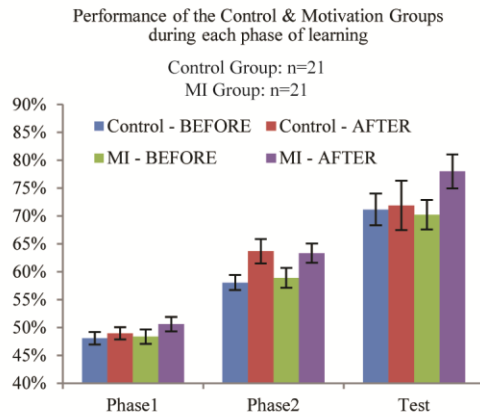
Study 2

Figure 8. Experiment 2a: Behavioral Pilot Performance-Motivation Correlations. Relationship between motivation change and change in BEFORE to AFTER learning task performance.
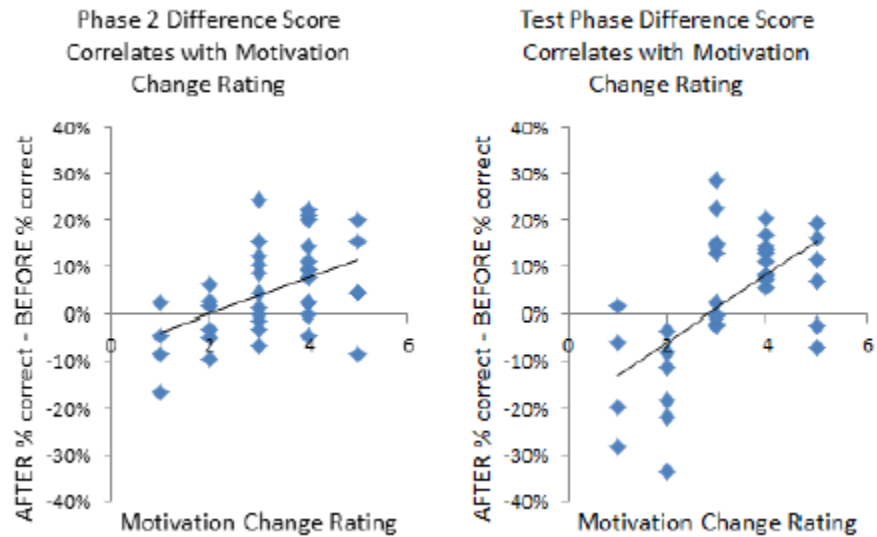
Study 2b

Figure 9. Experiment 2b: Behavioral results. A. The percentage of correct responses for each learning phase are contrasted between the learning sessions BEFORE and AFTER the motivation manipulation. Percent correct responses was significantly higher for learning phase 2 AFTER the manipulation than BEFORE. B. Ratings of the extent to which motivation changed from BEFORE to AFTER the manipulation were correlated with changes in task performance from BEFORE to AFTER the manipulation, both for Learning Phase 2 (shown) and Test performance.
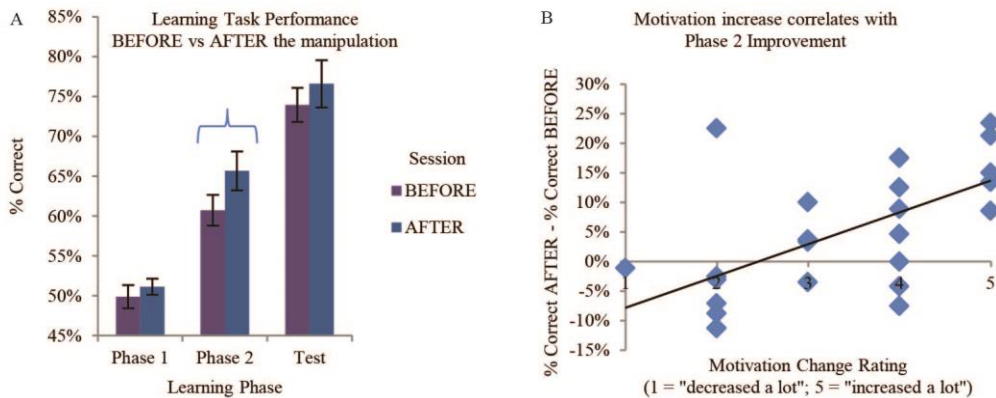
Study 2b

Figure 10. Experiment 2b: Positive > Negative Feedback Contrast. Results of the conjunction analysis performed to identify regions that were modulated by feedback valence in both Learning Phase 1 and Learning Phase 2. Regions demonstrating sensitivity to feedback valence for both Phase 1 feedback and Phase 2 feedback included ventral striatum (VS), ventromedial prefrontal cortex (vmPFC), posterior cingulate cortex (PCC), and the medial temporal lobes (MTL).
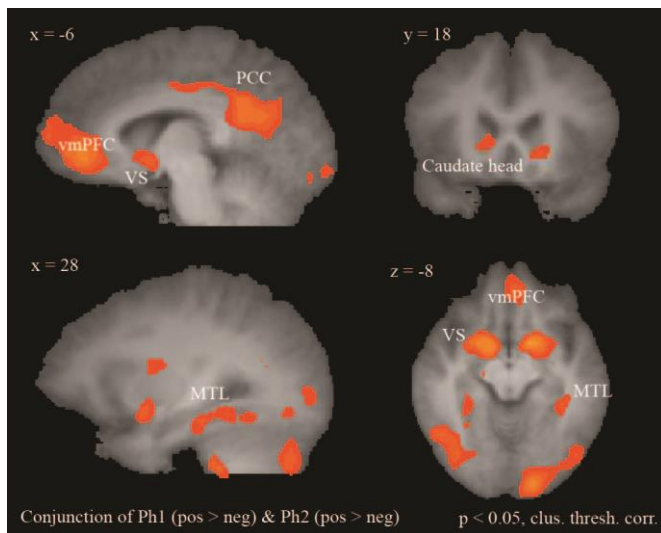
Study 2b

