Learning and motivation in the human striatum
Daphna Shohamy

The past decade has seen a dramatic change in our understanding of the role of the striatum in behavior. Early perspectives emphasized a role for the striatum in habitual learning of stimulus–response associations and sequences of actions. Recent advances from human neuroimaging research suggest a broader role for the striatum in motivated learning. New findings demonstrate that the striatum represents multiple learning signals and highlight the contribution of the striatum across many cognitive domains and contexts. Recent findings also emphasize interactions between the striatum and other specialized brain systems for learning. Together, these findings suggest that the striatum contributes to a distributed network that learns to select actions based on their predicted value in order to optimize behavior.

Address
Department of Psychology, Columbia University, New York, NY 10025, United States

Corresponding author: Shohamy, Daphna
(shohamy@psych.columbia.edu)

Current Opinion in Neurobiology 2011, 21:408-414
This review comes from a themed issue on Behavioral and Cognitive Neuroscience
Edited by Ann Graybiel and Richard Morris
Available online 12th June 2011
0959-4388/$ – see front matter © 2011 Elsevier Ltd. All rights reserved.
DOI 10.1016/j.conb.2011.05.009

Introduction
It is hard to believe that only a decade ago it was still hotly debated whether the striatum or other basal ganglia nuclei contribute to cognitive function, in addition to their obvious role in motor control. In recent years the question has reversed itself: Given the wealth of reports indicating a broad role for the striatum in many aspects of cognitive function – ranging from sequence learning to social cooperation – it seems that the crucial question now is: when does the striatum not contribute to cognition? That is, how can we understand the specific and selective role of the striatum in cognitive function?

Recent reports indicating that the striatum contributes to learning and motivation have been largely inspired by findings from systems and computational neuroscience demonstrating an important role for the striatum and its dopaminergic inputs in learning to predict reward. Together with extensive converging evidence indicating a role for the basal ganglia in habitual learning of stimulus–response associations [1–4], addiction [3], and movement [5,6], these findings emphasized a crucial role for this circuit in learning to predict rewards and acting to obtain them.

Here, we focus on recent human functional magnetic resonance imaging (fMRI) studies of the striatum. Together, these studies suggest an even broader role for the striatum in learning than previously recognized. This conclusion emerges from three complementary directions. First, recent fMRI studies have aimed to characterize the specific nature of learning signals in the striatum, raising questions about its selective role in reward-driven habits. Second, emerging data indicate that the striatum contributes to a wide range of sophisticated behaviors and to the representation of many kinds of outcomes. Third, new studies are taking advantage of the ability of fMRI to characterize broad neural networks and are providing a more detailed understanding of how interactions between the striatum and other specialized learning systems in the brain shape behavior. The following review focuses on these novel insights, considers the challenges they pose for developing an integrated understanding of the role of the striatum in learning, and discusses promising future directions that may help address these challenges.

The striatum and feedback-based learning
Understanding the selective role of the striatum in human learning

In the past decade there have been substantial advances in understanding the role of midbrain dopamine neurons and their striatal targets in learning from reward (for review [7]). The emergence of these findings has had an enormous influence on our understanding of the neural bases of learning. Although it had been previously recognized that the striatum plays an important role in learning, the common view was that it is specialized for implicit (i.e. unconscious) learning of habits (e.g. [1,2]). The novel emphasis on reinforcement, however, suggested a special role for the striatum in learning that is based on trial-by-trial feedback, regardless of whether it is implicit or not. This idea and the data that support it led to a novel conceptualization of the role of the striatum and helped resolved previous inconsistencies in the literature (e.g. [8,9]).

These ideas also led a wealth of fMRI studies in humans, which aimed to identify the selective role of the striatum in learning. Converging evidence indicates that the striatum supports the ability to gradually learn, based
Feedback-based learning of habits, goals, or both?

An important question which these studies leave open is to what extent is feedback-based learning in the human striatum truly habitual in nature. To get at this question, one approach has been to test, after learning, how people use what they learned. Habits are typically defined as behavior that is not sensitive to the value of its outcomes and in that respect is rigid or inflexible. In rodent conditioning studies, a series of studies demonstrate a key role for dorsolateral striatum in driving habitual responses that are expressed even when the animal no longer desires their outcomes (assessed using a devaluation procedure; for review [15]). Adapting this approach to humans learning to respond for food rewards, fMRI has revealed that the emergence of habits is associated with changes in activation in the dorsal striatum during learning [16] (see Figure 1).

