

The Involvement of Corticostriatal Loops in Learning Across Tasks, Species, and Methodologies

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Abstract The basal ganglia contribute to a variety of forms of learning. The first goal of this chapter is to review the different tasks (instrumental conditioning, visual discrimination, arbitrary visuomotor learning, rule learning, categorization, and decision making) that have been used to study basal-ganglia-dependent learning in rodents, monkeys, and humans. These tasks have several features in common: in each, the subject is first presented with a stimulus within a behavioral context, is then required to respond with an appropriate behavior, and finally receives a reward or positive feedback for correct behavior. The second goal of this chapter is to examine how these different features (stimulus, response, and reward) involve the independent corticostriatal loops that connect the basal ganglia with cerebral cortex. The visual corticostriatal loop is involved in aspects of visual stimulus processing; the motor corticostriatal loop is involved in response selection; and the executive and motivation corticostriatal loops are involved in processing feedback and reward. The chapter concludes with a discussion of how the corticostriatal loops interact during learning.

1 Introduction

Recent years have seen an increased appreciation of the contributions made by the basal ganglia to cognitive domains other than motor processing. In particular, the basal ganglia are involved in a wide variety of learning tasks which have in common the requirement for the subject to learn via trial and error to associate a given stimulus or experimental context with a given response or behavior. In this chapter, I will first describe these tasks individually, emphasizing the features they have in common. I will then discuss the different corticostriatal loops and how each loop may subserve some of the features common to basal-ganglia-dependent learning tasks.

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2 Basal-Ganglia-Dependent Learning Tasks

In this section, I will describe several of the commonly used tasks developed to study basal-ganglia-dependent learning in humans, monkeys, and/or rodents. Although these tasks are basal ganglia dependent, task performance does not rely on only the basal ganglia; instead, the basal ganglia interact with cortex and other neural systems in performing the behavior. Cortical contributions to performance will be mentioned here when they are particularly prominent, but space considerations preclude a full discussion of cortical contributions to each task.

The tasks discussed here are used along with multiple experimental methodologies. In nonhuman animal models the most prominent methodologies include experimental lesion, chemical manipulation, and electrophysiological recording of individual neurons. In human models, the most commonly used methodologies are studies of patients with neuropsychological disorders of the basal ganglia (e.g., Parkinson's disease), and functional brain imaging using functional magnetic resonance imaging (fMRI) or positron emission tomography (PET). Due to the depth of the basal ganglia within the head and the cellular anatomy of the basal ganglia, there are many research methods that cannot currently be used to study the basal ganglia, including electroencephalography, magnetoencephalography, optical imaging, and transcranial magnetic stimulation.

Across species and methodologies, learning tasks that recruit the basal ganglia typically involve three common features: presentation of a stimulus within a behavioral context, an overt motor response, and reward or feedback. First, the subject is placed into a particular behavioral context (e.g., a rat may enter a Skinner box; a human may enter the laboratory and be seated in front of a computer monitor), and is faced with particular stimuli (e.g., a lever; or a visual image on the computer screen). Second, the subject must decide what the correct behavior is and then execute the behavior (e.g., by pressing a lever; or a key on a computer keyboard). Third, the subject is given feedback or a reward indicating whether he or she responded correctly (e.g., a drop of fruit juice; or the word "Correct!" on the computer screen). Tasks differ in terms of which of these features are manipulated by the researcher and are thus considered to be of primary importance. For example, in visual discrimination learning the visual stimuli are manipulated; in arbitrary visuomotor learning, the particular motor response performed by the subject is manipulated. Nevertheless, both these tasks include all three features: the subject is presented with a stimulus, performs a response, and receives feedback.

2.1 *Tasks from the Rodent Literature*

2.1.1 Instrumental Conditioning

In instrumental conditioning, subjects learn to perform desired behaviors in response to cues in order to receive rewards. These tasks are most commonly used with rodents. A common experimental context is provided by a maze (such as a T maze, plus maze, or the Morris water maze); when placed in the maze, the subject must learn

to perform the same behavior on each trial (e.g., turn right, or go to a visually cued location). The striatum has been shown to be involved in these tasks in experiments involving induced lesions of the basal ganglia (Packard et al. 1989; Packard and McGaugh 1992), chemical manipulation of neural activity and neural plasticity (Atallah et al. 2007; Brightwell et al. 2008), and electrophysiological recording of striatal neurons (Jog et al. 1999; Barnes et al. 2005).