Figure 11. Experiment 2b: Decrease in feedback sensitivity from BEFORE to AFTER the manipulation. (A) In the ventral striatum, feedback sensitivity declined AFTER the manipulation. (B) However, throughout this region, the decline in feedback sensitivity was strongest for those reporting the lowest levels of motivation at the mid-point of the study. Those who were most motivated showed an attenuated decline in ventral striatal feedback sensitivity.
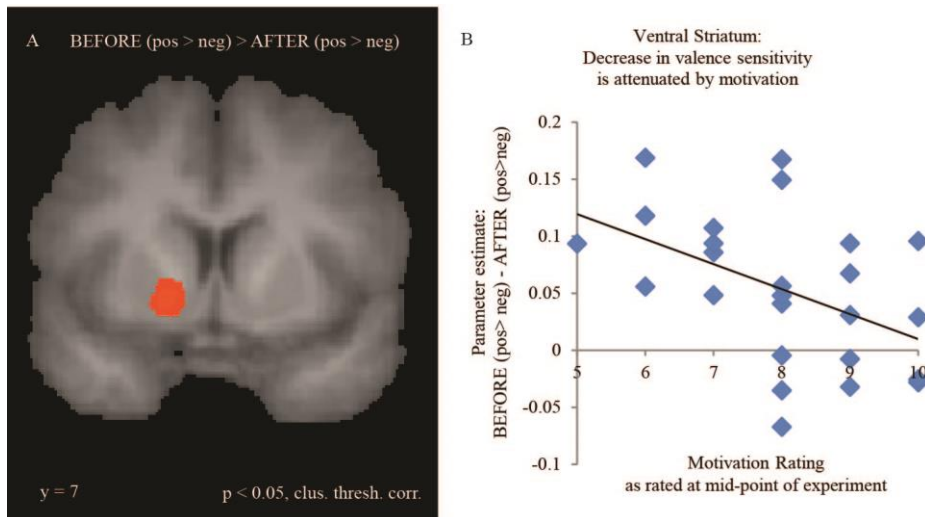
Study 2b

Figure 12. Experiment 2b: Motivation increase correlates with increasing valence sensitivity in MTL. (A) A whole-brain ANCOVA revealed a region in left MTL where increasing motivation from BEFORE to AFTER the manipulation correlated with increasing sensitivity to positive > negative feedback from BEFORE to AFTER the manipulation (both learning phases). (B) The same correlation was exhibited in the superior temporal sulcus. Scatterplots use parameter estimates extracted from the entire ROIs identified in the whole-brain ANCOVA.
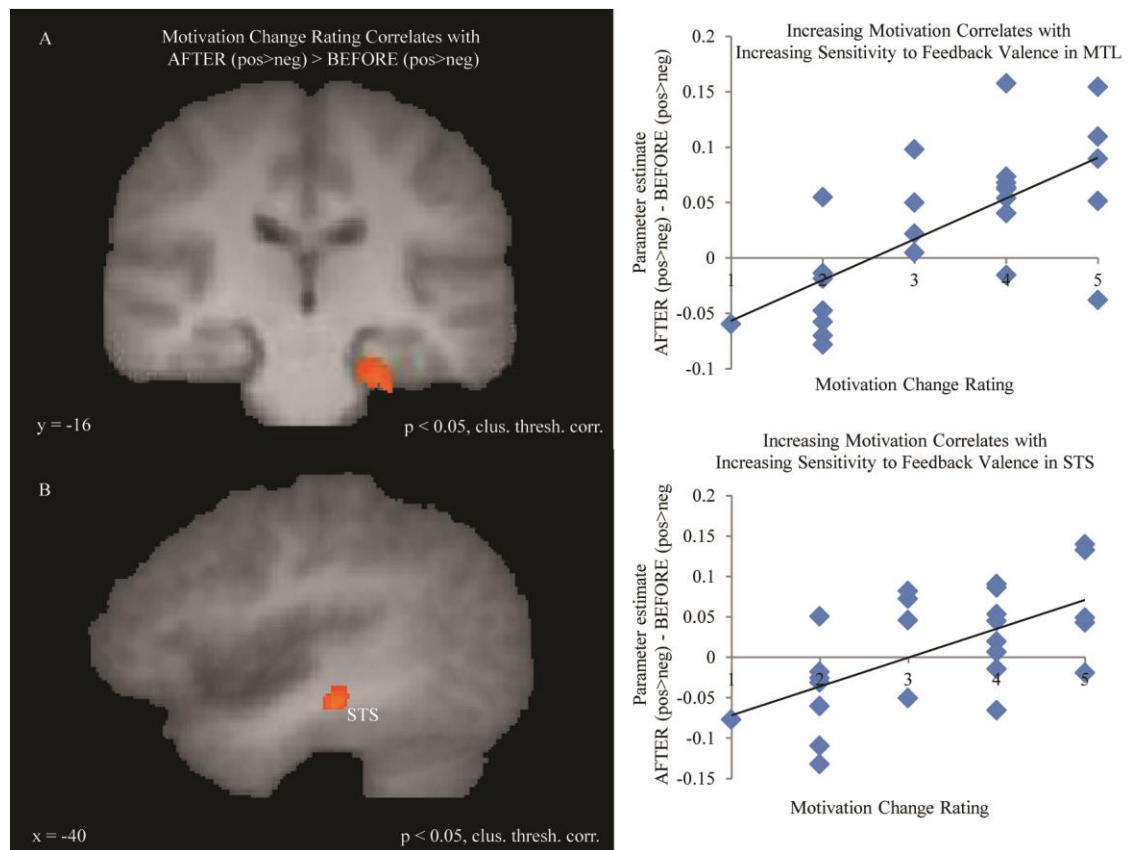
Study 2

