Dissociation between Striatal Regions while Learning to Categorize via Feedback and via Observation

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Abstract

■ Convergent evidence from functional imaging and from neuropsychological studies of basal ganglia disorders indicates that the striatum is involved in learning to categorize visual stimuli with feedback. However, it is unclear which cognitive process or processes involved in categorization is or are responsible for striatal recruitment; different regions of the striatum have been linked to feedback processing and to acquisition of stimulus–category associations. We examined the effect of the presence of feedback during learning on striatal recruitment by comparing feedback learning with observational learning of an information integration task. In the feedback task, participants were shown a stimulus, made a button press response, and then received feedback as to whether they had made the correct response. In the observational task, participants were given the category label before the stimulus appeared and then made a button press indicating the correct category membership. A region-of-interest analysis was used to examine activity in three regions of the striatum: the head of the caudate, body and tail of the caudate, and the putamen. Activity in the left head of the caudate was modulated by the presence of feedback: The magnitude of activation change was greater during feedback learning than during observational learning. In contrast, the bilateral body and tail of the caudate and the putamen were active to a similar degree in both feedback and observational learning. This pattern of results supports a functional dissociation between regions of the striatum, such that the head of the caudate is involved in feedback processing, whereas the body and tail of the caudate and the putamen are involved in learning stimulus–category associations. The hippocampus was active bilaterally during both feedback and observational learning, indicating potential parallel involvement with the striatum in information integration category learning. ■

INTRODUCTION

Effective and appropriate behavior in the human environment requires the ability to form categories of objects, people, and events, and to link these categories with appropriate responses. The striatum is involved in forming these links: Many diseases that affect the striatum (including Parkinson's and Huntington's diseases, schizophrenia, obsessive–compulsive disorder, and Tourette syndrome) cause impairments in learning to categorize. Category learning involves multiple cognitive functions, including visual analysis, response performance, association formation; and executive functions, including strategy selection, feedback processing, and set switching; it is unknown which of these functions are critically dependent on the striatum. Furthermore, the striatum interacts with the cortex in multiple independent networks or "loops"; it is unclear if and how each individual loop contributes to categorization. Our goal was to begin to map some of these cognitive functions onto particular corticostriatal loops. We manipulated the presence of feedback and examined its effect on three regions of the striatum: the head of the caudate, body and tail of the caudate, and the putamen.

Previous functional imaging research associating striatal activity with category learning has used tasks that share common features: (1) subjects learn to classify stimuli into two (or more) categories or classes of outcomes, (2) subjects indicate category membership via independent motor responses, and (3) training takes place with feedback on a trial-and-error basis. These tasks include information integration (Nomura et al., 2007; Seger & Cincotta, 2002) and probabilistic classification (both multiple cue variants, Aron et al., 2006; Aron, Gluck, & Poldrack, 2004; Poldrack et al., 2001; Poldrack, Prabhakaran, Seger, & Gabrieli, 1999; and simpler variants, Seger & Cincotta, 2005). Additionally, performance on these tasks is impaired in people with compromised striatal functioning due to Huntington's disease (Filoteo, Maddox, Salmon, & Song, 2005; Filoteo, Maddox, & Davis, 2001; Knowlton, Squire, et al., 1996), Parkinson's disease (Shohamy, Myers, Onlaor, & Gluck, 2004; Sage et al., 2003; Witt, Nuhsman, & Deuschl, 2002; Maddox & Filoteo, 2001; Knowlton, Mangels, & Squire, 1996, but see also Ashby, Noble, Filoteo, Waldron, & Ell, 2003), Tourette syndrome (Keri, Szlobodnyik, Benedek, Janka, & Gadoros, 2001), focal right striatal lesion (Keri et al., 2002), schizophrenia (Beninger et al., 2003; Keri et al., 2000), and obsessive–compulsive disorder (Roth et al., 2003). Feedback appears to be particularly

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important for striatal recruitment: Neuropsychological studies using probabilistic classification and artificial grammar learning tasks have shown that people with Parkinson's disease are impaired when learning via feedback but not impaired when learning via a different strategy, such as observation (Smith & McDowall, 2006; Shohamy, Myers, Grossman, et al., 2004). Behavioral studies support both the necessity of feedback for high levels of performance in categorization learning (Ashby, Maddox, & Bohil, 2002; Ashby, Queller, & Berretty, 1999), and the time-sensitive nature of feedback (Maddox, Ashby, & Bohil, 2003).

Different regions of the striatum participate in independent corticostriatal loops. The head of the caudate interacts with the dorsolateral prefrontal cortex as part of the "cognitive" corticostriatal loop, the body and tail interacts with inferior temporal areas as part of the "visual" corticostriatal loop, and the putamen interacts with premotor areas as part of the "motor" loop (Lawrence, Sahakian, & Robbins, 1998; Middleton & Strick, 1996). Given these differing anatomical connections, it is likely that these striatal regions will play different roles in classification learning (Ashby, Alfonso-Reese, Turken, & Waldron, 1998). The head of the caudate has been shown to be sensitive to the presence of feedback in many cognitive tasks, including gambling tasks (Delgado, Stenger, & Fiez, 2004; Delgado, Nystrom, Fissell, Noll, & Fiez, 2000) and instrumental learning tasks (Haruno et al., 2004; O'Doherty et al., 2004) as well as in categorization learning (Tricomi, Delgado, McCandless, McClelland, & Fiez, 2006). Furthermore, the head of the caudate is sensitive to feedback valence, with most studies finding greater activity for positive than negative feedback (Filoteo, Maddox, Simmons, et al., 2005; Seger & Cincotta, 2005; Delgado et al., 2000, 2004; Tricomi, Delgado, & Fiez, 2004). Early Parkinson's disease has its strongest effects on anterior portions of the striatum (including the head of the caudate nucleus; Dauer & Przedborski, 2003), and patients with early Parkinson's disease are impaired in learning via feedback but learn normally on observational tasks (Smith & McDowall, 2006; Shohamy, Myers, Grossman, et al., 2004).

The body and tail regions of the caudate have been theorized to represent associations between the visual stimulus and motor response, indicating category membership (Ashby & Casale, 2003; Ashby et al., 1998). In the visual corticostriatal loop, the inferior temporal cortex projects to the body and tail of the caudate (Middleton & Strick, 1996; Yeterian & Pandya, 1995; Updyke, 1993; Webster, Bachevalier, & Ungerleider, 1993; Saint-Cyr, Ungerleider, & Desimone, 1990; McGeorge & Faull, 1989). A major projection from the body and tail goes to premotor areas of cortex (via the basal ganglia output nuclei), particularly Brodmann's area (BA) 8, also known as the frontal eye fields (Passingham, 1993). Research in nonhuman animals indicates that the visual loop is necessary for visual association learning (Fernandez-Ruiz, Wang, Aigner, & Mishkin, 2001; Teng, Stefanacci, Squire, & Zola, 2000; Buffalo et al., 1999; Buffalo, Stefanacci, Squire, & Zola, 1998). Models of the visual corticostriatal loop give feedback-associated dopamine release, a crucial role in forming associations. The striatal synapse is tripartite: The synapses of glutamatergic cortical projection neurons onto striatal spiny cells are modulated by dopaminergic projections from the midbrain, and strengthening of these synapses only occurs when dopamine is present (Reynolds & Wickens, 2002). Ashby and Casale (2003) and Ashby et al. (1998) propose that dopamine-mediated plasticity in corticostriatal synapses is the neural mechanism that underlies information integration category learning. This theory is supported by research finding that disruption of dopaminergic input to the striatum impairs stimulus–response learning in rats (Faure, Haberland, Conde, & El Massioui, 2005). Two studies have dissociated the contributions of head, and body and tail regions of the caudate to learning within in the same experiment. Seger and Cincotta (2005), using a simple probabilistic classification task with eight discrete stimuli, found that activity associated with successful classification learning was localized in the body and tail, whereas the head of the caudate was sensitive to feedback valence. Another study used a rule learning task and found that the head of the caudate was sensitive to feedback valence and was active primarily at the beginning of rule learning (perhaps due to working memory updating or task shifting demands), whereas the body and tail of the caudate was active across the time course of classification and was greater in successful learners than unsuccessful (Seger & Cincotta, 2006).