Modern learning theory has identified two forms of instrumental conditioning: goal-directed learning, sometimes called Action–Outcome–Reward (A–O–R) learning, and habit learning, sometimes called S–R learning (Yin and Knowlton 2006; Balleine et al. 2007). Goal-directed learning tends to predominate early in training. It is reliant on the dorsomedial striatum in rodents, which is roughly homologous to the head of the caudate nucleus/anterior putamen in primates. As training progresses, goal-directed behavior shifts to habit learning. The main distinction between habit learning and goal-directed learning is that habit is resistant to incentive devaluation. For example, an animal might be trained to run a maze in order to receive water. Water can be devalued as an incentive by giving the animal ad libitum water before the session. Goal-directed responding will be impaired by incentive devaluation, whereas habitual responding is not. Habit learning is reliant on the dorsolateral striatum in rodents, which is roughly equivalent to the posterior putamen in primates. It should be noted that the use of the term “habit learning” is inconsistent across researchers and tasks: some reserve the term habit for only S–R learning, whereas others use it for any learning of repeated behavior in response to a situation.

2.2 Tasks from the Monkey Literature

2.2.1 Visual Discrimination

In this task the subject views two visual stimuli or objects, and has to choose one of them, typically by touching it on a computer screen (Gaffan and Eacott 1995), grasping the object, or uncovering an adjacent food well (Teng et al. 2000; Fernandez-Ruiz et al. 2001). The subject learns across trials to choose the item that is rewarded. This task is typically used with macaque monkey, which has a better developed visual system than rodents. This task was developed primarily to answer questions about visual memory and visual form processing, but has also been considered to be a monkey test of habit learning. Visual discrimination learning is often studied in conjunction with visual cortical regions. Monkeys with lesions to either the striatum or the visual cortex are impaired in visual discrimination learning (Gaffan and Eacott 1995); in addition, striatal neurons are active when performing this task (Brown et al. 1995).

2.2.2 Arbitrary Visuomotor Learning/Conditional Response

In this task the subject views a single stimulus which serves as a cue to perform a motor action; correct performance is followed by a reward. The relationship

between the visual cue and the response is arbitrary (e.g., the visual stimulus does not include any information about the desired direction of movement). The emphasis in this task is on the motor action, and on the association between cue and action. Arbitrary visuomotor learning studies in monkeys have shown that both acquisition (Wise and Murray 2000) and performance of previously learned relationships (Nixon et al. 2004) are impaired by striatal lesions. Electrophysiological studies find that striatal cell activity increases during learning (Hadj-Bouziane and Boussaoud 2003; Brasted and Wise 2004). In humans, functional imaging studies of the arbitrary visuomotor association task have also found striatal activation (Toni et al. 2002; Grol et al. 2006). Arbitrary visuomotor learning often is accompanied by activation of premotor and motor cortex.

2.2.3 Rule Learning

The term rule learning is used for at least two types of experiment. One type stems from the monkey learning literature and is very similar to arbitrary visuomotor learning. In both tasks, the subject is trained to implement a particular relationship across the length of the study (Murray et al. 2000). However, in rule learning the relationship between stimulus and response is often more complex than in arbitrary visuomotor learning. For example, the rule “same” requires the subject to learn to choose whichever stimulus is the same as a previously presented stimulus. Both lesion and electrophysiological studies indicate that the striatum is important for learning and performing abstract rules (Murray et al. 2000; Muhammad et al. 2006).

A second type of rule learning experiment uses tasks that emphasize switching between rules, or reversing a previously learned association. In both humans and monkeys, the striatum is active while switching (Monchi et al. 2001; Cools et al. 2004; Seger and Cincotta 2006), and when relearning after a rule reversal (Cools et al. 2002; Pasupathy and Miller 2005). Both types of rule learning tasks often have heavy reliance on prefrontal cortical regions in conjunction with the striatum (Bunge et al. 2005).

