THE ROLE OF FEEDBACK IN LEARNING AND MOTIVATION

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ABSTRACT

Performance feedback about whether responses are correct or incorrect provides valuable information to help guide learning. Although feedback itself has no extrinsic value, it can produce subjective feelings similar to “rewards” and “punishments.” Therefore, feedback can play both an informative and a motivational role. Over the past decade, researchers have identified a neural circuit that processes reward value and promotes reinforcement learning, involving target regions of dopaminergic input (e.g., striatum and ventromedial prefrontal cortex). Importantly, this circuit is engaged by performance feedback even in the absence of reward. Recent research suggests that feedback-related brain activity can be modulated by motivational context, such as whether feedback reflects goal achievement, whether learners are oriented toward the informative versus evaluative aspect of feedback, and whether individual learners are motivated to perform well relative to their peers. This body of research suggests that the brain responds flexibly to feedback, based on the learner’s goals.

Keywords: Learning; motivation; feedback; striatum; dopamine; reward
In the classroom and in life, there are many ways to learn new information. However, few are as powerful as learning directly through experience. Making a choice and experiencing the outcome allows an individual to adjust responses that should be improved. Educators, clinicians, and parents often use informative feedback, such as praise for desirable responses and critiques of missteps, to help guide such learning. Feedback is a term

![Fig. 1. Components of the Corticostriatal Loops. Notes: Dorsal striatum is comprised of the caudate nucleus and putamen, while the ventral striatum primarily refers to the nucleus accumbens. The striatum receives projections from diverse areas, from the anterior cingulate (ACC) and ventromedial prefrontal cortex (vmPFC) to the amygdala and hippocampus.](image-url)
borrowed from cybernetics; it describes a process by which a response is controlled by its effects (Hill, 1997). In psychological studies of human behavior, the term most often describes stimuli that signal performance accuracy, which can then be used to modify future performance (Kluger & DeNisi, 1996). To motivated learners, feedback not only provides information but also plays an emotive role (Elliott, Sahakian, Michael, Paykel, & Dolan, 1998). The term “positive feedback” indicates an accurate response and can also convey task success, whereas “negative feedback” denotes an inaccurate response and can signify failure or poor task performance.

Most of the time, learners are pleased to receive positive feedback, causing positive feedback to have appetitive value, and thus to serve as a reward (Elliott, Frith, & Dolan, 1997). Since rewards act as reinforcers, which are events that increase the frequency of a behavior (Hill, 1997), positive feedback motivates learners to perform in a way that will maximize their chance of earning more positive feedback. Negative feedback can be viewed either as the omission of the positive hedonic value associated with positive feedback or as an outcome with negative hedonic value (Holroyd & Coles, 2002). In either case, negative feedback typically acts as a punishment, which is an event that decreases the frequency of a response (Miller & Escobart, 2002). Note that punishment should not be confused with negative reinforcement, which refers to the removal of a stimulus of negative hedonic value, which increases the tendency to perform a behavior (e.g., a baby’s cry, which is eliminated when the baby is picked up; Miller & Escobart, 2002). Negative feedback can thus motivate learners to adapt their behavior in order to minimize the potential for further negative feedback.

Although lab-based learning tasks involving externally provided feedback may seem artificial, they closely mimic ever-present real-life learning situations. In the classroom, many types of feedback can be used to guide learning, including praise/criticism from teachers, marks on exams, grades, etc. Additionally, in many cases, performance of a task itself provides feedback (Goodman, 1998). For example, matching jigsaw puzzle pieces together and shooting a basketball through the hoop provide clear indications of response success, which are simply inherent to the tasks themselves. Learning on the basis of this “task feedback” might be assumed to proceed in a similar way as learning based on external feedback, with the only major difference being whether the source of the feedback is intrinsic to the task or externally generated. This chapter will primarily focus on the effects of external feedback, which is easier to manipulate experimentally and has therefore been studied more extensively.
In this chapter, we will begin with a discussion of the neural circuits underlying feedback processing, with a particular emphasis on the striatum, a key brain region in the reward circuit. We will then discuss the effects of motivation on feedback processing during learning, and we will conclude by discussing the implications of this research for education.

**BRAIN CIRCUITS INVOLVED IN PROCESSING REWARD-RELATED INFORMATION**

The processing of reward-related information is carried out via corticostriatal “loops,” or brain circuits, connecting various subregions of the prefrontal cortex involved in valuation and decision making processes, with the subdivisions of the striatum, which has been implicated in reward, motivation, and action control (Fig. 1). The striatum, the primary input unit of the basal ganglia, receives convergent projections from regions throughout the prefrontal cortex, and sends information back to the prefrontal cortex via the globus pallidus and thalamus (Alexander, DeLong, & Strick, 1986).