In addition to caudate nucleus regions, the putamen is also often active during category learning. The putamen interacts with the motor and somatosensory cortices of the frontal and parietal lobes in the motor loop (Lawrence et al., 1998). Seger and Cincotta (2005) found that the putamen activity pattern was similar to that of the body and tail of the caudate in that it increased across the course of learning. However, putamen activity was not correlated with learning success. In categorization studies, a motor response is required on each trial, and one possibility is that the putamen is recruited due to its role in initiating motor responses.

We were also interested in examining what role the hippocampus might play in information integration category learning. Studies using multiple cue probabilistic classification tasks have found an antagonistic relationship between striatal and medial-temporal activity (Poldrack et al., 1999, 2001). Poldrack et al. (2001) compared feedback-based learning with a paired associates observational learning task. They found greater hippocampal activity during observational learning than during feedback learning, and greater striatal activity during feedback learning than during observational learning;

furthermore, striatal and hippocampal activity was negatively correlated across tasks and subjects. Within feedback learning, hippocampal activity decreased across learning, whereas striatal activity increased. Seger and Cincotta (2005) found that caudate activity was positively correlated with classification accuracy, whereas hippocampal activity was negatively correlated with classification accuracy. Previous studies of information integration category learning did not report hippocampal activity when categorization was compared with baseline (Seger & Cincotta, 2002) or when correct categorization trials were compared with incorrect trials (Nomura et al., 2007). However, Nomura et al. (2007) did find greater activity in the hippocampus for rule-based categorization than information integration categorization.

We directly compared feedback learning with observational learning within subjects in an information integration task (Ashby et al., 2002). Each participant performed both a feedback and an observational task. During feedback learning, participants learned in a trial-and-error manner, receiving feedback on each trial. During observational learning, participants were told the category membership of each stimulus prior to its presentation, then indicated the category membership with a button press. Test trials were identical for both the feedback and the observational tasks; participants were neither given feedback nor told the category label. Our primary goal was to examine activity associated with feedback and observational learning separately in the head of the caudate, body and tail of the caudate, and the putamen to determine which of these systems was affected by feedback. Secondary goals included examining hippocampal recruitment during the task, and identifying cortical areas of activation that may interact with the striatum during learning.

METHODS

Participants

Participants were 13 members of the Stanford community, 7 men and 6 women, with an average age of 24.4 years (range = 20–42 years). Participants were right-handed, fluent speakers of English, met the criteria for MRI scanning (no metallic implants, no claustrophobia, head size compatible with the custom head coil), and were neurologically healthy (no known neurological or psychiatric injury or disease, not taking any psychoactive medication or drugs).

Materials

Two sets of stimuli were developed, both of which incorporated one feature that varied on the basis of spatial extent, and one that varied the basis of angle. As shown in Figure 1, one set of stimuli (LA) was constructed of two lines; one varied in length and the other varied

in the angle at which it intersected the other line. A second set of stimuli (DA) was constructed of a circle, which varied in diameter, with a line extending from center to edge, which varied in angle from horizontal. The baseline stimulus was an outline of a square. Two categories, A and B, were defined for each stimulus set. Category members for the two categories were constructed according to the Ashby et al. (2002) Experiment 1 diagonal category structure. The category structures and the parameter values are shown in Table 1. Each category distribution is specified by a mean and a variance on each dimension and by a covariance between dimensions. The stimuli from each category were generated by sampling randomly from a bivariate normal distribution. Categories A and B had different means; however, the covariance matrix was identical for both categories, except that the covariance of the DA stimuli was negative (Diag-Neg in Ashby et al., 2002) and the covariance of the LA stimuli was positive (Diag-Pos in Ashby et al., 2002). The stimuli that have a negative covariance increase in length or diameter as the angle decreases and the stimuli that have a positive covariance increase in length or diameter as the angle increases.

Procedure

Each participant completed two tasks, feedback and observational, in one session. Each task was approximately 18 min long. Each participant was presented with both stimulus sets; one during the observational task and the other during the feedback task. The order of the tasks and assignment of stimulus sets (LA or DA) to tasks were counterbalanced across participants. Two hundred forty stimuli were generated for each task, 120 in Category A and 120 in Category B. Of the 120, 100 served as training trial stimuli and 20 served as test trial stimuli.

Training trials in both feedback and observational tasks consisted of the following events: a blank screen for 100 msec, a cue letter for 450 msec, a stimulus (during which participants made a response) for 2000 msec, and finally, a letter string for 450 msec. On feedback training trials, the cue letter was always "F" (for "feedback") and the letter string was the feedback, either "correct" or "incorrect." On observational training trials, the cue letter indicated category membership of the stimulus ("A" or "B") and the letter string was always "XXXXXXXX."

The test and baseline trials were identical in the observational and feedback tasks. On test trials, the cue letter was "T" (meaning "test") and the letter string was always "XXXXXXXX." Thus, participants neither were told the category membership nor received feedback. On baseline trials, the cue letter was an "S" (meaning "square") and the letter string was always "XXXXXXXX."