Figure 13. Experiment 2b: Changes in feedback valence sensitivity in PCC correlate with changes in test phase performance. (A) A whole-brain ANCOVA identified clusters in left and right (shown) PCC where increasing valence sensitivity correlated with increasing test phase accuracy. (B) Correlation between test phase difference scores and parameter estimates from the contrast AFTER (positive > negative) – BEFORE (positive > negative) in the combined left and right PCC clusters.
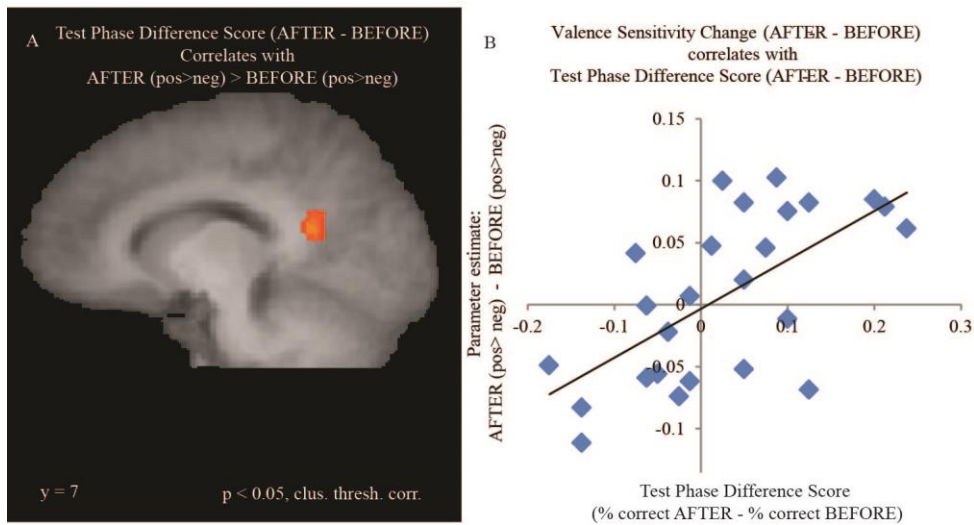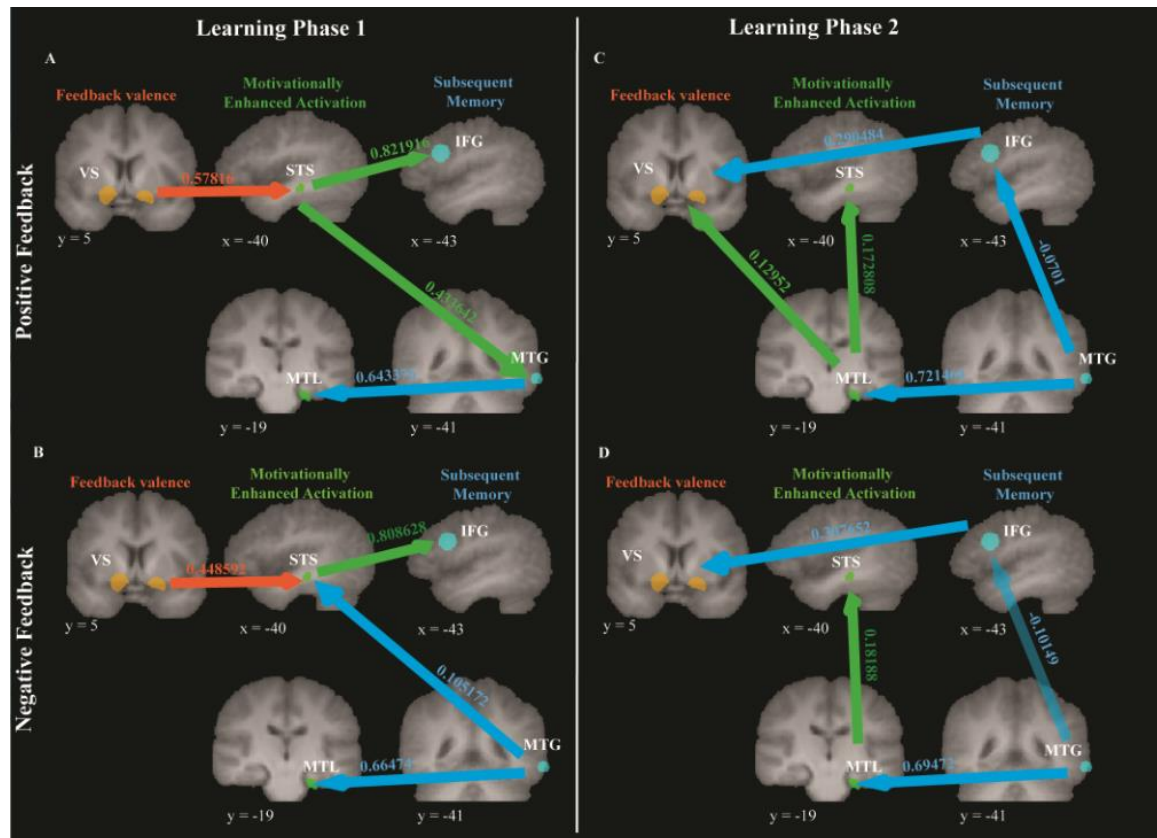
Study 2