The “limbic loop” connects the ventral striatum (i.e., the nucleus accumbens) and ventral caudate and putamen with the ventromedial prefrontal cortex (vmPFC), including the orbitofrontal and medial prefrontal regions (Haber, Kunishio, Mizobuchi, & Lynd-Balta, 1995). In addition to prefrontal input, the nucleus accumbens also receives projections from other limbic regions, such as the amygdala and hippocampus (Haber & McFarland, 1999). This “limbic loop” is involved in motivational and value-related processes (Haber, 2011). The “associative loop” includes the caudate nucleus, located in the dorsal striatum (DS), and the dorsolateral prefrontal cortex (DLPFC), an area that is involved in executive functions, such as working memory, response selection and inhibition, and attentional shifting (Niendam et al., 2012; Packard & Knowlton, 2002). This loop is thought to play a role in cognitive functions, including incentive-based associative learning of whether particular responses lead to positive or negative outcomes (Haber, Kim, Mailly, & Calzavara, 2006).

Importantly, both the prefrontal cortex and the striatum receive modulatory dopaminergic input from the midbrain, and the striatum also projects heavily to the midbrain, forming striatonigrostriatal circuits (Haber, Fudge, & McFarland, 2000). Electrophysiological research in nonhuman primates has demonstrated that dopaminergic neurons in the midbrain play a key role in coding for reward-related information.
These neurons respond with bursts of activity to unpredicted rewards, such as delivery of juice, and show effects of learning; if a reward is consistently preceded by a conditioned stimulus, the neuronal activity occurs at the onset of the predictive stimulus, rather than the reward itself. The absence of a predicted reward, however, causes depression in neuronal firing at the time at which the reward would have occurred (Schultz, Dayan, & Montague, 1997). Thus, the dopaminergic signal can be thought of as coding for both positive and negative “prediction errors,” that is, the difference between the reward received and the expected reward (Schultz & Dickinson, 2000), an important signal for learning and shaping of decisions.

Functionally, the striatum has been implicated by both electrophysiological and neuroimaging studies in the processing of primary and secondary rewards (Delgado, 2007). Human neuroimaging studies demonstrate that this region shows activation for expectation and receipt of primary rewards, such as juice (McClure, Berns, & Montague, 2003; O’Doherty, Dayan, Friston, Critchley, & Dolan, 2003), and secondary rewards, such as money (Delgado, Nystrom, Fissell, Noll, & Fiez, 2000; Elliott, Friston, & Dolan, 2000; Knutson, Westdorp, Kaiser, & Hommer, 2000). Typically, rewards produce a signature response of sustained striatal activation, whereas punishments produce a dip below baseline in striatal signal, before it returns to baseline (Delgado et al., 2000). As the magnitude of a reward, such as monetary value, increases, the striatal reward response also increases (Delgado, Locke, Stenger, & Fiez, 2003). The ventral striatum responds to reward prediction errors (Garrison, Erdeniz, & Done, 2013), and is required for the modulation of action vigor by motivational signals (Cardinal, Parkinson, Hall, & Everitt, 2002). Information from the ventral striatum reaches the DS through ascending striatonigrostriatal loops (Haber et al., 2000), and the DS uses reward-related information to acquire action-outcome associations (Yin, Ostlund, Knowlton, & Balleine, 2005). Together, these data suggest that striatal processing of rewards is important for both learning to predict rewards and learning to act in ways that maximize positive outcomes.

One frontal region that projects to the striatum is the anterior cingulate cortex (ACC), a region that has been widely implicated in a diversity of affective and cognitive functions. The ACC is believed to be the source of the “error-related negativity,” a component of the event-related potential that is elicited during error detection, and is therefore thought to play an important role in performance monitoring (Holroyd & Coles, 2002). Given its anatomical connections and functional roles in self-control, performance monitoring and effortful cognition, it has been proposed that the ACC...
integrates emotional and cognitive information to guide intelligent behavior (Allman, Hakeem, Erwin, Nimchinsky, & Hof, 2001). In addition to its connections with the striatum, the ACC is reciprocally connected with the basolateral amygdala (BLA), which itself has been implicated in value and expectancy processes (Belova, Paton, Morrison, & Salzman, 2007). Inputs from the BLA to the striatum are critical for acquisition of striatal responses to reward-associated cues and reward-seeking behavior (Ambroggi, Ishikawa, Fields, & Nicola, 2008). Finally, the hippocampus plays a key role in learning and memory, and especially in declarative memory (Squire, 2004); interestingly, this region also receives dopaminergic innervation, which may facilitate hippocampus-dependent memory formation (Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006; Lisman & Grace, 2005).