Figure 1. Category structure and sample stimuli used in the experiment. Top: Length–angle stimulus structure. Bottom: Diameter–angle stimulus structure. Each triangle denotes an individual exemplar of Category A and each dot denotes an exemplar of Category B. The diagonal line represents the optimal decision bound. The solid arrow points at the mean or prototypical stimulus dimensions. Three exemplars of each category are shown, with an arrow to the point representing their stimulus dimensions.
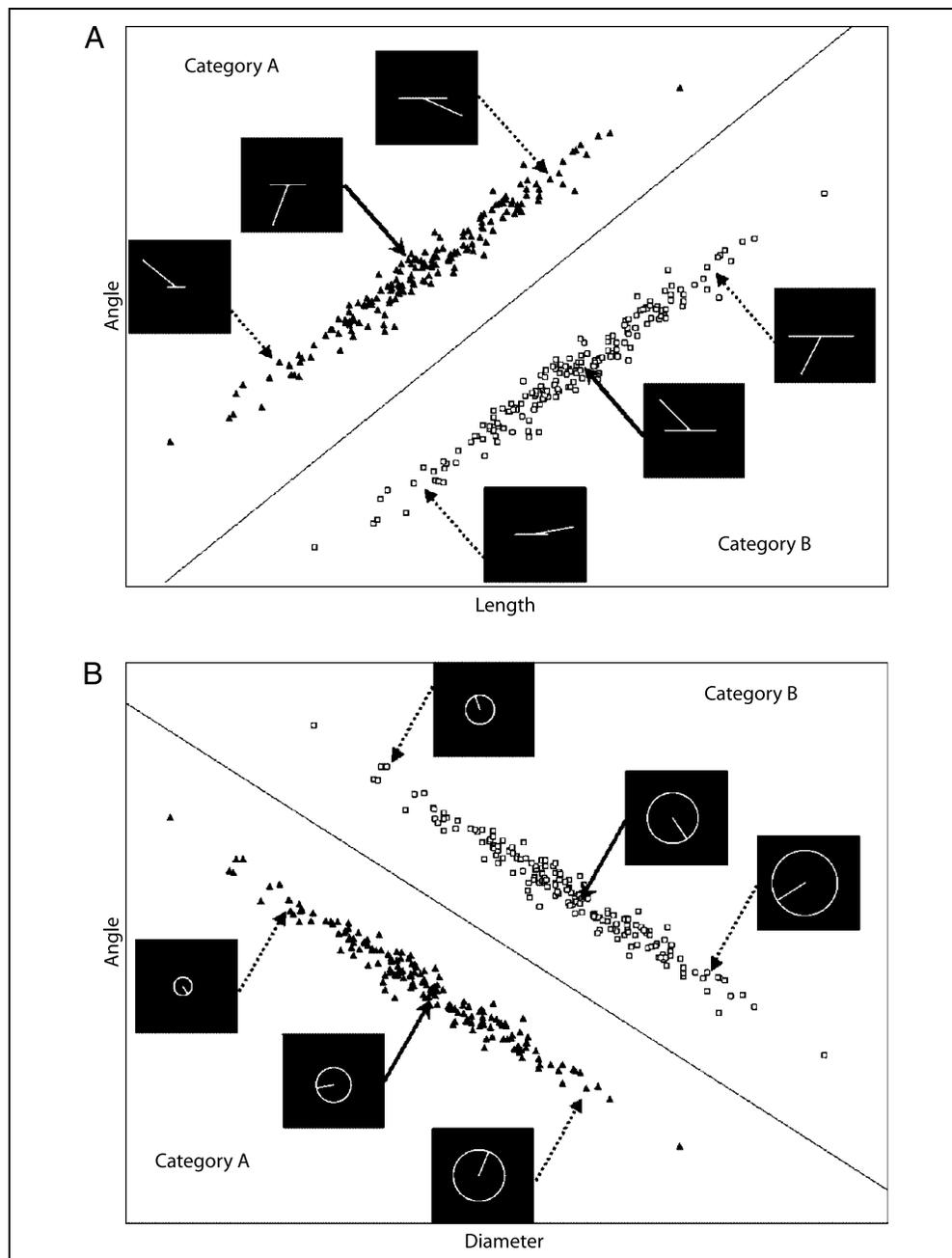
We used a block design. Block designs have the advantage of being more sensitive to differences in blood oxygen level dependent (BOLD) signal than event-related designs, but with a block design it is not possible to attribute activations to particular events within a trial. For each task, there were 20 training blocks, 4 test blocks, and 24 baseline blocks, for a total of 48 blocks. Each task was broken into four quartiles.

Table 1. Category Distribution Parameters

Condition	Category A					Category B				
	μ_x	μ_y	σ_x	σ_y	cov_{xy}	μ_x	μ_y	σ_x	σ_y	cov_{xy}
LA Stimuli	243	249	4538	4538	4463	357	135	4538	4538	4463
DA Stimuli	243	190	4538	4538	−4463	357	304	4538	4538	−4463

μ = mean for each dimension; σ = variance for each dimension; cov = covariance between dimensions.

Each quartile included five training blocks (50 trials total), one test block (10 trials total), and six baseline task blocks. Training and test blocks alternated with baseline blocks, with the test block being the final block within each quartile. Each training and test block was 10 trials and each baseline block was 5 trials, resulting in each training and test block lasting for 30 sec and each baseline block for 15 sec.

fMRI Image Acquisition

Imaging was performed with a custom-built whole head coil in a 3.0-Tesla MRI Signa LX Horizon Echospeed (General Electric Medical Systems, Milwaukee, WI). Head movement was minimized for participants using a ''bite-bar'' formed with the participant's dental impression. In addition to the functional scans, three anatomical scans were performed: a coronal T1-weighted localizer scan, a three-dimensional high-resolution T1-weighted spoiled gradient-echo scan with 124 contiguous 1.5 mm slices [minimum full echo time (TE), 30° flip angle, 24 cm field of view, 256 × 256 acquisition matrix], and an in-plane anatomical T1-weighted spin-echo scan with 22 contiguous 5-mm axial slices [minimum full TE; repetition time (TR) = 500 msec, 24 cm field of view, 256 × 256 acquisition matrix]. Functional scanning was performed using a T2*-sensitive gradient-echo spiral in–out pulse sequence (Preston, Thomason, Ochsner, Cooper, & Glover, 2004; Glover & Law, 2001) [TE = 30 msec; TR = 1500 msec; 65° flip angle; 24 cm field of view; 64 × 64 acquisition matrix] of the same 22 contiguous 5-mm axial slices as the in-plane images.

Stimuli were presented using a magnet-compatible projector (Resonance Technology, Van Nuys, CA) that back-projects visual images onto a screen mounted above the participant's head. E-prime software (Psychology Software Tools, Pittsburgh, PA) running on a personal computer was used to generate visual stimuli and control experimental parameters. Responses were obtained using a magnet-compatible response system.

Image Processing

Image analysis was performed using Brain Voyager QX 1.1 (Brain Innovation, Maastricht, The Netherlands). The functional data were first subjected to preprocessing, consisting of three-dimensional motion correction, slice scan time correction, and temporal data smoothing with a high-pass filter of three cycles in the time course and linear trend removal. Each participant's high-resolution anatomical image was normalized to the Tailarach and Tournoux (1988) brain template. The normalization process in Brain Voyager consists of two steps, an initial rigid body translation into the AC–PC plane, followed by an elastic deformation into the standard space performed on 12 individual sub-

volumes. The resulting transformations were applied to the participant's functional image volumes to form volume time-course representations to be used in subsequent statistical analyses. Finally, the volume time-course representations were spatially smoothed with a Gaussian kernel, full width at half maximum of 6.0 mm.

Statistical Analysis

Because of the a priori prediction that striatal and hippocampal structures would be important for categorization, the primary statistical analysis was limited to eight regions of interest (ROIs) in the striatum and hippocampus: the right and left head of the caudate nucleus, the right and left body and tail of the caudate nucleus, the right and left putamen, and the right and left hippocampus. These areas were defined anatomically using a single subjects' high-resolution normalized anatomical image, and were confirmed to encompass the structure in all participants. The ROIs were drawn with generous margins in order to ensure coverage of each structure across subjects; thus the borders of the ROIs extended into surrounding white matter and ventricles, but not into gray matter areas such as the thalamus, insula, or globus pallidus. The resulting ROIs are shown in Figure 2. The ROI general linear model (ROI GLM) tool of Brain Voyager QX 1.1 was used to analyze contrasts between conditions, separately within each ROI.

In addition to the ROI analysis of striatal and hippocampal structures, a whole-brain analysis was performed to identify additional structures that may be associated with category learning. Brain Voyager was used to analyze contrasts between conditions, using the GLM with separate subject predictors and random effects analysis. Again, only contrasts with potential theoretical interest were analyzed. The False Discovery Rate (FDR) method with a threshold of $q < .05$ was used to control for proportion of false positives; $q < .05$ results in no more than 5% of the voxels being significantly active by chance (Genovese, Lazar, & Nichols, 2002).