Using a somewhat different approach, another recent study has shown that the dorsal striatum supports learning of inflexible stimulus–response associations particularly when people are distracted while they are learning [17]. Here, learning involved cognitive feedback (rather than primary rewards); habits were defined as the inability to flexibly express the learned associations on a later probe test. Notably, in both of these studies, as in many others, the selective role for the striatum in habit learning is thought to be complemented by other distinct brain regions that are specialized for other forms of learning (e.g. goal-directed behaviors in the orbitofrontal cortex (OFC) [18] or mnemonically flexible behaviors in the hippocampus [2,17,19]).

Recent findings, however, raise questions about this parcellation and especially about the unique role of the striatum in feedback-based learning of habits, as detailed below. Rather than focusing on post-learning behaviors, these studies have combined computational models with fMRI to identify brain regions where trial-by-trial fluctuations in the BOLD signal vary with specific computational variables, as learning takes place [11,20**,21–24].

Early fMRI studies in humans focused on classical conditioning paradigms and primary rewards such as juice, literally replicating paradigms from animal electrophysiological studies [23,24]. The ubiquitous finding is that a reward prediction error – computationally equivalent to that signaled by midbrain dopamine neurons – correlates with BOLD activation in the ventral striatum, presumably reflecting dopaminergic inputs there (e.g. [22–26]; for review [27]). This signal is thought to be central to the learning of habitual stimulus-reward associations and is referred to computationally as ‘model-free’ learning (because it involves learning directly from experience rather than using an existing model of the task structure).

Expanding on these findings, recent studies have been using this approach to compare different kinds of learning signals and their neural substrates [8,20**,21]. For example, one recent study revealed that activation in the striatum during learning was related to multiple forms of learning [20**]. Specifically, activation in the ventral striatum correlated with ‘model-free’ learning of habitual stimulus-reward associations, as shown previously. But, an overlapping region in the ventral striatum also correlated with so-called ‘model-based’ learning, which involves more abstract learning about task structure and states, rather than stimulus–response associations (for a related study see also [21]).

This surprising result stands in contrast to other evidence for clear anatomical segregation between different learning signals, both within the striatum (e.g. [14]; for review see [15]) or between the striatum and other brain regions (e.g. [13,21]; for review see [18])

The striatum supports learning and motivation across domains

In parallel to the attempts to characterize distinct types of learning and their neural substrates, there has also been much effort to determine whether these neurobiological learning mechanisms encompass the wealth of stimuli, outcomes and contexts which are characteristic of, and in some cases unique to, human learning.

Learning signals across domains

There is now ample evidence that reward prediction error signals in the ventral striatum are generated by expectations and receipt of a wide variety of rewards, including money, verbal and cognitive feedback, food, and music [12,25,26,28–36]. Of particular importance for neurobiological theories of learning, recent findings in both animals and humans indicate that the striatum supports learning to predict both positive and negative outcomes [37–42]. Beyond simple reinforcement, however, these signals also account for a wide variety of complex social behaviors, including reciprocity in rewards [43], social fairness [44*], social learning [45–47], and overbidding in auctions [41].
Motivation to learn
Collectively, these findings suggest a broad role for the striatum in learning to modify actions based on predicted outcomes. This provides an obvious link to motivated, goal-directed behavior. Notably, truly motivated behavior has traditionally been dissociated from habitual responses to obtain rewards, again demonstrating quite a broad role for the striatum in many different processes.

One important recent advance has been the demonstration that striatal signals encode not just extrinsic rewards, but also intrinsic motivation [48**]. This study leverages a well-known psychological phenomenon whereby extrinsically controlled rewards, such as money, can hamper intrinsic motivation. Here, performance and brain activation were compared between two groups that both played a simple ‘stopwatch’ computer game that required rapid responding to cues on a computer screen. One group received performance-based rewards (money), while another group played the same game but did not receive performance-based rewards. When given the option to keep playing the game during their ‘free’ time, the group that received performance-based rewards was much less likely to choose to play compared with the group that did not receive rewards. In parallel to this behavioral difference between the groups, fMRI revealed that the decrease in motivation due to extrinsic reward was related to decreased responses in the anterior striatum and in the prefrontal cortex (PFC), suggesting a key role for the striatum in the integration of extrinsic reward value and intrinsic motivation. Other negative effects due to extrinsic reward (in this case ‘overmotivation’) also appear to operate via motivational signals in the striatum [49] (see Figure 1).