Figure 14. Experiment 2b: Subsequent memory. Activation during the Phase 1 predicted accuracy in Phase 2, in the left PFC (IFG/MFG,), and middle temporal gyrus (MTG).
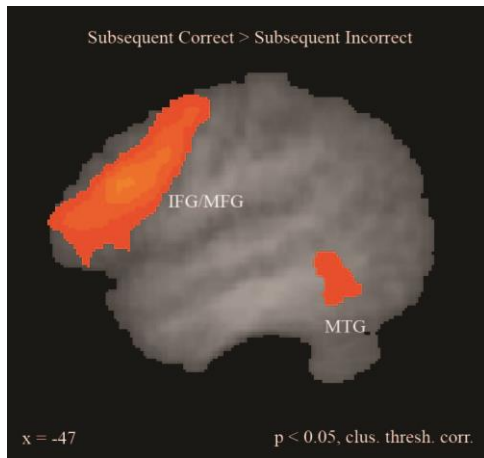
Study 2

Figure 15. Experiment 2b: Effective connectivity between the ventral striatum, motivationally modulated temporal regions, and subsequent memory regions. The arrows represent directed connections, and are color coded according to the origin of the connection. Arrows are labeled with the average connection weights across subjects.

Study 3

Figure 16. Experiment 3: Experimental Design. Each trial required subjects to learn a word pair, with two opportunities to learn each pair (Study Phase and Learning Phase) followed by a test phase. During the Study Phase, the correct word was highlighted in green. Feedback during the Learning Phase reflected the accuracy of participants' memory for the correct pairs, and promoted further learning. The self-paced test phase resembled the learning phase but did not include feedback.
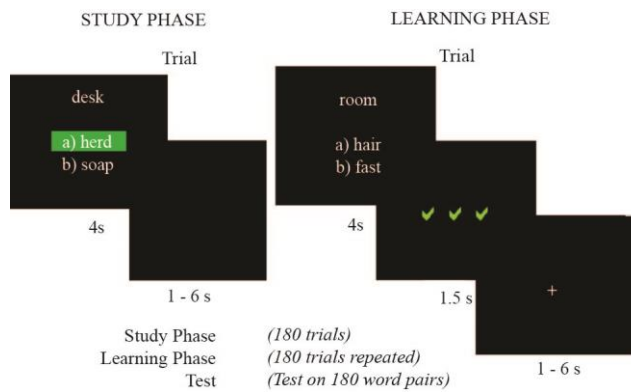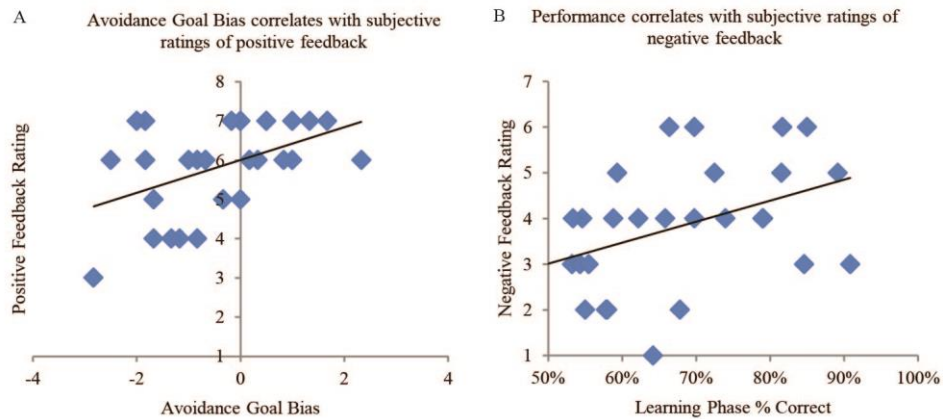
Study 3

Figure 17. Experiment 3b: Task Performance. Performance was greater than chance (50%) in both the feedback and test phases. Test phase performance exceeded feedback phase performance, suggesting that additional learning took place during the feedback phase.
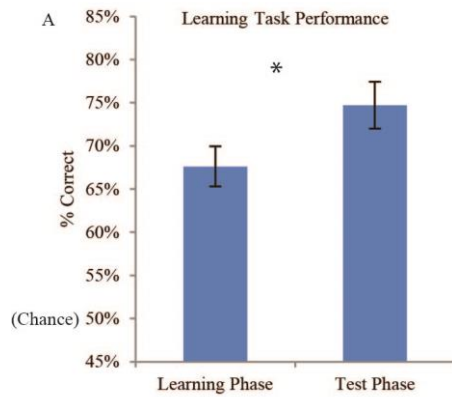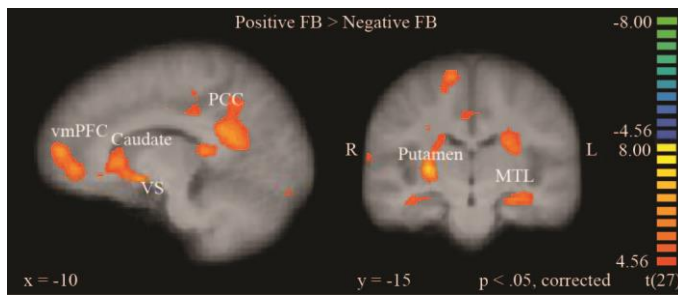
Study 3