RESULTS
Behavioral Results: Accuracy Measures

Feedback Task

A 2 (learning task: feedback training and feedback test) × 4 (quartile) repeated measures analysis of variance (ANOVA) indicated a main effect of quartile, $F(3,36) = 12.12$, $p < .001$, such that overall accuracy increased across trials (see Figure 3). There were no other significant interactions or main effects ($ps > .1$). In conclusion, participants learned to classify across quartiles, and performance on the test quartiles was similar to that on the training quartiles.
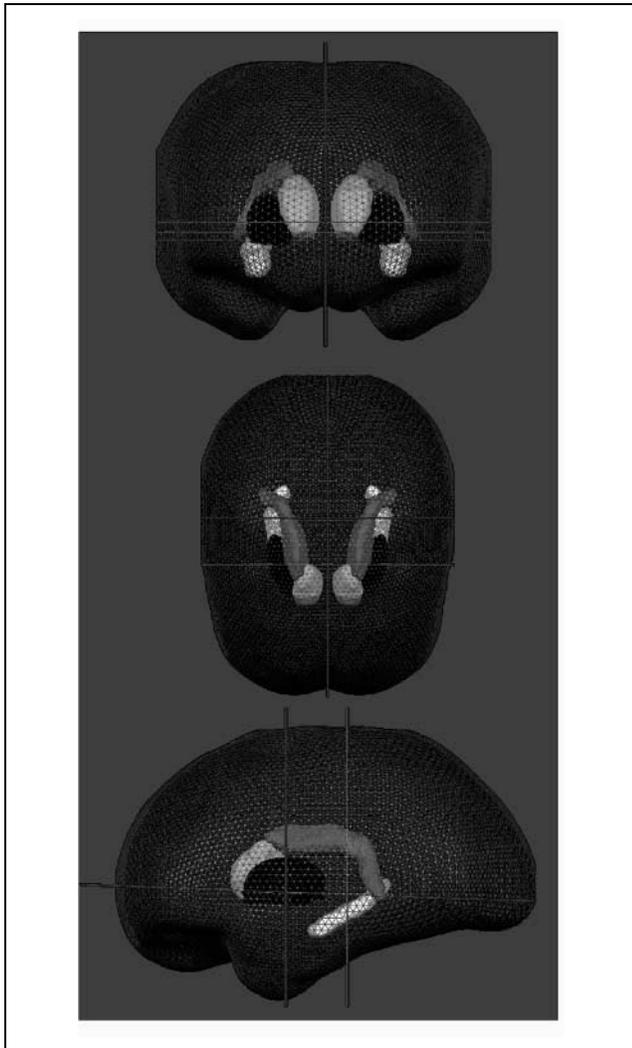
Figure 2. Three-dimensional rendering of the striatal and hippocampal regions of interest, viewed from the left, from above, and from the front. The white mesh indicates the approximate borders of cortex in order to show the relative locations of the ROIs in the brain. Dark gray: body and tail of the caudate. Light gray: head of the caudate. Black: putamen. White: hippocampus. White lines indicate the planes of $z = 0$, $x = 0$, $y = 0$, and $y = −20$, as used in Talairach and Tournoux (1988) atlas. Within the caudate nucleus, the border between the head and the body and tail ROIs was along an oblique plane angled at 45° from horizontal running between the lines defined by $y = 0$, $z = 14$ and $y = 10$, $z = 24$. The head of the caudate ROIs extended inferiorly to $z = −1$ and laterally from the ventricles to $x = ±13$. The body and tail of the caudate ROIs extended superiorly to $z = 28$, inferiorly in the body portion to $z = 16$, in the tail portion to $z = −3$, laterally from approximately $x = ±9$ to $x = ±22$ in the body region, and posteriorly to $y = −38$ at the tip of the tail. The putamen ROIs extended from $z = −1$ to $z = 15$, from $y = −15$ to $y = +15$, and from $x = ±15$ to $x = ±33$. The hippocampus ROI extended from $z = 6$ to $z = −18$, from $y = −0$ to $y = −43$, and from $x = ±20$ to $x = ±34$.
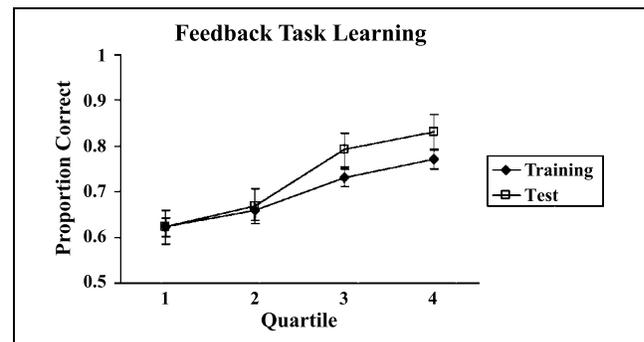
Observational Task

Because participants were told the category membership for stimuli on observational training trials, accuracy was high: 98.8% across the entire scan. The rate of missed responses was 14.5%; subjects may have omitted re-

sponses because there was no signal indicating that the response was not received. The observational test blocks provide the best measure of learning. Across the four quartiles, participants had accuracies of 0.83 ($SD = 0.18$), 0.67 ($SD = 0.23$), 0.76 ($SD = 0.22$), and 0.78 ($SD = 0.25$), respectively. Because a monotonically increasing learning curve was not seen, we performed a one-sample t test to determine if participant's accuracy rates varied significantly from chance (0.50 in this task). For each quartile during the observational test, mean accuracy rates differed significantly from chance [Quartile 1: $t(12) = 6.64$, $p < .001$; Quartile 2: $t(12) = 2.63$, $p < .05$; Quartile 3: $t(12) = 4.25$, $p < .001$; Quartile 4: $t(12) = 4.09$, $p < .01$). The high accuracy in the first quartile is probably due to an unintended grouping of unusually easy-to-categorize stimuli in this quartile. In both the LA and DA stimulus sets, the 10 Quartile 1 stimuli were either very similar to the prototype of the category, or were stimuli with extreme values that made them very dissimilar from the prototype of the alternate category.

Comparison of Feedback and Observational Learning

The best comparison of learning between conditions is on the test quartiles in which the trial structure was identical for both observational and feedback tasks. A 2 (learning task: feedback and observational) × 4 (quartile) repeated measures ANOVA was performed on participant's accuracy on test quartiles to examine learning across the tasks. There was a significant interaction of Learning task by Quartile, $F(3,36) = 5.39$, $p = .004$, which was probably driven by the unusually high performance on the first quartile of the observational task. In addition, there was a main effect of quartile, $F(3,36) = 3.93$, $p = .016$, such that accuracy increased across quartiles for both tasks combined. Accuracy on the feedback test portion ($M = 0.72$, $SD = 0.14$) was not significantly different from that on the observational test portion ($M = 0.76$, $SD = 0.20$), $F(1,12) = 0.29$, $p > .1$. Similar accuracy in observational and feedback learning is consistent with Ashby et al. (2002), who found similar levels of accuracy

Figure 3. Mean proportion correct across quartiles in feedback learning in training blocks and test blocks. Error bars show standard error.

for feedback and observational learning during early training blocks; differences in accuracy between groups in their study did not emerge until later in training.

To investigate whether there were any effects of the order in which the tasks were performed, a 2 (learning task: feedback and observational) × 2 (order: observational first, feedback first) ANOVA was performed on participants' accuracy levels on the test quartiles. For this analysis, we were solely interested in whether or not there was an interaction between accuracy for each task and order in which the tasks were performed. There was no significant interaction ($F < 1.0$).