2.3 *Tasks from the Human Literature*

2.3.1 Categorization and Classification

In categorization and classification tasks, subject view visual stimuli, and decide for each which category or group it belongs to. Typically subjects indicate the category via a button press on a computer keyboard, then receive feedback (usually verbal, either indicating whether the response was correct or incorrect, or indicating the actual category membership of the stimulus). These tasks were developed primarily to investigate the effects of stimulus similarity on learning, and the ability of subjects to generalize to novel stimuli. However, the basal ganglia are commonly

involved regardless of categorical structure (Ashby and Waldron 1999; Seger 2008). Some commonly used tasks that recruit the basal ganglia are trial and error prototype learning in which stimuli are formed as distortions of a prototypical stimulus (Vogels et al. 2002), information integration learning in which stimuli are grouped on the basis of a decision bound in abstract feature space (Seger and Cincotta 2002; Ashby and Maddox 2005; Cincotta and Seger 2007; Nomura et al. 2007), probabilistic classification learning in which multiple-independent features are correlated with category membership (Knowlton et al. 1996a, b; Poldrack et al. 1999, 2001), and arbitrary categorization tasks in which stimuli in each group share no identifiable common characteristics and the category membership of each must be learned independently (Seger and Cincotta 2005).

2.3.2 Decision Making

In decision making and gambling tasks, subjects view a set of options (often pictured as cards or slot machines), choose one of them, and receive reward (often points, sometimes actual money). Unlike categorization tasks, the stimuli remain the same across the task and the emphasis is primarily on learning about the reward or feedback. Some studies manipulate the presence and valence (loss vs. gain, or reward vs. punishment) of the reward (Delgado et al. 2000; Knutson and Cooper 2005; Yacubian et al. 2007). Other studies manipulate the relationship between stimulus, decision, and reward to examine how subjects make decisions faced with ambiguity (unknown contingency) or risk (known probabilistic contingency; Delgado et al. 2005; Kuhnen and Knutson 2005; Huettel et al. 2006; Preuschoff et al. 2006). Sometimes these reward features are varied across the time course of learning to examine how subjects adjust to changing contingencies (Daw et al. 2006).

3 Roles of Corticostriatal Loops in Learning

Given the complexity of basal-ganglia-dependent learning tasks, and the many features that these tasks have in common, it is unclear whether the basal ganglia are important for all aspects of task performance, or just a subset of the task features. Furthermore, the basal ganglia are not a single isolated brain structure; instead, the basal ganglia are closely connected with cerebral cortex and other subcortical regions, and participate in multiple-independent neural networks known as corticostriatal loops. In my laboratory, we try to take fine-grained view of both learning task demands and basal ganglia anatomy in order to identify specific linkages between particular learning task features and particular corticostriatal loops. Our main methodology is fMRI, which has excellent spatial resolution that allows us to localize specific regions within the human basal ganglia.

Within the scope of this chapter, I will illustrate the patterns we have found primarily in reference to one study, which used a simple categorization task

(Seger and Cincotta 2005). In this task, the subject views a single visual stimulus, such as an abstract pattern of lines, a house, or a face. While the stimulus is visible, the subject must decide which of the two arbitrary categories it belongs to (e.g., group 1, or group 2), and press the button corresponding to the category. The subject then sees a feedback screen consisting of either the word “Right” or “Wrong.” The relationship between each individual stimulus and the categories can be deterministic, random, or probabilistic. A deterministic relationship means the stimulus is always in one of the categories, and subjects receive consistent feedback to that effect. When the relationship is random the stimulus is in each category half of the time; in this situation, the subject cannot learn any regular stimulus-category pairings. In a probabilistic relationship, the stimulus might be in category 1 80% of the time and category 2 the other 20%. Subjects can learn probabilistic stimulus–category relationships, but on some trials they will receive feedback that is counter to the pre-dominant membership. In this task, we operationally defined learning-related trials as deterministic and probabilistic trials in which the subject responded correctly and received positive feedback. In addition we examined feedback processing by comparing the response to positive (“Right”) and negative (“Wrong”) feedback on random trials; this manipulation serves to isolate feedback processing in the absence of learning. Figure 1 shows the patterns of recruitment of different striatal regions during successful categorization learning and during feedback valence processing in this simple categorization task.