The projections of the vmPFC to the ventral striatum position it to play a critical role in the brain’s reward circuitry (Haber et al., 1995). The vmPFC has been implicated in the encoding of reward value and expected reward value of both primary and secondary rewards (O’Doherty, 2004). The medial orbitofrontal cortex (mOFC) is more active following reward than punishment, with activation that is correlated with reward magnitude (O’Doherty, Kringelbach, Rolls, Hornak, & Andrews, 2001) and prediction error (O’Doherty, Dayan, et al., 2003). Neurons in the OFC are more sensitive to the specific nature of the reward than dopaminergic neurons; that is, different neurons are tuned to different types of rewards (Schultz, Tremblay, & Hollerman, 1998). With its ability to distinguish the specific nature of different rewards, the OFC may be an important substrate of comparing potential rewards. Both neuroimaging studies and neuropsychology work in patients with vmPFC lesions indicate that this region plays a prominent role in decision making (Bechara, Tranel, & Damasio, 2000; O’Doherty, Critchley, Deichmann, & Dolan, 2003), and animal work suggests a role in the weighing of cost-benefit tradeoffs in reward-based decision making, particularly relating to risk and delay (Walton, Rudebeck, Bannerman, & Rushworth, 2007). Furthermore, the vmPFC may play a particularly important role in guiding behavior based on abstract information, such as social cues (Fellows, 2007; Hampton, Bossaerts, & O’Doherty, 2006; Tricomi, Rangel, Camerer, & O’Doherty, 2010), consistent with evidence suggesting its responses to rewards are modulated by the social context (Ho, Gonzalez, Abelson, & Liberzon, 2012). In light of this evidence, it seems that the contribution of the vmPFC to the “limbic loop” may involve the integration of information about reward value and possible response costs with contextual factors, including motivational states.
Importantly, reward representations in the brain do not depend on absolute values of the rewards, but instead are modulated by contextual influences (De Martino, Kumaran, Seymour, & Dolan, 2006; Nieuwenhuis, Heslenfeld, et al., 2005). For example, the brain is sensitive to “counterfactual comparisons” between the reward obtained and the other possible outcomes, suggesting that rewards and punishments are relative. Brain regions involved in reward processing, including the striatum and the prefrontal cortex, show a “reward” response to earning no money when the alternative is losing money, but show a “punishment” response to earning no money when the alternative is winning money (Breiter, Aharon, Kahneman, Dale, & Shizgal, 2001; Nieuwenhuis, Heslenfeld, et al., 2005). Similarly, activation in the striatum is influenced by information about the value of unchosen outcomes, and this information influences future choices (Li & Daw, 2011; Lohrenz, McCabe, Camerer, & Montague, 2007). Thus, the brain represents value in a flexible way that takes into account subjective interpretation based on relative preferences.

LEARNING FROM FEEDBACK RECRUITS THE BRAIN’S REWARD SYSTEM

For the affective information provided by rewards and punishments to shape our behavior, we must be able to associate them with the actions that produced them. As a part of the “associative loop,” the DS, including the caudate nucleus, plays an important role in learning these associations. A study involving a series of three fMRI experiments found that the head of the caudate nucleus was not significantly activated by monetary rewards and punishments presented randomly in time, nor was it recruited when an anticipatory cue signaled an impending reward or loss. Robust activation in the caudate was found, however, when participants had to respond to a cue by choosing one of two responses and were told that the outcome would depend on whether they chose the correct response; these responses also differentiated between reward and punishment trials. A second condition, for which subjects were told that the required button press did not determine the outcome, produced only weak and nondistinct responses in the caudate (Fig. 2). Therefore, the perception of an action-outcome contingency was found to be the critical factor that governs the recruitment of the caudate nuclei. These results suggest a role for the caudate not as...
a simple reward processor but as a region which associates actions with positive or negative consequences (Tricomi, Delgado, & Fiez, 2004).