Behavioral Results: Model-based Analysis

Using the model fitting methods outlined in Ashby et al. (2002), we examined which of three possible strategies best characterized each subject's categorization performance: unidimensional rule, conjunctive rule, or information integration. Classification using a unidimensional rule involves ignoring one of the dimensions, and classifying stimuli solely on the basis of the second dimension, with items above a criterion value in one category, and stimuli below criterion in the other; this translates into a verbalizable rule such as "If it is wide, then it is in Category A; if it is narrow, in Category B." Classification using a conjunction rule involves evaluating each dimension against a separate criterion, then combining the results of the two decisions to make a final decision. This translates into a verbalizable rule such as "if the stimulus is both narrow and has an angle close to horizontal, then it is in Category B, otherwise it is in Category A." Information integration was measured by fitting the general linear classifier, which assumes a linear decision bound between the categories; it requires linear integration of perceived length and orientation. The main difference between a conjunctive rule and information integration is the point at which the information is combined across dimensions: For the conjunctive rule, it is after each dimension is independently evaluated, whereas in information integration, the integration is predecisional.

The percentage of subjects whose best fitting strategy was a linear rule, conjunctive rule, or information integration is shown in Table 2. Due to the limited number of trials in the observational test and feedback test conditions, we were not able to examine strategy change across quartiles. Also in Table 2 are the corresponding values from Ashby et al. (2002). Most participants in both observational and feedback conditions had patterns of classification performance that were best fit by an information integration model.

Striatal and Hippocampal ROI Analysis

For each ROI, six contrasts were examined. ROIs included the right and left head of the caudate; the body and

Table 2. Percentage of Participants whose Data were Best Fit by Rule-based or Information Integration Models

	Present Study		Ashby et al. (2002)	
	Training	*Test*	*Block 1*	*Block 2*
Observational Learning				
Rule-based (total)	NA	15	30	60
Unidimensional		8		
Conjunctive		8		
Information integration	NA	85	70	40
Feedback Learning				
Rule-based	23	38	70	70
Unidimensional	23	38		
Conjunctive	0	0		
Information integration	77	62	30	30

Data from Ashby et al. (2002) were taken from their Experiment 1, which corresponds closest to the stimulus structure used in the present study. These data can be found in their Table 2, top section (response training, diagonal category structure); only Blocks 1 and 2 (of 5 total) are included here. Due to the difference in experimental design and number of trials per block, Ashby et al. transfer block 1 (trials 81–160) is roughly comparable to the present study quartiles 2 and 3 (trials 70–180, of which trials 111–120 and 171–180 are test trials); quartile 4 (trial 240) ends at the point where Ashby et al. transfer block 2 (trials 241–320) begins.

tail of the caudate; the putamen; and the hippocampus. The contrasts examined were each of the observational tasks versus baseline, each of the feedback tasks versus baseline, observational versus observational test, feedback versus feedback test, observational versus feedback, and observational test versus feedback test. Each contrast was calculated separately for each ROI. The t values for significant differences are given in Table 3, and bar graphs of percent signal change difference between learning tasks and baseline are provided in Figures 4, 5, 6, and 7.

As illustrated in Figure 4, the bilateral head of the caudate was significantly less active during both feedback learning and observational learning than during the baseline task. The greatest decrease in activity was during feedback training, when participants were actively receiving feedback: In the left head of the caudate, feedback learning was significantly less active than observational learning, and in both the left and right head of the caudate, feedback learning was less active than during feedback test blocks (in which feedback was omitted). The direction of the difference (lower activity than baseline rather than higher than baseline) is consistent with other studies of category learning (e.g., Filoteo, Maddox, Simmons, et al., 2005); possible reasons for the relative reduction in activity will be discussed further below.

Table 3. Comparison of Conditions with Baseline Task in Striatal and Hippocampal ROIs

	Observational	Obs. Test	Feedback	Feedback Test
Right head caudate	**−2.7****	ns	**−2.3****	ns
Left head caudate	**−7.4*****	ns	**−6.7*****	**−4.0****
Right body/tail caudate	2.9**	3.2***	3.2***	2.6**
Left body/tail caudate	2.2**	3.9***	2.0*	3.1***
Right putamen	1.7*	2.4**	4.4***	3.8***
Left putamen	ns	ns	1.8*	2.2**
Right hippocampus	2.3**	2.7**	2.6**	2.9**
Left hippocampus	ns	4.0***	2.9**	3.9***

Comparisons between Conditions

	Obs > Feed	Obs-T > Feed-T	Feed-T > Feed	Obs-T > Obs
Right head caudate	ns	2.2*	4.6***	3.4***
Left head caudate	2.7**	3.0**	2.5**	3.9***
Right body/tail caudate	ns	ns	ns	3.0**
Left body/tail caudate	ns	ns	ns	ns
Right putamen	ns	ns	ns	ns
Left putamen	ns	ns	ns	2.3**
Right hippocampus	ns	ns	ns	ns
Left hippocampus	2.1*	ns	ns	2.9***

Bold font indicates negative t values corresponding to lower activity during the condition than baseline. Obs = Observational; Obs-T = observational test blocks; Feed = feedback; Feed-T = feedback test blocks. For all t tests, $df = 12$, ns = not significant, $p > .1$.

*$p < .1$.

**$p < .05$.

***$p < .01$.

As shown in Figure 5, activity was significantly greater than baseline for both feedback and observational learning in the body and tail of the caudate bilaterally; activity did not differ in this area between observational and feedback learning either on training or test trials. There was, however, greater activity during test than training trials for observational learning on the right side. The pattern of activity was similar in the putamen, as illustrated in Figure 6: Activity was greater than baseline for all tasks, and tasks did not differ in activation from each other (except for greater activity in the left putamen in observational test blocks than observational learning).

The right and left hippocampi were recruited for both observational and feedback learning. As shown in Figure 7, activity was higher than baseline for all four testing conditions in both the left and right hippocampi. Observational and feedback learning were similar in their degree of recruitment of the hippocampus, although there was a trend for higher activity during observational than during feedback learning in the left hippocampus.

Whole Brain Analysis of the Cortex

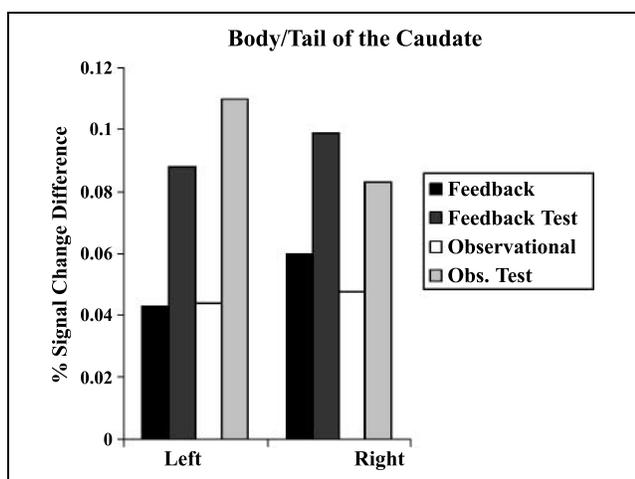### Conjunction Observational Learning and Feedback Learning versus Baseline