3.1 *Corticostriatal Loops: Anatomy*

All lobes of the cortex project to the striatum (consisting of the caudate nucleus, putamen, and ventral striatum including the nucleus accumbens) and from there to the output structures of the basal ganglia and back to the cortex thus forming “loops.” Different cortical areas project to different striatal areas (Alexander et al. 1986; Lawrence et al. 1998). Cortical regions project to the striatum in rough correspondence with the proximity of the cortical region to the particular striatal region. Although there are no strict borders between various corticostriatal loops, on the basis of the predominant cortical inputs to particular striatal regions it is possible to divide the corticostriatal systems into at least three types (Parent and Hazrati 1995): limbic (referred to here as motivational), associative, and sensorimotor (referred to here as motor). The largest of these, the associative loop, is sometimes subdivided further. In this chapter, we follow the lead of Lawrence et al. (1998) who split the associative loop into two loops; these are described in more detail below and in Table 1.

Overall, projections follow a gradient from the most anterior–medial–ventral portions on up to the most posterior–lateral–dorsal regions. In primates this corresponds to a gradient running from ventral striatum (motivational loop), to the head of the caudate/anterior putamen (executive loop), then to the body/tail of the caudate (visual loop), and finally to the posterior putamen (motor loop). In addition, there are various neurochemical processes that follow the same gradient. The most prominent

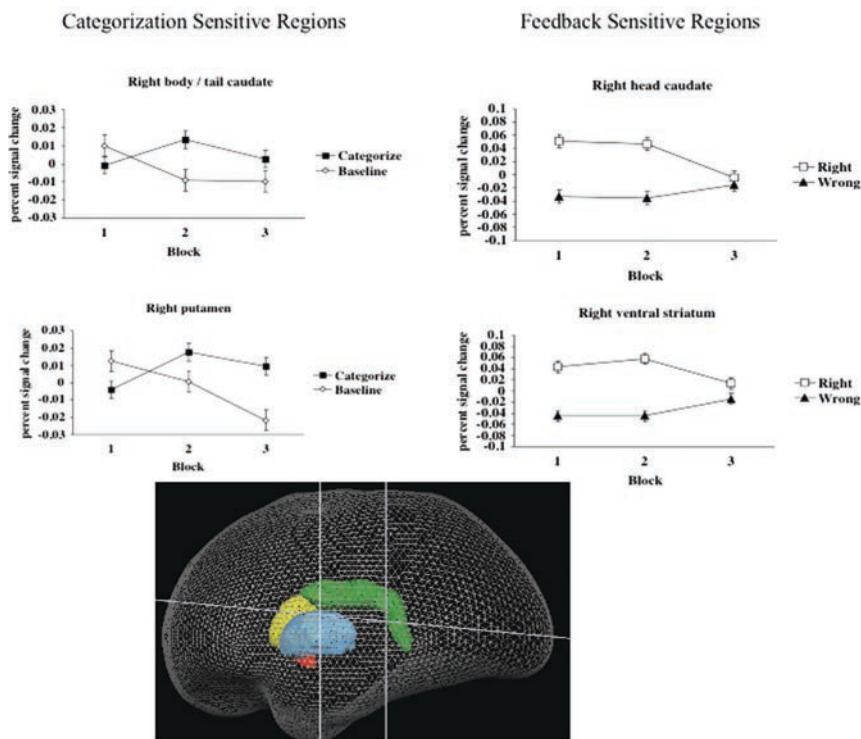


Fig. 1 *Left:* Activity in the body/tail of the caudate and putamen regions of interest during correct categorization in comparison with baseline across blocks of training. *Right:* Activity in the ventral striatum and head of the caudate regions of interest in response to positive (“Right”) and negative (“Wrong”) feedback on random trials across blocks of training. In all graphs, activity is measured as percent blood oxygen level-dependent (BOLD) signal change from the beginning of each trial, and is averaged for all voxels within the particular region of interest. *Bottom:* Regions of interest within the striatum, lateral view; *Red:* ventral striatum; *Yellow:* Head of the caudate; *Green:* Body and Tail of the caudate; *Blue:* Putamen. For simplicity only right-sided activity is shown; left-sided basal ganglia activity did not differ significantly