Further studies also support the idea that activity in the DS is linked to action. For example, both rewarding and nonrewarding stimuli can activate the caudate if they are behaviorally relevant (Zink, Pagnoni, Martin, Dhamala, & Berns, 2003; Zink, Pagnoni, Martin-Skurski, Chappelow, & Berns, 2004). Additionally, brain regions in the reward circuit, and especially the head of the caudate, have been found to be more active when performing feedback-based learning tasks oneself than when learning based on observing the choices and outcomes for another person (Bellebaum, Jokisch, Gizewski, Forsting, & Daum, 2012; Kobza & Bellebaum, 2015). These action-dependent effects may be particularly apparent in the dorsal, rather than ventral, striatum (O’Doherty et al., 2004), though recent reports have found that the ventral striatum is also sensitive to action contingency and behavioral relevance (FitzGerald, Schwartenbeck, & Dolan, 2014).
The idea that the caudate is involved in adapting behavior based on the consequences of one’s actions suggested that it might be sensitive to performance feedback indicating whether one’s responses are correct or incorrect during learning, as well as to extrinsic rewards and punishments. To test this hypothesis, one fMRI study investigated whether receipt of performance-dependent feedback in a learning task would activate the caudate in a similar way as extrinsic monetary rewards in a guessing task. The study used as a model system the acquisition of the non-native /r/-/l/ phoneme distinction by native Japanese speakers (Tricomi, Delgado, McCandliss, McClelland, & Fiez, 2006), using a phoneme identification training paradigm that had been shown to be effective only when performance feedback was present (McCandliss, Fiez, Protopapas, Conway, & McClelland, 2002). Positive and negative performance feedback produced caudate activation similar to that elicited by monetary rewards and punishments in the guessing task (Fig. 3). Moreover, in contrast to performing the learning task with feedback, phoneme identification practice with no feedback produced neither striatal activation nor successful learning. These results demonstrated that the intrinsic rewards and punishments of positive and negative performance feedback elicit similar neural activity as extrinsic rewards and punishments, and suggested that recruitment of the caudate facilitates feedback-based learning.

Further studies have confirmed that brain regions in the reward system, including the dorsal and ventral striatum, midbrain, and posterior cingulate cortex respond more to positive than negative feedback (Aron et al., 2004; Marco-Pallares, Muller, & Munte, 2007; Nieuwenhuis, Slagter, Alting von Geusau, Heslenfeld, & Holroyd, 2005), and show responses that correlate with reward prediction error (Garrison et al., 2013; Shohamy, 2011). Furthermore, individual differences in feedback-based learning performance correlate with activation in the DS (Schonberg, Daw, Joel, & O’Doherty, 2007) and ventral striatum (Vink, Pas, Bijleveld, Custers, & Gladwin, 2013). The ACC, interestingly, responds more to positive outcomes when they are less frequent than negative outcomes, but more to negative outcomes when they are less frequent than positive outcomes, highlighting this region’s role in processing outcomes that are unexpected (Jessup, Busemeyer, & Brown, 2010; Zanolie, Van Leijenhorst, Rombouts, & Crone, 2008). Meanwhile, the prefrontal cortex, including the dorsolateral PFC and inferior frontal gyrus, produces the greatest response to negative feedback when it is the most informative (Tricomi & Fiez, 2008; Zanolie et al., 2008).
Along with neuroimaging work highlighting the role of the reward system in feedback processing, neuropsychology studies of patients with Parkinson’s Disease, a disease which depletes the brain of dopamine, provide converging evidence for the importance of dopaminergic corticostriatal systems to feedback-based learning. Individuals with Parkinson’s Disease are impaired on some learning tasks, but not others. Shohamy and colleagues (2004) found that Parkinson’s patients were impaired at feedback-based learning, but were not impaired on a non-feedback version of the

![Fig. 3. Positive (“Correct”) and Negative (“Incorrect”) Feedback Elicit Similar Responses as Monetary Rewards/Punishments.](image)

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same task. This study thus provided critical evidence that feedback processing in particular is dependent on dopaminergic brain systems, and fMRI research confirms striatal dysfunction in Parkinson’s patients during the processing of positive feedback (Keitz et al., 2008). Further evidence comes from the work of Frank and colleagues, who investigated how Parkinson’s patients learn from positive versus negative feedback (Frank, Seeberger, & O’Reilly, 2004). In healthy participants, learning from negative feedback is more difficult than learning from positive feedback (Hearst, 1991; Kim, Shimojo, & O’Doherty, 2006; Wachter, Lungu, Liu, Willingham, & Ashe, 2009). In contrast, Parkinson’s Disease patients learn better from negative feedback than from positive feedback. When these patients are given medication to increase dopamine levels, they become better at learning from positive than from negative feedback (Frank et al., 2004). Frank et al. (2004) suggest that these effects reflect attenuated dopamine neuron firing “bursts” to rewards and augmented “dips” in firing to punishments in Parkinson’s patients, a pattern which dopamine medication reverses. Since activity in the striatum and other reward-sensitive brain regions is thought to reflect dopaminergic input, one implication of this theory is that the efficacy of learning from positive and negative feedback should depend on the strength of the “reward” and “punishment” responses they generate in the brain, respectively.