This contrast identified common cortical areas of activation during observational and feedback categorization learning. A conjunction analysis was performed, which identified areas that were active for both conditions when each was compared to its baseline. As shown in Table 4, feedback training and observational training both activated widespread areas in the frontal lobe: the left and right inferior frontal gyri and anterior insula, the right and left middle and superior frontal gyri, and bilateral medial frontal gyri; all but the latter activations are illustrated in Figure 8. Feedback and observational test blocks (which had identical trial structures across
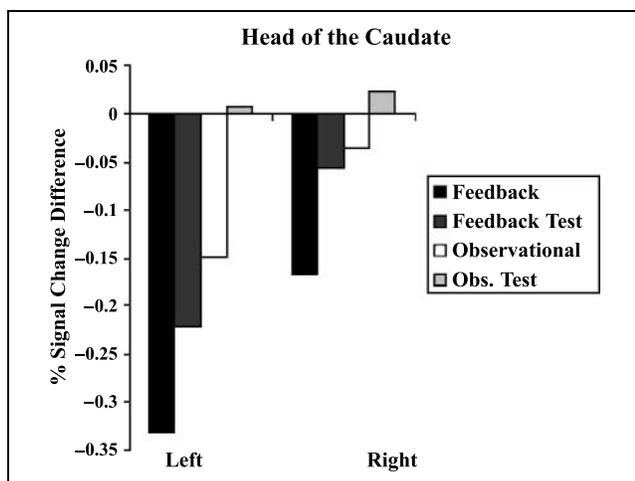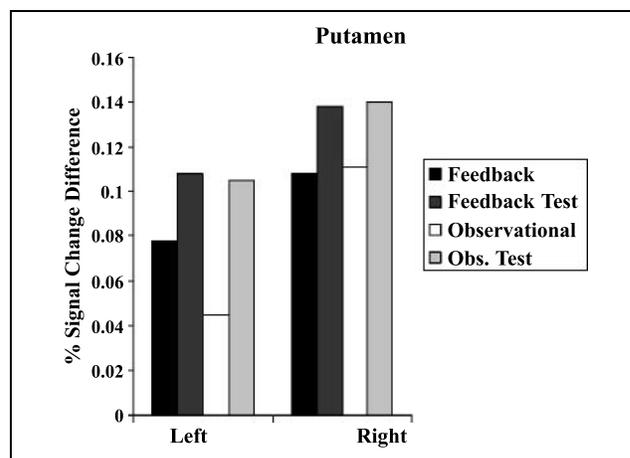
Figure 4. Activity during feedback and observational learning in the right and left head of the caudate. The *y*-axis indicates the difference in percent BOLD signal change between categorization blocks and baseline blocks. Feedback = feedback learning training blocks; Feedback Test = feedback learning test blocks; Observational = observational learning training blocks; Obs. Test = observational learning test blocks.

Figure 6. Activity during feedback and observational learning in the right and left putamen. The *y*-axis indicates the difference in percent BOLD signal change between categorization blocks and baseline blocks. Feedback = feedback learning training blocks; Feedback Test = feedback learning test blocks; Observational = observational learning training blocks; Obs. Test = observational learning test blocks.

tasks) also activated common areas in the frontal lobe, including the right and left inferior frontal gyrus/anterior insula, the right and left middle and superior frontal gyrus, and the right cingulate gyrus (see Figure 8).

Several areas were more active during the baseline condition than during the observational and feedback training conditions, including a large cluster that encompassed parts of the right inferior frontal gyrus, right precentral gyrus, right postcentral gyrus, and right inferior

parietal lobule. Additionally, portions of the left precentral gyrus, left inferior parietal lobule, and bilateral cuneus were more active during baseline trials.

Comparisons between Observation and Feedback

We compared the observational and feedback tasks via two contrasts, feedback versus observational and

Figure 5. Activity during feedback and observational learning in the right and left body and tail of the caudate. The *y*-axis indicates the difference in percent BOLD signal change between categorization blocks and baseline blocks. Feedback = feedback learning training blocks; Feedback Test = feedback learning test blocks; Observational = observational learning training blocks; Obs. Test = observational learning test blocks.
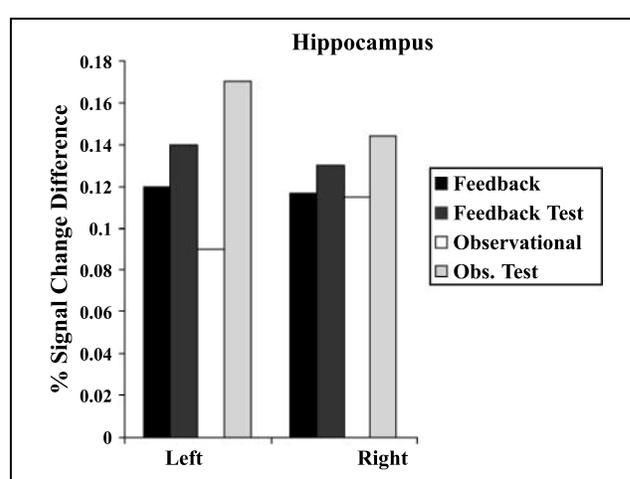

Figure 7. Activity during feedback and observational learning in the right and left hippocampus. The *y*-axis indicates the difference in percent BOLD signal change between categorization blocks and baseline blocks. Feedback = feedback learning training blocks; Feedback Test = feedback learning test blocks; Observational = observational learning training blocks; Obs. Test = observational learning test blocks.

**Table 4.** Areas of Activation for Feedback and Observational Learning Outside the Hippocampus and Striatum

	BA	x	y	z	Voxels
Conjunction Observational and Feedback > Baseline					
L Inferior Frontal Gyrus/Anterior Insula	47	−25	27	−1	1305
R Inferior Frontal Gyrus/Anterior Insula	47	31	25	−2	9472
R Middle and Superior Frontal Gyri	8, 9	35	43	47	11,293
L Middle and Superior Frontal Gyri	8, 9	−36	36	49	2643
B Medial Frontal Gyri	8	3	23	61	155
Baseline > Conjunction Observational and Feedback					
R Inferior Frontal, Precentral and Postcentral Gyri, and Inferior Parietal Lobule	4, 6, 40, 43, 44	54	−16	29	10,365
L Precentral Gyrus	4, 6	−57	3	21	2978
L Inferior Parietal Lobule	40	−43	−31	44	4033
B Cuneus	18, 19	2	−87	21	7683
Conjunction Observational Test and Feedback Test > Baseline					
R Inferior Frontal Gyrus/Anterior Insula	47	32	24	−1	9689
L Inferior Frontal Gyrus/Anterior Insula	47	−27	27	−1	2873
R Middle and Superior Frontal Gyri	8, 9	36	43	45	7480
L Middle and Superior Frontal Gyri	8, 9	−37	35	49	1942
R Cingulate Gyrus	31	13	−38	33	286
Baseline > Conjunction Observational Test and Feedback Test					
No significant clusters					

The FDR threshold was set to q = .05. Areas of activation falling in the areas reported in the ROI analysis (striatum and hippocampus) are not included in this table. BA = Brodmann's area; x, y, z = Talairach coordinates (Talairach & Tournoux, 1988) of the central voxel of the activated cluster; L = left; R = right; B = bilateral; voxels = size of the cluster in mm³.

feedback test versus observational test. These comparisons revealed no differences in activation when the FDR was set to q < .05. Because the presence of any differences between these conditions would be of theoretical interest, we performed an exploratory random effects analysis using a threshold of p < .0017, uncorrected for multiple comparisons; the results are give in Table 5. Most notably, feedback learning resulted in more activ-