The idea that the striatum may contribute to multiple mechanisms that underlie motivated behavior also has implications for more abstract forms of knowledge, such as memory for facts, events or objects [50*,51–53]. Intriguingly, in such cases, activation in the ventral striatum predicted the beneficial effects of motivation on long-term memory, along with cooperative interactions between midbrain dopamine regions and the hippocampus [50*]. Finally, responses in the striatum also relate to goal satisfaction in tests of episodic memory retrieval [54,55]. Notably, these learning situations do not involve repeated responses, nor extrinsic rewards, nor any outcome or feedback, and thus differ substantially from the repeatedly reinforced stimulus–response associations typically associated with the striatum (see also [56]).

Feedback, motivation and learning
The demonstration of such a wide variety of motivational signals in the striatum raises questions about whether this region plays a role that is much broader than learning from feedback, or, alternatively, whether our traditional framing of feedback as explicit reinforcement is too narrow. Interestingly, in the birdsong literature it has been shown that performance itself – without additional explicit reinforcement – serves as a form of feedback that supports learned behaviors in the avian basal ganglia [57]. As in the studies reviewed above, these behaviors do not fit the canonical definition of a feedback-based learning task that typically involves the selection of a specific action in order to obtain a specific reward. Together, these varied findings emphasize the broad importance of feedback in driving behavior even when this feedback is not explicit (see also [58]).

Interactions between the striatum and other learning systems
The striatum is known to interact with a wide network of cortical regions [59]. Recent years have seen exciting progress in understanding the specific role of the OFC in learning value and interacting with the striatum to guide actions (for review [18,60]). As nicely demonstrated in a recent rat lesion study, the OFC together with the ventral striatum represent not only reward value, but also reward identity, suggesting, yet again, that both these regions may encode rather richer representations of outcomes than previously thought [61].

New advances in fMRI data analysis make it increasingly possible to ask questions not only about parallel contributions of interconnected regions, but also their dynamic interactions over the course of learning. For example, one recent study used dynamic causal modeling of BOLD activity to demonstrate that striatal prediction error responses can tune plasticity in visual and motor cortex [62*].
Finally, there has been a surge of interest in understanding interactions between the striatum and other specialized learning systems, most notably the hippocampus [13,63–66,67*]. Although the striatum and the hippocampus were traditionally thought to support two distinct and independent memory systems [2], an emerging literature has focused on characterizing their joint and interactive contributions to learning [13,17,65,66,68]. Anatomically, both the striatum and the hippocampus connect with PFC, a likely pathway for mediating interactions between them [59,69–72]. Functionally, both competitive and cooperative interactions between the hippocampus and the striatum, as well as parallel contributions, have been reported [17,66,68,73]. These have emerged in a number of recent studies that involve multi-trial reinforcement learning paradigms (e.g. [13,28,67*]).

Notably, cooperative interactions between the hippocampus and the striatum also emerge in very different kinds of learning situations, even those which involve no choice or feedback, and indeed no real ‘performance’ beyond passive viewing [50*,74]. Providing a possible explanation for these varied effects, a recent study reported that responses in the striatum encode value even during passive viewing, and that such responses predict later choice behavior [75]. Yet other findings indicate that in contrast to its traditional depiction as a neutral ‘cognitive’ memory store, long-term memory in the hippocampus is also modulated by dopamine, expectations and value [53,63,76,77]. Together, these findings suggest that information about affect and value may be encoded by multiple interacting brain systems for learning (for review [63]). These findings also emphasize the link between mnemonic processes, learning and decision making (for review [78]), an idea that has received recent empirical support [79].

Challenges and open questions

Determining the necessary role for the striatum in learning and motivation

An important limitation of fMRI is that it cannot indicate the causal, essential role of a brain region for a particular function. Thus, moving forward, it will be crucial to test predictions that emerge from fMRI research in both animal and human lesion studies that can test the necessary role of the striatum across varied learning situations.

Some important progress on this front has emerged from studies with Parkinson’s disease patients, which in its early stages involves relatively selective loss of nigro-striatal dopamine projections. Indeed, Parkinson’s patients have provided important insight into the role of the striatum in learning (for review see [80–82]), including evidence directly relevant to the role of the striatum in feedback and reward based learning [9,81,83–85]. Notably, data from Parkinson’s patients so far indicate a rather selective pattern of deficits in learning from reinforcement. Future studies are necessary to test the selectivity of these effects in light of the recent broad findings from fMRI to allow a more precise understanding of when the striatum is involved, and necessary, for learning.