Figure 18. Experiment 3b: Correlations for Subjective Feedback Ratings. A. *Task avoidance bias* was positively correlated with subjective ratings of how rewarding participants found positive feedback during learning. B. Subjective ratings of how negative participants felt receiving negative feedback were related to task performance in both the feedback phase (shown) and the test phase.
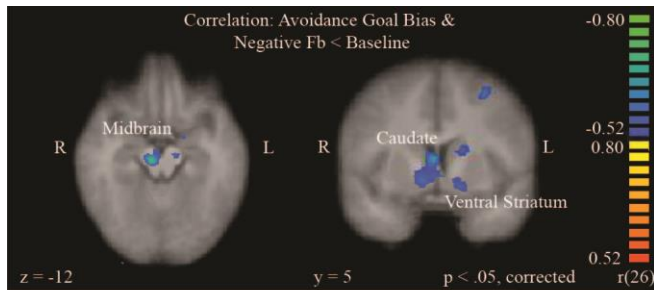
Study 3

Figure 19. Experiment 3b: Positive > Negative Feedback Contrast. Regions that were modulated by feedback valence during learning included ventral striatum (VS), dorsal striatum (Caudate & Putamen), ventromedial prefrontal cortex (vmPFC), posterior cingulate cortex (PCC), and the medial temporal lobes (MTL).
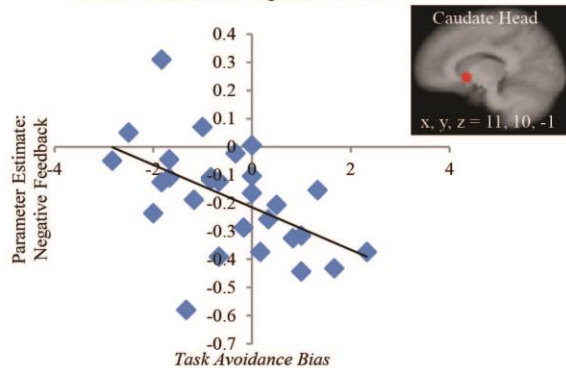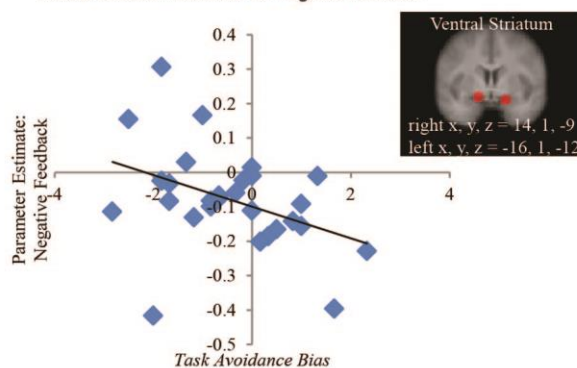
Study 3

Figure 20. Experiment 3b: Negative Correlation between *Task Avoidance Bias* and Neural Responses to Negative Feedback. A. Regions where negative feedback processing was modulated by *task avoidance* bias. B. Parameter estimates for negative feedback negatively correlated with *task avoidance bias* in the a priori caudate ROI. C. Same correlation in ventral striatum ROI.
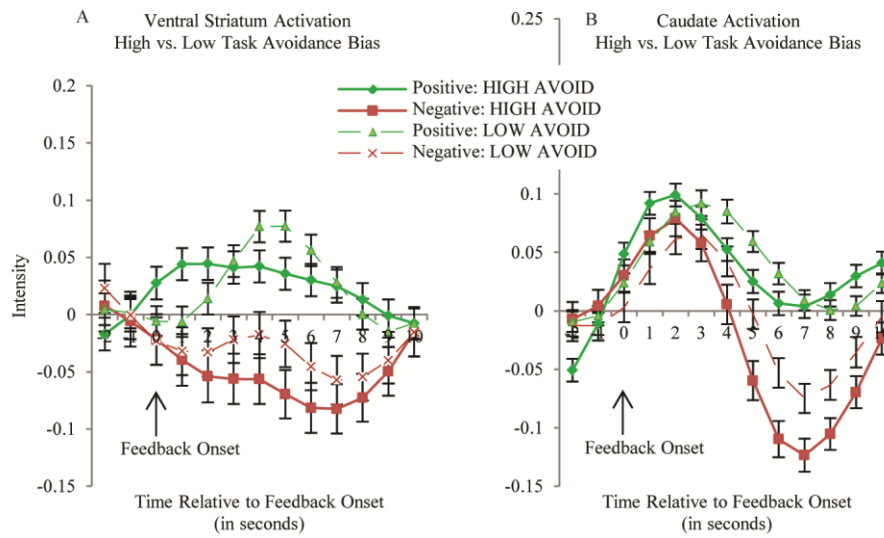
Study 3