of these is the density of dopaminergic projections from the VTA/SNc (Voorn et al. 2004; Haber et al. 2006). Calbindin immunoreactivity (a measure of the presence of the calcium-binding protein, calbindin) also follows this gradient, with greatest binding in the anterior–medial–ventral portions (Karachi et al. 2002).

3.2 Corticostriatal Loops: Function

On a cellular level, all corticostriatal loops have a similar pattern of neural connectivity. This implies that there should be a similarity of function across loops as well. One general function served by the basal ganglia is the selection or gating of representations

Table 1 Cortical, striatal, and dopaminergic systems interacting within each corticostriatal loop

	Cortical projections	Striatal target:	Striatal target:	Dopaminergic
Loop name	Primate	Primate	Rodent homolog	innervation
Motivational	Orbitofrontal	Ventral striatum	Nucleus accumbens	High
	Anterior cingulate	Nucleus accumbens	Shell and core	
	Amygdala	Ventral putamen		
	Hippocampus	Ventral caudate		
Executive	Dorsolateral prefrontal	Head of the caudate	Dorsomedial	Intermediate
	Posterior parietal	Anterior putamen		
Visual	Inferior temporal	Body of the caudate	Dorsomedial	Intermediate
	Middle temporal	Tail of the caudate	Bordering	
	Superior temporal		Dorsolateral	
	Ventrolateral prefrontal			
	Frontal eye fields			
Motor	SMA	Posterior putamen	Dorsolateral	Low
	Lateral premotor cortex			
	Primary motor			
	Primary somatosensory			

Note. SMA supplementary motor area

in cortex (Redgrave et al. 1999; Gurney et al. 2004). Cortex is characterized by the simultaneous activation of many different possible representations (e.g., possible movements in motor cortex, possible strategies in the frontal lobes, possible object categories in visual cortex). The basal ganglia modulate these cortical representations in two ways. First, they exert a broad tonic inhibition on these representations. Second, they can effectively select a particular representation by phasically reducing the inhibition for it. Researchers currently have identified three pathways (direct, indirect, and hyperdirect) between the striatum/STN and BG output nuclei. These allow for inhibition and selection of cortical representations across different timescales (see Frank 2006, for a review).

3.3 Visual Corticostriatal Loop

The visual corticostriatal loop links temporal and occipital extrastriate visual cortex with the body and tail of the caudate (Webster et al. 1993; Middleton and Strick 1996). In addition, visually related frontal lobe regions such as the ventrolateral prefrontal cortex (involved in visual working memory; Inoue and Mikami 2007) and the frontal eye fields (involved in eye movement planning; Lau and Glimcher 2007) also project to the body and tail of the caudate. The visual corticostriatal loop may contribute to selection within the cortex in two ways. One is by modulating representations within visual cortex, such as selection of a particular interpretation

of an ambiguous visual scene or updating visual working memory. In addition, there are output projections from visual loop to motor cortex that may enable selection of appropriate motor plans on the basis of current visual processing (Ashby et al. 1998, 2007).

In our laboratory we have found that the body and tail of the caudate participate in categorization learning. As shown in Fig. 1, the body and tail of the caudate is more active overall during correct categorization than on baseline trials. Furthermore, activity in the body and tail increases across the time course of learning, and more successful learners (those who achieved greater accuracy) were more likely to recruit this area than less successful learners. We also found activity associated with learning in the body and tail of the caudate when using information integration categorization tasks (Cincotta and Seger 2007), and in simple rule learning tasks (Seger and Cincotta 2006). Current work in progress in our lab is investigating how the body and tail of the caudate interact with visual cortical regions during learning.