Figure 8. (A) Areas in the prefrontal cortex that were more active in a conjunction analysis of feedback (FEED) and observational (OBS) training blocks than baseline (BASE) blocks. (B) Areas in the prefrontal cortex that were more active in a conjunction analysis of feedback test (FEED-T) and observational test (OBS-T) blocks than baseline (BASE) blocks. (C) Area in the superior frontal gyrus (BA 8) that was more active in feedback training than in observational training.
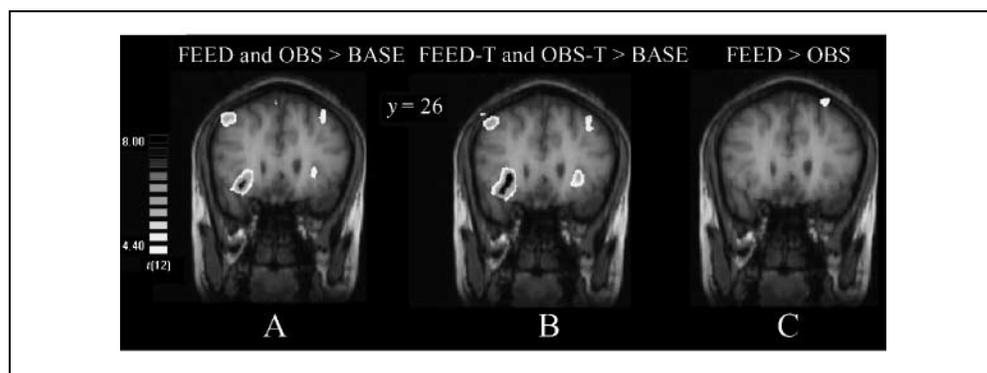
ity than observational learning in an area of the left superior frontal gyrus (BA 8); this area is shown in Figure 8. In addition, there were small areas of greater activation in the left anterior cingulate gyrus, and the bilateral supramarginal and superior temporal gyrus. Observational test led to greater activity than feedback test for areas in the left inferior parietal lobule, the right cuneus, and the right lingual gyrus. No cortical areas were significantly more active in observational training than in feedback training, or in feedback test than in observational test.

DISCUSSION

The presence of feedback differentially affected regions of the striatum: Feedback modulated activity in the head of the caudate, but not in the body and tail of the caudate or putamen. Both the body and tail of the caudate and the putamen were more active during categorization than during baseline during all conditions, indicat-

Table 5. Areas of Differential Activation for Feedback and Observational Learning Outside of the Hippocampus and Striatum

	BA	x	y	z	Voxels
Observational Learning > Feedback Learning					
No significant clusters					
Feedback Learning > Observational Learning					
L Anterior Cingulate Gyrus	24	−12	33	−3	176
L Superior Frontal Gyrus	8	−28	31	57	1207
R Supramarginal/Superior Temporal Gyri	39	37	−49	27	214
L Supramarginal/Superior Temporal Gyri	39	−41	−46	31	190
Observational Learning Test > Feedback Learning Test					
L Inferior Parietal Lobule	40	−45	−56	45	363
B Cuneus	17	5	−80	6	3846
R Lingual Gyrus	19	22	−59	−4	169
Feedback Learning Test > Observational Learning Test					
No significant clusters					

The voxelwise significance threshold was set to $p = .0017$, uncorrected for multiple comparisons. Areas of activation falling in the areas reported in the ROI analysis (striatum and hippocampus) are not included in this table. BA = Brodmann's area; x, y, z = Talairach coordinates (Talairach & Tournoux, 1988) of the central voxel of the activated cluster; L = left; R = right; B = bilateral; voxels = size of the cluster in mm^3.

ing a potential role in learning stimulus–category response associations.

Head of the Caudate

The head of the caudate was the only part of the striatum in which activity was modulated by feedback. During feedback learning, the head was more active during baseline blocks than during feedback training blocks, indicating a relative deactivation of the head of the caudate with feedback. Furthermore, activation was lower on feedback training blocks than on feedback test blocks, during which feedback was absent, implying that activity modulation is related to some aspect of receiving and processing feedback. Finally, cross task comparisons found lower activity during feedback learning than during observational learning.

These results are broadly consistent with previous research finding modulation of the head of the caudate with feedback. Tricomi et al. (2006) and Filoteo, Maddox, Simmons, et al. (2005) found differences in activation in the head of the caudate when comparing categorization with feedback against baseline tasks and categorization without feedback, respectively. Previous results are mixed as to whether feedback-related modulation is measured as a comparative increase or decrease of activity in the head of the caudate. Tricomi et al. found overall greater activity during feedback learning in the head of the caudate, whereas the current study found less activity, in comparison with baseline. The apparent deactivation of the head of the caudate may be due to several factors, each of which will be discussed further below: choice of baseline task, valence of feedback, subject expectations about feedback, and the time lapsed following feedback.

First, choice of baseline task is important in determining the direction of activity change. Baseline tasks in studies examining striatal activity are typically undemanding, as in the current study: viewing a repeated visual stimulus and making a simple motor response. The effects of baseline task have been studied in most detail in research on the medial-temporal lobe. This research finds that learning-associated changes in the brain are often apparent deactivations rather than activations (Stark & Squire, 2001); the specific pattern of activity is due to a combination of the memory demands of the baseline task itself, and the presence of incidental memory encoding and retrieval during "daydreaming" when undemanding baseline tasks are used.

Second, many studies have shown greater activity in the head of the caudate in response to positive feedback than to negative feedback (Filoteo, Maddox, Salmon, et al., 2005; Filoteo, Maddox, Simmons, et al., 2005; Seger & Cincotta, 2005; Delgado et al., 2000, 2004; Tricomi et al., 2004). This pattern of results is consistent with electrophysiological studies of reward finding increased activity in the striatum following a reward

than trials without reward, or with punishment (Schulz, 1998). Filoteo, Maddox, Salmon, et al. (2005) found that decrease of activity relative to baseline was greater for incorrectly classified trials than correct trials in a deterministic rule learning task. Third, the activity changes in the striatum to positive and negative feedback are modulated by the expectations of the subject (Delgado, Frank, & Phelps, 2005; Delgado, Miller, Inati, & Phelps, 2005; Seger & Cincotta, 2005). The electrophysiological literature shows that missing an expected reward leads to a dip in dopamine and an associated dip in activity in the striatum, whereas receiving an unexpected reward leads to a burst of dopamine and an associated rise in activity (Schultz, 1998).

Fourth, studies using an event-related design that examine BOLD signal change across an extended period (approximately 12 sec) typically find a strong immediate increase in activation after positive feedback that is followed by a sustained depression of activity (Delgado, Miller, et al. 2005). A similar pattern is present in ventral striatal regions adjacent to the head of the caudate in tasks involving receiving monetary reward (Larkin et al., submitted; Knutson, Fong, Adams, Varner, & Hommer, 2001) When averaged across trials in a block design (as in the present study), the net result may be an apparent depression of activity. In summary, it is likely that whether overall the activity of the head caudate will appear as an activation or deactivation will depend on the choice of baseline comparison task, the proportion of positive and negative feedback trials in each condition, timing of trials, and the expectations that subjects have.

In addition to feedback processing, the head of the caudate has been linked to some forms of task switching, including switching between objects (Cools, Clark, & Robbins, 2004; Monchi, Petrides, Petre, Worsley, & Dagher, 2001) and reversing stimulus–response associations (Cools, Clark, Owen, & Robbins, 2002; Rogers, Andrews, Grasby, Brooks, & Robbins, 2000). Switching may be integrally related to feedback processing, as negative feedback indicates that a switch is required. In the present study, feedback learning has greater switching demands than observational learning. In feedback learning, the correct response was often unknown, and subjects needed to update their mental representations upon the receipt of negative feedback. These demands were absent in observational learning, in which the correct response was given on each trial.