Figure 21. Experiment 3b: Correlation between *Task Avoidance Bias* and Positive > Negative Feedback Contrast. A. Regions where the contrast between Positive and Negative feedback processing was modulated by *task avoidance* bias. B. Parameter estimates for Positive > Negative Feedback contrast correlated with *task avoidance bias* in the a priori caudate ROI.
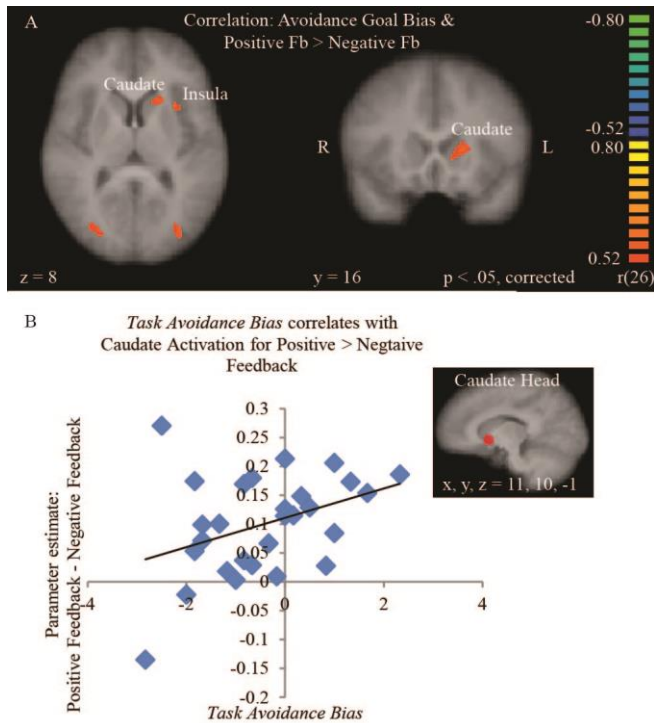
Study 3

Figure 22. Experiment 3b: Comparison of Time course in Ventral Striatum & Caudate ROIs for High vs Low Task Avoidance Bias. Time course of activation is displayed for Ventral Striatum (A) and Caudate (B). A median split was used to plot the averages separately for individuals who were highest and those lowest in *task avoidance bias*.

Study 3

Figure 23. Experiment 3b: Comparison of Time Course in Caudate ROI for High vs Low Normative Goals. Individuals with high scores on the normative questions from the Achievement Goal Questionnaire exhibited an attenuated response to negative feedback relative to those lower in normative goals.

Caudate Activaion:
High vs Low Normative Goals (task-specific)
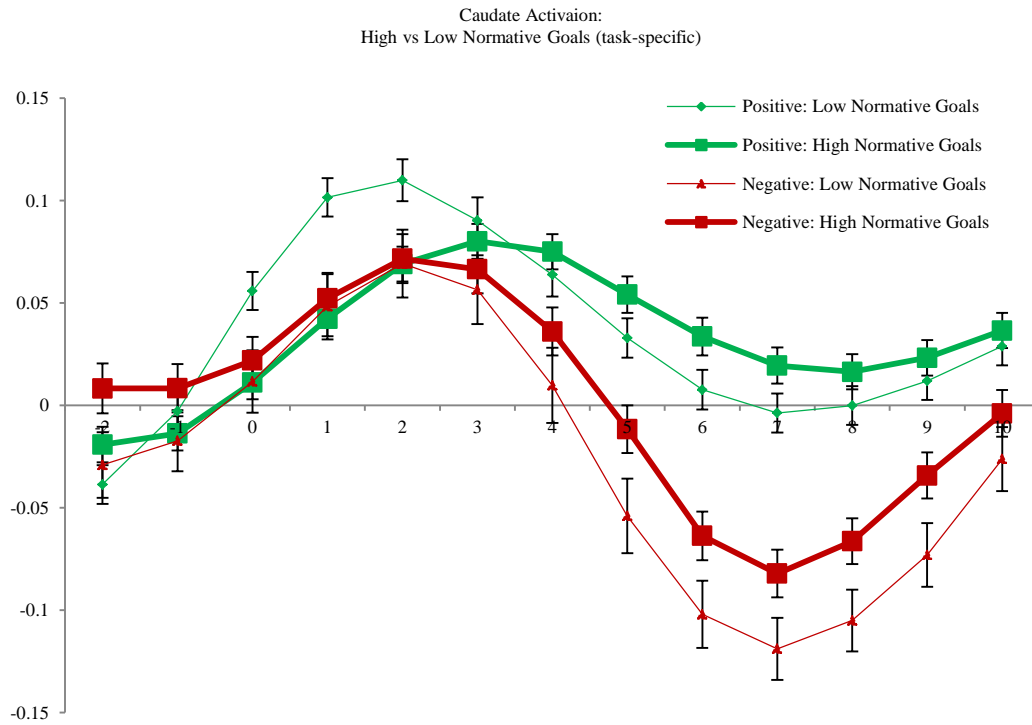
Appendix

SUPPLEMENTAL: EXPERIMENT 1

Supplemental Methods: Whole-brain Analyses:

We performed a whole-brain ANOVA to identify main effects of labeled difficulty ("EASY" or "HARD"), actual difficulty (low or high), and feedback valence. To explore the direction of the main effects, whole-brain contrasts were used to detect differences in brain responses to positive and negative feedback under different task difficulty expectations (positive versus negative when labeled "EASY," positive versus negative when labeled "HARD"). We additionally conducted a whole-brain Analysis of Covariance (ANCOVA) to explore relationships between normative goals and the effect of expectations on the pattern of feedback activation.