The visual loop has also been implicated in learning in studies involving other methodologies, species, and tasks. In humans, neuropsychological research has found that categorization is impaired in cases of basal ganglia damage (Knowlton et al. 1996a, b; Shohamy et al. 2004; Ashby and Maddox 2005), but typically these studies cannot isolate specific corticostriatal loops. Research using the concurrent visual discrimination task finds that the tail of the caudate (Brown et al. 1995; Teng et al. 2000; Fernandez-Ruiz et al. 2001) and temporal lobe visual processing area TE (Buffalo et al. 1998) both must be intact for monkeys to learn concurrent visual discrimination tasks. Conversely, visual discrimination learning is preserved when all other connections from visual areas of the inferior temporal lobe other than the connection to the striatum are severed (Gaffan and Eacott 1995).

3.4 *Motor Corticostriatal Loop*

The motor loop connects the motor and somatosensory cortexes of the frontal and parietal lobes with the putamen (Lawrence et al. 1998). Motor cortex is organized hierarchically, from primary motor cortex (involved in representing particular directions of motor effectors) to supplementary motor area (SMA) and premotor cortex (involved in motor programming) to preSMA and other prefrontal structures (involved in higher order programming and goal setting). Within the motor loop, the basal ganglia selection function is expressed in the realm of overt motor behavior (Redgrave et al. 1999; Gurney et al. 2004). Basal ganglia disorders typically result in oversuppression of movement (hypokinesia) or undersuppression of movement (hyperkinesia).

Categorization tasks require that the subject select and perform an appropriate motor responses, even in tasks in which motor performance is not the main focus of attention. In our laboratory, we have examined recruitment of the putamen during categorization learning. As shown in Fig. 1, the pattern of activation in the putamen is similar to the pattern found in the body and tail of the caudate.

This study, however, was not designed to tease apart the different roles that putamen and body and tail of the caudate may play in learning; other studies have indicated that overall the caudate nucleus is more involved during acquisition of stimulus–response relationships, whereas the putamen is more involved in skilled, habitual, or automatic performance (Haruno and Kawato 2006; Williams and Eskandar 2006; Balleine et al. 2007). Tasks in which motor demands are prominent (e.g., arbitrary visuomotor learning) are especially likely to report putamen involvement in learning (Brasted and Wise 2004). In addition, electrophysiological studies that have isolated basal ganglia responses to stimulus, response, and feedback have found that the putamen is more likely than other striatal regions to be active during the response phase (Yamada et al. 2007).

3.5 *Executive Corticostriatal Loop*

The executive corticostriatal loop links the head of the caudate and anterior regions of the putamen to the dorsolateral prefrontal cortex and interconnected regions of the posterior parietal cortex (Lawrence et al. 1998). Executive function involves monitoring performance, correcting for errors, and initiating, stopping, and switching between complex cognitive procedures. Within the realm of the basal-ganglia-dependent learning tasks discussed in this chapter, executive functioning is especially required for interpreting feedback or reward and using this information as a cue to initiate a strategic plan, update working memory, or switch between associations.

In our laboratory, we have investigated the role of the head of the caudate and interacting cortical regions across a series of studies. One approach we have taken is to examine how feedback valence affects caudate activity. As shown in Fig. 1, in the simple categorization task (Seger and Cincotta 2005), we found greater activity in the head of the caudate for positive feedback than for negative feedback. This difference was modulated by experience: as training continued (and presumably subjects learned that feedback would not be helpful in learning the category membership of the random stimuli), the differential sensitivity of the head of the caudate was eliminated. We found a similar pattern in a rule learning task that involved hypothesis testing: greater activity in the head of the caudate in response to positive feedback than negative (Seger and Cincotta 2006). Other studies have found a similar pattern of feedback valence sensitivity. In the domain of rule learning, Monchi et al. (2001) found greater activity for negative feedback than positive in the Wisconsin Card Sorting task, whereas tasks in which feedback valence is randomly determined (e.g., gambling tasks) generally show greater activity for positive than negative feedback (Delgado et al. 2000; Tricomi et al. 2004; Seger and Cincotta 2005).