Traditionally, the striatum had been associated with nondeclarative learning, that is, learning without a verbalizable strategy and without an explicit awareness of what is being learned. Yet the use of performance feedback as an instructional tool for the acquisition of declarative knowledge (explicit knowledge of facts and events) is extremely common. If the caudate plays an important role in processing performance-dependent feedback, it would seem unlikely for this role to be limited to nondeclarative learning tasks. Indeed, the deficits shown by Parkinson’s patients suggested that the striatum may be particularly important for tasks involving feedback, rather than for all nondeclarative learning tasks (Shohamy et al., 2004; Smith & McDowall, 2006). Further research indicated that the brain’s dopamine-mediated reward system facilitated memory formation that was dependent on the hippocampus, a brain structure associated with declarative learning. A feedback-based declarative word pair learning task was developed to test the hypothesis that the striatum would be involved in feedback processing even during declarative memory acquisition. The caudate nucleus does indeed show reward and punishment responses to positive and negative feedback in this task, supporting the notion that this region is critically involved in feedback processing across different types of learning, rather than being solely involved in nondeclarative
learning (Tricomi & Fiez, 2008). Furthermore, since the words used on each trial of this task are unique, the experimental design allows caudate activation to be compared for trials associated with high and low confidence on a subsequent post-test. This analysis showed that caudate activation following positive feedback was associated with increased confidence for the same item on the post-test, supporting the role of the caudate in facilitating feedback-based declarative memory acquisition (Tricomi & Fiez, 2012). The results from other studies have also provided converging evidence for the revised view that the striatum and hippocampus are part of interactive, rather than competing, memory systems (Dickerson, Li, & Delgado, 2011; Shohamy & Adcock, 2010; Wittmann et al., 2005).

More recent work on feedback processing has investigated how robust the brain signals to feedback are if they are presented after a delay. Associative learning studies tend to emphasize the close temporal proximity of the response and the corresponding feedback, yet humans are capable of learning from outcomes that are quite delayed from the actions that produced them, such as when a student learns from a graded test that is handed back a week after taking the test. Research with Parkinson’s patients found that a delay of only 6 seconds between the response and the feedback was enough to eliminate impairments relative to healthy participants, indicating that dopaminergic brain signals can aid linking actions and outcomes only when they are spaced closely in time (Foerde & Shohamy, 2011). However, an fMRI experiment with healthy participants using the declarative word pair learning task found that if learners are reminded of their original response prior to getting feedback, the same neural structures that respond to immediate positive and negative feedback also respond in a similar way when feedback is delayed by about 25 minutes from the original response. Furthermore, performance was also similar for items learned from immediate and from delayed feedback (Dobryakova & Tricomi, 2013). These findings suggest that the brain structures involved in associative learning are actually quite flexible, and can still be recruited to facilitate learning despite obstacles such as a delay between an action and its consequences.

**EFFECTS OF MOTIVATION ON FEEDBACK PROCESSING DURING LEARNING**

Recent research on feedback-based learning has investigated how the motivational significance of feedback influences neural processing and consequent
learning. Motivation is what drives behavior; thus for feedback to motivate learning, it must be perceived by the learner as aiding in the goal of task mastery. Generally, feedback is treated as having a fixed reward value (“correct”/positive vs. “incorrect”/negative). The subjective value of feedback to an individual, however, can vary depending on how motivated that individual is to earn positive feedback or avoid negative feedback. Correspondingly, feedback signals in the brain have been found to be modulated by the subjective value of the feedback to the individual, not only when feedback is accompanied by monetary reinforcement (Knutson, Taylor, Kaufman, Peterson, & Glover, 2005) but also when no extrinsic reinforcers are present (DePasque & Tricomi, 2015; DePasque Swanson & Tricomi, 2014). For example, a brief motivational interview was used in one study to influence the value learners placed on the goal of doing well on learning task (DePasque & Tricomi, 2015). Based on a technique from motivational interviewing, we used an “importance ruler,” in which participants first rated the importance of performing well during the task, on a scale from 0 to 10, and were then asked to explain why they did not indicate a lower number (Miller & Rollnick, 2002). The interview prompted subjects to generate their own personally meaningful reasons to strive for success on the task, with the rationale that self-generated motivational statements would enhance intrinsic motivation for the task more effectively than externally provided reasons (Deci & Ryan, 1987). In a behavioral experiment, those individuals whose motivation increased the most after the interview exhibited the greatest gains in task performance, supporting the notion that within-subject increases in motivation are associated with gains in task performance. In an fMRI adaptation of the experiment, striatal feedback responses were sensitive to individual differences in motivation. Specifically, while many subjects reported increases in boredom or sleepiness during the second half of the scan and evinced decreases in striatal feedback responses after the manipulation, subjects with higher levels of motivation showed attenuation or even reversal of the decrease in striatal feedback responses (Fig. 4).