Clusters of voxels identified by the feedback-onset GLM analysis at an uncorrected statistical threshold of $p < 0.001$ were subjected to the cluster-level statistical threshold estimator in BrainVoyager, which provided a contiguity threshold for each contrast to produce a cluster level false positive alpha rate of 0.05.

Supplemental Table 1. Brain regions showing a main effect of feedback valence ($p < 0.05$, cluster threshold corrected).

Region of Activation	BA	Size (# voxels)	Peak Talairach Coordinates (x, y, z)			Maximum F Value
Positive feedback > Negative Feedback						
Cerebellum, posterior lobe, declive (R)		31022	38	-65	-18	45.29
Middle Frontal Gyrus (R)	46	742	53	40	18	28.92
Striatum (R)						
Putamen (ventral, anterior) (R)		13528	20	7	-6	93.18
Putamen (dorsal)(R)			*26*	*-5*	*12*	*42.64*
Globus Pallidus(R)			*26*	*-17*	*3*	*44.39*
Superior Parietal Lobule (BA 7)(R)	7	349	26	-68	42	20.40
Precuneus (BA 7)(R)	7	351	20	-56	51	21.23
Paracentral Lobule (BA 5)(R)	5	1995	5	-38	54	62.64
Posterior Temporal & Occipital Cortex (L)						
Occipital lobe, fusiform gyrus (BA 19) (L)	19	33659	-43	-71	-12	52.36
Occipital lobe, lingual gyrus (L)	19		*-31*	*-71*	*6*	*43.61*
Temporal lobe, fusiform gyrus	37		*-46*	*-38*	*-15*	*33.66*
Striatum (L)						
Putamen (ventral, posterior) (L)		14176	-28	-11	-6	61.32
**Caudate Body (L)*			*-21*	*4*	*21*	*27.23*
White matter (parietal/frontal lobe sub-gyral) (L)		354	-28	-29	30	26.34
Negative Feedback > Positive Feedback						
No regions exhibited greater feedback activation for negative than for positive feedback						

BA, Brodmann Area.

*To better identify the separate brain areas encompassed within the larger clusters, the threshold was increased until the larger clusters separated into smaller ones and those peaks are also reported.

Supplemental Table 2. Brain regions showing a main effect of actual task difficulty ($p < 0.05$, cluster threshold corrected).

Region of Activation	BA	Size (# voxels)	Peak Talairach Coordinates (x, y, z)			Maximum F Value
High Difficulty > Low Difficulty						
Middle Frontal Gyrus (R)	8	148	44	19	42	20.24
Insula (R)		113	35	10	6	23.04
Cerebellum, anterior lobe, culmen (R)		154	20	-23	-27	26.11
Thalamus (R)		161	5	-20	18	37.29
Inferior Frontal Gyrus (L)	11	66	-10	37	-18	30.72
Low Difficulty > High Difficulty						
No regions exhibited greater feedback activation during low difficulty blocks						

BA, Brodmann area.

Supplemental Table 3. Brain regions showing a main effect of labeled difficulty ($p < 0.05$, cluster threshold corrected).

Region of Activation	BA	Size (# voxels)	Peak Talairach Coordinates (x, y, z)			Maximum F Value
"HARD" > "EASY"						
Inferior Frontal Gyrus (R)	47	164	-34	25	-15	22.024
"EASY" > "HARD"						
No regions exhibited greater feedback activation during "EASY"-labeled blocks						

BA, Brodmann area.

Supplemental Table 4. Brain regions showing an interaction between feedback valence and difficulty label ($p < 0.05$, cluster threshold corrected).

| Region of Activation	BA	Size (# voxels)	Peak Talairach Coordinates (x, y, z)			Maximum F Value
Middle Temporal Gyrus (R)	21	612	56	-20	-3	34.04
Inferior Temporal Gyrus (R)	20	59	53	-47	-9	23.89
Precuneus (L)	31	85	-7	-62	23	21.55
Superior Parietal Lobule (L)	7	98	-28	-47	57	23.17
Insula (L)	13	145	-37	-23	5	32.39

BA, Brodmann Area.

Supplemental Table 5. Brain regions showing a main effect of actual difficulty in sustained activation throughout the duration of each block ($p < 0.05$, cluster threshold corrected).

Region of Activation	BA	Size (# voxels)	Peak Talairach Coordinates (x, y, z)			Maximum F Value
High difficulty > Low difficulty						
Superior Frontal Gyrus	9	219	29	55	31	5.601711
Putamen		129	20	16	-3	4.558174
Lingual Gyrus	18	211	11	-68	3	4.764969
Thalamus		185	5	-20	18	6.096312
Anterior Cerebellum (Culmen)		1166	-22	-41	-15	6.724807
Insula	13	415	-37	13	15	4.805342