Another approach we have taken is to compare learning tasks that involve trial and error feedback with those that are observational (that is, in which subjects are told the category membership on each trial, then tested on their learning later). We found that activity in the head of the caudate was modulated by presence of

feedback during learning (Cincotta and Seger 2007). Neuropsychological studies have found that people with basal ganglia disorders are impaired in learning via feedback but learn normally on observational tasks (Shohamy et al. 2004; Smith and McDowall 2006). Electrophysiological studies have shown that cells in the head of the caudate are more likely to be active after receiving feedback than during stimulus processing or response execution (Yamada et al. 2007).

3.6 *Motivational Corticostriatal Loop*

The motivational loop connects the ventral striatum with predominantly limbic regions. In primates, the ventral striatum consists of the nucleus accumbens and the most ventral and anterior portions of the caudate and putamen. The motivational loop receives projections from ventral and medial frontal regions (including orbito-frontal cortex and the anterior cingulate), the hippocampus and the amygdala (Lawrence et al. 1998). The projections to striatum from midbrain dopaminergic regions such as the ventral tegmental area and substantia nigra pars compacta are particularly pronounced in the ventral striatum.

How selection is exhibited in the motivational loop is controversial. Some studies indicate that rather than being involved directly in response selection, the ventral striatum may maintain information from past experience, such as the results of the previous trial (Kim et al. 2007) or the stimulus and behavioral context of several seconds in the past (Nicola 2007). Research on reward processing finds that the ventral striatum is sensitive to reward valence, whereas more dorsal areas of the striatum such as the head of the caudate are sensitive to reward only when subjects must make actions contingent on the rewards (O'Doherty et al. 2004).

In our categorization study (see Fig. 1), we found that the ventral striatum was sensitive to feedback valence and showed a similar pattern as the head of the caudate across the time course of learning. In other classification learning tasks, ventral striatal activity has been found to be sensitive to the degree of prediction error for negative feedback (Rodriguez et al. 2006) and to the degree of categorization uncertainty (Grinband et al. 2006).

4 Interactions between Corticostriatal Loops

So far this chapter has focused on the role that each individual corticostriatal loop plays in learning. However, the corticostriatal loops do not act in isolation: there is interaction between the loops, and different loops take on different roles across the time course of learning. There are at least three anatomical bases for interactions between corticostriatal loops. Many of the interactions between loops follow the gradient from motivational to motor loop, as described above and in Table 1. First, the output projections from the thalamus can target a different cortical area than the

one providing the input to the loop. For example, the visual loop has output projections that target premotor areas in the frontal lobe (Passingham 1993; Ashby et al. 1998). Second, there is interaction between loops at the level of projection from the striatum to basal ganglia output nuclei (Joel and Wiener 1994). Finally, there are reciprocal projections between the striatum and the SNc/VTa: the return projections from striatum to SNc/VTa terminate at cells that in turn project back to striatum, but to relatively more dorsal, lateral, and posterior regions (Haber et al. 2000).

During learning, there are shifts between corticostriatal loops. Many of these shifts appear to follow the ventromedial-anterior to dorsolateral-posterior gradient, such that activity in the executive loop precedes activity in the motor loop. In instrumental conditioning (Yin and Knowlton 2006; Balleine et al. 2007), early learning has been characterized as goal directed and shown to be reliant on the head of the caudate (dorsomedial striatum in rodents); later phases of learning have been characterized as habit learning, are relatively more automatic in the sense that it is resistant to incentive devaluation, and have been shown to be reliant on the putamen (dorsolateral striatum in rodents). Researchers using computational modeling techniques have found that the caudate nucleus is most active when learning rate is the highest (Williams and Eskandar 2006) and when subjects are making the most use of feedback to change their mental representations (Haruno and Kawato 2006). In contrast, activity in the putamen generally follows behavioral performance, increasing as accuracy increases even to the point of automaticity (Haruno and Kawato 2006; Williams and Eskandar 2006). Foerde et al. (2006) manipulated the degree of automaticity of performance by requiring subjects to perform a categorization task under dual task conditions, which limited the amount of attention they could pay to the task. In dual task conditions, in which attention was limited, learning tended to rely on the putamen, whereas in single task conditions where the subject could apply full attention to learning the caudate was recruited.

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