The idea that responses to feedback in the DS relate to the motivation of the learner is further supported by a study in which the learning goals of participants were manipulated within the context of a single learning task. Han, Huettel, Raposo, Adcock, and Dobbins (2010) used performance-linked monetary rewards to incentivize different types of responses (i.e., “old” vs. “new” judgments) in a declarative memory task. In the absence of monetary incentives, the caudate was generally more active for “old” judgments (identification of words that had been previously studied) than “new,” yet when incentivized to make “new judgments,” activation in the caudate increased for “new” judgments, even when no feedback was
presented. Once again, activation in the caudate appears to relate not specifically to whether a response is correct or incorrect, but rather to whether an outcome satisfies the current goals of the learner.

Another example of how a learner’s goals can influence feedback-related brain activation comes from an experiment that compared feedback signals when the feedback provided useful information, but did not indicate performance, versus when it signaled task success. The experiment used a multiple-choice word pair learning task, in which each trial featured a new word pair to learn. Initial feedback provided information about whether the learner had happened to guess correctly, but did not provide evaluative information about task success, since the choices were arbitrary and task success was not under the learner’s control. Next, learners were tested again on the same pairs and were instructed to try to pick the correct answer based on their memory from the first set of trials. Feedback during this second phase was thus evaluative, and reflected whether learners were achieving their goal of learning the word pairs. The caudate nucleus was more responsive to positive and negative feedback when it was evaluative than when it was merely informative (Tricomi & Fiez, 2008). Thus, in this example, the DS was engaged by feedback only when the feedback was evaluative of the subject’s performance. In contrast, a separate experiment using a similar paradigm with two versus four response options found that varying the amount of information provided by positive and negative
feedback could also influence caudate recruitment (Tricomi & Fiez, 2012). With two response options and no initial knowledge of the correct answer, positive and negative feedback provide equal amounts of information: both allow the learner to determine the correct answer. In contrast, with four response options, positive feedback provides more information than negative feedback, since positive feedback indicates that the chosen option is correct, while negative feedback only eliminates one of four possibilities. When responses were arbitrary, positive and negative feedback elicited differential responses in the caudate nuclei with four options, but not with two options. Furthermore, increased caudate activation following positive feedback was associated with better performance for the same item on a post-test. These results suggest that when a learner is oriented to the informational value provided by feedback, even feedback that is not evaluative can engage the caudate and facilitate learning.

Further evidence that feedback signals in the striatum depend on whether feedback is viewed as evaluative versus informative comes from a study which found that simply mixing trials with and without feedback produces different responses in the ventral striatum and head of the caudate to negative feedback and to no feedback, compared to a blocked design of the same experimental task (Lempert & Tricomi, 2015). Whereas positive feedback is typically both rewarding and informative, negative feedback is often punishing, but still informative. When learners did not know whether feedback will be received, however, they reported a preference for negative feedback over no feedback, since even negative feedback provides information necessary to achieve the goal of improving task performance. Correspondingly, the “punishment” signal to negative feedback is attenuated in this “mixed feedback” design, relative to the “blocked feedback” design, within subjects (Lempert & Tricomi, 2015). Because the blocked feedback trials emphasized the evaluative nature of negative feedback (i.e., that negative feedback signals poor performance), they led to the signature “punishment” response of a dip below baseline, relative to no feedback. In contrast, the “mixed feedback” design served to highlight the informative nature of negative feedback, leading to an attenuation of this punishment response (Fig. 5). Thus, even very simple changes in a learning task are capable of shifting the subjective interpretation of feedback and the neural responses it produces.

Much research has shown that reward-related brain signals are strongly influenced by experience-driven expectations, based on the prediction error difference between the value of actual and expected outcomes (Shohamy, 2011). Interestingly, even subjective expectations, such as expectations
based on task instructions, can also influence the neural processing of reward (Delgado, Frank, & Phelps, 2005) and performance-related feedback. For instance, one study employed a trial-and-error categorization task in which separate blocks of trials were labeled either “easy” or “hard.” Feedback sensitivity in the caudate was enhanced during blocks that were expected to be more difficult, especially for individuals who scored high in normative goals, which reflect a desire to outperform other students (Fig. 6) (DePasque Swanson & Tricomi, 2014).