BA, Brodmann Area.
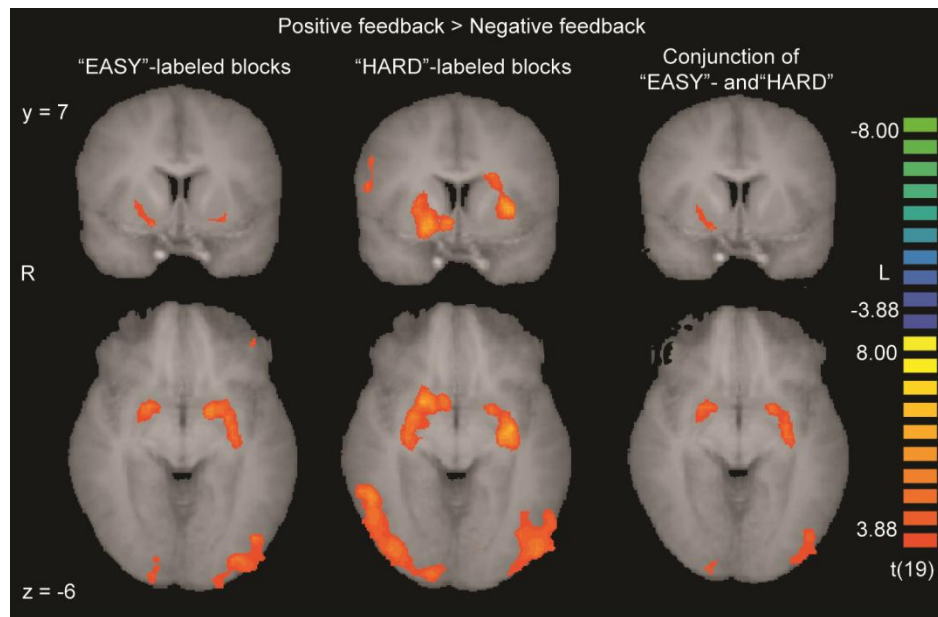
Supplemental Figure 1. Valence sensitivity in "EASY"- and "HARD"-labeled blocks. Positive > Negative feedback contrast activated the striatum in both "EASY"-labeled blocks (shown at left, $p < 0.05$, cluster threshold corrected; max $t = 7.07$) and "HARD"-labeled blocks (shown at center, $p < 0.05$, cluster threshold corrected; max $t = 6.80$), including the ventral striatum, putamen, and the body of the caudate nucleus. Posterior cortical regions including the fusiform and middle occipital gyri were also sensitive to feedback valence, as well as smaller regions in DLPFC, precuneus, and the paracentral lobule. Conjunction of "EASY" and "HARD" blocks is shown at right ($p < 0.05$, cluster threshold corrected).
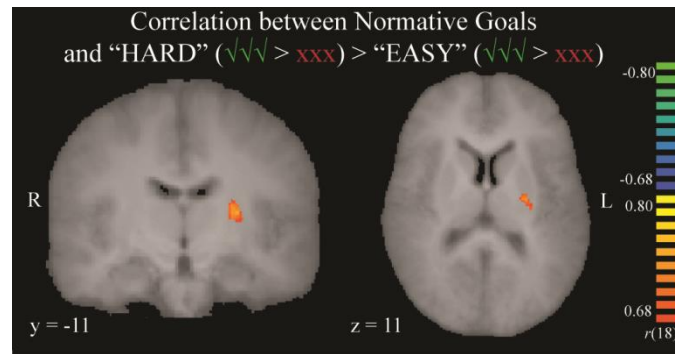
Supplemental Figure 2. Correlation between normative goals and expectation by valence interaction. In the dorsal putamen, normative goals were significantly positively correlated with the difference in "HARD" positive > negative feedback processing versus "EASY" positive > negative feedback processing (peak $r(18) = .75$, $p < 0.05$ corrected).

Samantha DePasque Swanson

Curriculum Vitae

sswanson@psychology.rutgers.edu

EDUCATION

2009 - 2014   Rutgers University
               PhD, Psychology
               Dissertation: *Motivational Influences on Feedback Processing During Learning.*
               Advisor: Elizabeth Tricomi, Ph.D.

2005 – 2007   Fairleigh Dickinson University
               MA, Clinical/Counseling Psychology

2000 – 2004   University of Rochester
               BA, Brain & Cognitive Sciences (*cum laude,* high honors in BCS)
               Minor: Clinical & Social Sciences in Psychology

PUBLICATIONS

DePasque Swanson, S., and Tricomi, E. (2014). Goals and task difficulty expectations modulate striatal responses to feedback. *Cognitive, Affective, and Behavioral Neuroscience, 14,* 610-620.

MANUSCRIPTS UNDER REVIEW

DePasque Swanson, S., Boukrina, O., and Tricomi, E. (2014). Effects of motivation on feedback processing during learning. *Under review.*

CONFERENCE PRESENTATIONS

Swanson, S.D., and Tricomi, E. (2014). Avoidance goals influence striatal processing of negative feedback during learning. Nanosymposium to be presented at the Society for Neuroscience annual meeting. Washington, DC.

Swanson, S. and Tricomi, E. (2013). Motivational influences on striatal responses to performance-related feedback. *Poster presented at the Society for Neuroscience annual meeting.* San Diego, CA.

Swanson, S. and Tricomi, E. (2013). Motivation modulates task performance and striatal activation during a feedback-based learning task. *Poster presented at the Social and Affective Neuroscience Society annual meeting.* San Francisco, CA.

Swanson, S. and Tricomi, E. (2012). Motivation and task difficulty expectations influence learning and striatal response to performance-related feedback. *Poster presented at the Social and Affective Neuroscience Society annual meeting.* New York, NY.

Swanson, S. and Tricomi, E. (2011). Expectations about task difficulty influence learning and neural response to feedback. *Poster presented at the Society for Neuroscience annual meeting.* Washington, D.C.

FELLOWSHIPS AND AWARDS

TNDA Postdoctoral Fellowship, UCLA, 2014

Dissertation Fellowship, Rutgers University, 2013

Mortimer D. Sackler, M.D. Summer Institute, Weill Cornell Medical College, July, 2012

Norman Samuels Fellowship, Rutgers University, 2009

Daniel S. Lehrman Fellowship, Rutgers University, 2009