The role for dopamine in learning in the striatum

A related challenge is to determine the crucial role of dopamine in learning and motivation. One approach to probe this question has been to use Parkinson’s disease as a model with which to directly test the role of dopamine in learning, by testing patients either on or off dopaminergic drugs [83,84,86]. Together with genetic studies and PET imaging [8,87–89,90*], such studies afford insight into dopaminergic mechanisms underlying learning, providing an important complement to BOLD fMRI, which does not provide insight about dopamine, per se.

Implications for disorders of learning and motivation

The many recent advances in our basic understanding of how and when the striatum contributes to learning and motivation have important implications for psychiatric and neurological disease and for changes in learning and motivation across the life span (e.g. [91–93]). Initial progress in these domains demonstrates the promising potential of leveraging basic findings from computational, neurophysiological and cognitive neuroscience to gain a better understanding of the neural mechanisms that support learning and motivation in both health and disease.

Acknowledgements

Thanks to R.A. Adcock, L. Atlas, E.K. Braun, N. Daw, K. Foerde, I. Kahn, G.E. Wimmer and S. Wood for helpful comments and to support from an NSF Career Development Award, a NARSAD Young Investigator Award, and the Michael J. Fox Foundation.

References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:


20. Daw N, Gerashan SJ, Dayan P, Dolan RJ: Model-based influences on humans’ choices and striatal prediction errors. Neuron 2011, 69:1204-1215. This paper used fMRI and computational models of learning and demonstrated overlapping responses to two distinct learning signals: one thought to correspond to retrospective learning of stimulus-reward associations (‘model-free’), the other thought to correspond to prospective learning of the task structure (‘model-based’).


44. Tricomi E, Rangel A, Camerer CF, O’Doherty JP: Neural evidence for inequality-averse social preferences. Nature 2010, 463:1089-1091. The authors examine the neural basis of inequality-averse preferences. Activity in a subject’s ventral striatum and ventromedial prefrontal cortex was more responsive to the transfer of money to others when the subject was first given a large endowment of money, while the opposite pattern was seen when the subject was not given the endowment.


The striatum and Learning

Shohamy


48. Murayama K, Matsumoto M, Izuma K, Matsumoto K: Neural basis of the underlying effect of monetary reward on intrinsic motivation. Proc Natl Acad Sci USA 2010, 107:20911-20916. The authors demonstrate that activity in the anterior striatum and prefrontal areas decreased along with the ‘undermining effect,’ the phenomenon in which performance-based extrinsic reward undermines a person’s intrinsic motivation to engage in a task.


50. Adcock RA, Thangavel A, Whitfield-Gabrieli S, Knutson B, Gabrieli JD: Reward-motivated learning: mesolimbic activation precedes memory formation. Neuron 2006, 50:507-517. The authors discover that cues indicating high-value rewards for memorizing upcoming scenes lead to greater activation in the VTA, nucleus accumbens, and hippocampus, along with superior memory performance later. Greater correlation between the hippocampus and VTA is associated with enhanced long-term memory, suggesting reward motivation may promote memory formation via DA release in the hippocampus before learning.


62. den Ouden HE, Dauizeau J, Roiser J, Friston KJ, Stephan KE: Striatal prediction error modulates cortical coupling. J Neurosci 2010, 30:3210-3219. The authors use a probabilistic, cue-stimulus association task to characterize the role of striatal trial-by-trial prediction error activity in controlling the efficacy of visuomotor connections. These data show the influence of surprising stimuli on premotor activity, and provide empirical evidence for a central role for prediction error-dependent plasticity in learning.


67. Mattfeld AT, Stark CE: Striatal and medial temporal lobe functional interactions during visuomotor associative learning. Cereb Cortex 2011, 21:847-858. The authors demonstrate coupling in activity in the ventral striatum and MTL during learning of an arbitrary associative learning task, and the opposite pattern in the associative striatum and MTL. Distinct areas throughout the striatum and MTL are modulated by probability correct or rate of learning.


69. Goldman-Rakic PS, Selemon LD, Schwartz ML: Dual pathways connecting the dorsolateral prefrontal cortex with the hippocampal formation and parahippocampal cortex in the rhesus monkey. Neuroscience 1984, 12:719-743.


90. Krugel UK, Biele G, Mohr PN, Li SC, Heekeren HR: Genetic variation in dopaminergic neuromodulation influences the ability to rapidly and flexibly adapt decisions. Proc Natl Acad Sci USA 2009, 106:17951-17956. The authors demonstrate an advantage in reward-based learning in those with the Val/Val genotype of the Val108Met COMT polymorphism, characterized by faster, more flexible learning, as well as greater and more differentiated striatal fMRI responses to predictions errors.