Fig. 5. Mixing Feedback With No-Feedback Reverses “Punishment” Response to Negative Feedback.
Because normative goals are inherently competitive, and difficult tasks could represent a potential opportunity to differentiate oneself from one’s competitors, these results imply that individual differences in achievement goals may modulate the subjective value of feedback, thus altering feedback responses in the DS.

These findings highlight the importance of considering individual differences when designing approaches to influence feedback processing during learning. Indeed, individual differences in approach motivation have been linked to exaggerated responses to reward receipt in the ventral striatum and orbitofrontal cortex (Simon et al., 2010), and extrinsic motivation has been found to correlate with neural responses to monetary rewards during probabilistic learning (Linke et al., 2010). Genetic differences in the dopamine transporter (DAT) gene have also been linked to individual differences in the effects of reward on memory, with increased dopaminergic
transmission being associated with increased striatal activation to motivational cues and better subsequent memory for those cues (Wittmann, Tan, Lisman, Dolan, & Düzel, 2013).

Together, these findings support the idea that both situational and dispositional factors can influence the subjective value attributed to performance-based feedback, modulating neural responses in networks that play an important role in effective learning and memory. Our research suggests that the effects of beliefs, values, and goals on learning success are tied to the extent to which they influence the incentive value of performance feedback as processed in the corticostriatal reward system of the brain.

THE MOTIVATIONAL CONTROL OF BEHAVIOR AFTER EXTENSIVE EXPERIENCE

Learning is often goal-directed; that is, it is motivated by the desire to achieve a goal, such as receiving positive feedback or mastering a task. However, as learning continues, and a particular response is repeated over and over, behavior may begin to become habitual. Habitual behavior is motivated not by the pursuit of a goal, but rather by a stimulus or context that has become associated with an action that leads to a goal (Dickinson & Balleine, 2002). For example, if someone turns left at a stop sign when driving to work, she may eventually no longer need to represent the goal of getting to work as she drives. Rather, the stop sign serves as a cue that elicits the habitual left turn, which can be executed without thinking about its consequences. This frees up mental resources to think about other things, but can be counterproductive if one’s goal changes. Indeed, the hallmark of habitual behavior is that it persists even once the outcome is no longer a behavioral goal. For example, one may still make the habitual left turn at the stop sign, even if one has a doctor’s appointment that requires turning right, rather than left.

In the lab, outcome sensitivity can be tested through a selective satiety devaluation procedure, in which individuals are pre-fed one of two food outcomes to satiety, so that the value of that outcome decreases while the value of the other food remains high. If behavior remains goal-directed, response rates should decrease for the devalued outcome relative to the still valued outcome following the devaluation procedure (Balleine & Dickinson, 1998; Colwill & Rescorla, 1985). If, however, behavior has become habitual, the cues associated with each response should elicit similar rates of responding irrespective of the outcome value. This procedure has been used with rats to
show that after extensive training, the response to a stimulus becomes independent of the outcome; even if the outcome is devalued, response rates remain high (Dickinson & Balleine, 2002). Further evidence from rodent studies has suggested that distinct subregions of the striatum may contribute to goal-directed and habitual behavior, with the dorsomedial striatum (DMS; equivalent to the caudate in humans) subserving goal-directed action, and the dorsolateral striatum (DLS; equivalent to the putamen in humans) supporting habit-based behavior (Yin & Knowlton, 2006). In rats with lesions to the DLS, habit learning is disrupted (Yin, Knowlton, & Balleine, 2004), whereas DMS lesions interfere with goal-directed learning (Yin et al., 2005); moreover, electrophysiological recordings of neuronal activity have confirmed that DMS neurons are more active early in training, whereas DLS neurons are more active later in training (Yin et al., 2009).

In humans, the selective satiety procedure has also been used successfully to test for outcome sensitivity (Gottfried, O'Doherty, & Dolan, 2003; O'Doherty et al., 2000). As with rodents, human behavior becomes demonstrably outcome-insensitive with extended training, demonstrating the transition from goal-directed to habitual behavior. Furthermore, after extensive training, there is a significant increase in task-related cue sensitivity in the human posterior putamen (Tricomi, Balleine, & O’Doherty, 2009). More recent investigation into the role of the posterior putamen in human habit learning has found that this region encodes reward value at the time a cue is presented requiring a motor response, but not at the time the associated outcome is revealed (Wunderlich, Dayan, & Dolan, 2012). This finding thus fits with the theory that the posterior putamen is not sensitive to outcome value, but rather represents motivationally salient cues. Additionally, Diffusion Tensor Imaging (DTI) has found that individual differences in the strength of the white matter tract between the posterior putamen and the premotor cortex, to which it projects, predict vulnerability to habitual actions toward outcomes that are no longer rewarding. Furthermore, this tendency toward habitual behavior is also related to gray matter density in the posterior putamen, measured with voxel-based morphometry (de Wit et al., 2012). Taken together, these results suggest a rodent-human homology in the neural structures governing goal-directed versus habitual behavior, and show that the distinction between behavior that is motivated by a goal and behavior that is motivated by response-associated cues is related to an underlying distinction in the corticostriatal systems supporting these two types of behavior (Balleine & O’Doherty, 2010; O’Doherty, 2015).

A related line of research has investigated “model-based” learning, in which a learner uses an internal model of the environment to make
decisions in a goal-directed way, compared to “model-free” learning, in which action values are learned slowly based on reinforcement history without an explicit model guiding behavior (Daw, Niv, & Dayan, 2005). Although this model-free learning is not insensitive to outcome consequences, it may be one mechanism by which habit learning occurs. Using a widely adopted paradigm with a two-step choice task that can differentiate model-based from model-free learning (Daw et al., 2011), research has found a bias toward model-free learning in individuals with psychiatric disorders related to compulsivity, such as obsessive-compulsive disorder, binge eating, and drug addiction (Deserno et al., 2015; Voon, Baek, et al., 2015; Voon, Derbyshire, et al., 2015); this fits with evidence using other experimental paradigms that habits play an important role in compulsivity, and that stress and anxiety exacerbate habitual tendencies (Alvares, Balleine, & Guastella, 2014; Gillan et al., 2011; Gillan, Robbins, Sahakian, van den Heuvel, & van Wingen, in press). Furthermore, a bias toward model-free learning is associated with lower gray matter volume in brain regions serving goal-directed behavior, such as the caudate and mOFC, suggesting that compulsivity may arise from an imbalance in contributions from the habit learning and goal-directed learning brain systems (Voon, Derbyshire, et al., 2015). Additionally, a bias toward model-free learning has been associated with increased functional connectivity between the putamen and supplementary motor area, again emphasizing that habit learning is subserved by a corticostriatal loop consisting of the putamen and motor regions of the cortex (Morris et al., 2015).

EDUCATIONAL IMPLICATIONS

An understanding of the multifaceted role that feedback plays in shaping learning has important implications for education and for motivating behavior toward healthy, rather than harmful goals. In trying to understand how to best tailor educational practices to the needs of the individual, influences on learning and performance other than ability need to be considered. Therefore, a better understanding of how motivation influences the neural mechanisms supporting learning and reward processing can inform educational and clinical practices. Our research shows that even in the absence of monetary or other extrinsic incentives, positive and negative feedback can activate learning systems in the brain much like rewards or punishments, particularly in contexts that elicit achievement goals.
consistent with the objectives of the task. This notion is consistent with studies of intelligence mindsets, in which beliefs about the stability or malleability of intelligence have been shown to influence both affective responses to feedback in the brain and the efficacy with which people learn (Mangels, Butterfield, Lamb, Good, & Dweck, 2006).

Learning can be a goal in itself, and individual differences in achievement goals may endow performance feedback with varying levels of reward value during learning. Interestingly, although performance feedback alone is able to activate the striatum, responses to feedback alone can be undermined by the presentation and subsequent removal of extrinsic monetary rewards. In other words, if an individual becomes accustomed to receiving monetary rewards and those rewards are then removed, striatal activation to feedback alone drops significantly below the response to feedback in a condition where no monetary rewards were ever present (Murayama, Matsumoto, Izuma, & Matsumoto, 2010). This mirrors the behavioral finding on the “undermining effect” of reward on performance; that is, extrinsic rewards such as money can undermine people’s intrinsic motivation to perform well on a task for its own sake (Deci, Koestner, & Ryan, 1999). Thus, it is important for educators (and others who wish to promote learning) to adopt an approach to instruction that will not undermine students’ intrinsic motivation to learn new material or improve their skills. Subtle changes in the learning context can orient learners toward different achievement goals, which in turn influence the motivational value of feedback. Furthermore, these contextual influences do not act on blank slates; pre-existing differences in individual students’ values, beliefs, and achievement goals can alter the way that the learning context affects feedback processing. Therefore, insights into the way that personality as well as contextual variables influence the brain’s response to feedback can go a long way in informing educators about how to tailor their practices to best support learning in students who come to the classroom with diverse goals and values.

REFERENCES