Body and Tail of the Caudate

Both feedback and observational learning led to more activity in the body and tail of the caudate than in baseline and did not differ in activity from each other. These results support the theory that the body and tail are involved in representation of associations between stimuli and responses or categories, and are consistent with studies finding activity in this area associated with learning to categorize (Seger & Cincotta, 2005, 2006). Furthermore, they indicate that learning associations can recruit the body and tail of the caudate even in the absence of explicit feedback. Other classification learning studies have also found body and tail activation without explicit feedback. Lieberman, Chang, Chiao, Bookheimer, and Knowlton (2002) examined learning to classify grammatical letter strings without feedback; they found greater body and tail of the caudate activity when subjects processed stimuli that followed the category rules in comparison with stimuli that did not.

These results provide a challenge for theories stating that the establishment of stimulus–category associations in the body and tail of the caudate is dependent on feedback. In the model proposed by Ashby and Casale (2003), synapses connecting projection neurons from the visual cortex with striatal spiny cells are strengthened on the basis of receipt of a time-sensitive dopaminergic reward signal from the midbrain. Without explicit feedback, this dopamine signal should be absent and learning should not occur. One possibility is that dopamine release occurred in the present task due to other task features than explicit feedback. First, all the stimuli were novel; novelty itself is rewarding in the sense of leading to dopamine release (Schulz, 1998), and novel stimuli are known to activate the caudate (Rolls, 1994; Cann, Perrett, & Rolls, 1984). Second, during observational learning, subjects made a response on each trial that they knew was correct (because they were told the category label at the beginning of the trial). Making a correct response may lead to an internally generated sense of reward, and thus, a dopamine signal to the caudate as a result of self-monitoring processes. It is known that another dopamine-regulated neural system, the medial frontal cortex, is sensitive to internally generated knowledge of correct or incorrect performance; this system provides the basis for the error-related negativity event-related potential component (Holroyd & Coles, 2002). Finally, recent research has found that corticostriatal synapses can be modulated in strength even in the absence of dopamine modulation (Fino, Glowinski, & Venance, 2005). However, feedback and observational learning do differ behaviorally, with feedback learning leading to better performance after extended training (Ashby et al., 2002). This implies that the dopamine release during observational learning is less effective than that during feedback learning for subserving learning in the long run; unfortunately, we were not able to test this possibility due to the limited length of the current study. One possibility is that the dopamine release from internally generated reward (during observational learning) may be qualitatively or quantitatively different from that in feedback, in which subjects receive a strong external feedback stimulus in addition to an internally generated sense of reward. Additional research is needed to determine whether caudate activity

during observational and feedback learning changes after extended training, as behavioral differences emerge.

The present results are also inconsistent with Poldrack et al. (2001), who found no caudate activation in a paired associates version of a multicue probabilistic classification task similar in stimulus presentation details to the observational learning task used here. One important methodological difference between the studies was that we required subjects to press a key indicating category membership on all trials, whereas Poldrack et al. merely required subjects to make a random button press. This suggests that the body and tail of the caudate may be active when stimulus–category pairings are accompanied by a relevant response, but not if a relevant response is absent. In general, the dorsal striatum is sensitive to action contingency, when an outcome and an action are meaningfully related (Tricomi et al., 2004). Behaviorally, Ashby et al. (2002) found stronger differences between feedback and observational learning of information integration categories when subjects were not required to make responses on each trial.

Putamen

The pattern of activity in the right and left putamen was similar to that in the body and tail of the caudate. Activity was significantly elevated in comparison with baseline and did not differ between the observational and feedback conditions. Seger and Cincotta (2005) also reported similar activation patterns in the putamen and the body and tail of the caudate: Both were more active in classification than in baseline, and their activity followed the time course of learning. The putamen primarily interacts with premotor, supplementary motor, and somatosensory cortices in the "motor" corticostriatal loop (Lawrence et al., 1998). Its activity is consistent with the motor planning demands of the feedback and observational tasks, both of which required making one of two button press responses on each trial. Nonhuman animal research suggests that the caudate is more related to induction of response associations, whereas the putamen is more related to performance of already learned responses. Williams and Eskandar (2006) found that activity in the caudate nucleus was greatest while learning was most rapid, whereas putamen activity increased in line with the learning curve, reaching a maximum as the automaticity of performance increased. In addition, microstimulation of the caudate, but not the putamen, led to improved learning. In rodents, lesions to the dorsomedial striatum (analogous to primate caudate nucleus) impair early learning of how actions taken in response to a stimulus result in particular outcomes or rewards (action–outcome learning). Lesions to the dorsolateral striatum (analogous to primate putamen) impair later stages of learning in which the animal acquires a habitual response to a stimulus (stimulus–response learning); during this phase, learning is insensitive to reinforcer devaluation (Yin & Knowlton, 2006).

Implications for Parkinson's Disease

Two studies, one using the probabilistic classification task (Shohamy, Myers, Grossman, et al., 2004) and one using the artificial grammar learning task (Smith & McDowall, 2006), have found that patients with Parkinson's disease are impaired at using feedback to learn but are not impaired when learning is via observation or other strategies. We found that feedback learning modulates activity in the head of the caudate but not other striatal regions. These results, taken together, imply that feedback-specific learning impairments in Parkinson's disease are due to the effects of the disease on the head of the caudate rather than the body and tail of the caudate. Consistent with this pattern of results, the head of the caudate is more strongly affected in early Parkinson's disease than the body and tail. Degeneration of the substantia nigra in Parkinson's disease typically begins in lateral portions of the substantia nigra and progresses to more medial portions (Dauer & Przedborski, 2003), which translates into primary initial involvement of the putamen and head of the caudate in the disease. Functionally, these results imply that the feedback-related learning impairment in Parkinson's disease will prove to be linked to the functions of the head of the caudate such as feedback processing and/or task switching, rather than the functions of the body and tail of the caudate, such as stimulus–category representations.

Hippocampal Contributions

The hippocampus was active during both feedback and observational learning. This indicates a potential role for the hippocampus in information integration learning. However, two previous fMRI studies of information integration learning did not find hippocampal activity. Seger and Cincotta (2002) did not report hippocampal activity when categorization was compared with a baseline task. Nomura et al. (2007) did not find a difference in hippocampal activity when comparing trials in which stimuli were correctly classified with those in which stimuli were incorrectly classified, indicating that the hippocampus is not involved in expressing categorical knowledge. It is possible that the stimulus features (means, covariance, and resulting distance between categories) used in the present study resulted in stimulus sets that were more amenable to hippocampally based learning strategies than those used in the previous studies; in the present study, the category distributions were more widely separated from each other than in the studies of Nomura et al. and Seger and Cincotta 2002 (in

this study, the category distributions actually overlapped). Alternatively, the hippocampal activity reported in the current study may not be due to expression of learned stimulus–category associations, but rather may be due to other aspects of the task. One possibility is encoding of novel stimuli and/or novel stimulus–category associations. All of the stimuli used in our tasks were novel. Strange, Fletcher, Henson, Friston, and Dolan (1999) required subjects to learn to classify letter strings via feedback and found that the hippocampus responded to novel letter strings that had behavioral significance, or that were processed using an active learning strategy (in comparison with passive viewing; Strange, Hurlemann, Duggins, Heinze, & Dolan, 2005). Accordingly, they argued that the hippocampal activity reflects active encoding of novel stimulus–category associations.

The finding of hippocampal activity during feedback learning is in contrast with studies of probabilistic classification tasks, which have found reductions in hippocampal activity during category learning with feedback (Poldrack et al., 1999, 2001). However, neuropsychological research indicates that the hippocampus is important for probabilistic classification: Hopkins, Myers, Shohamy, Grossman, and Gluck (2004) found impairment in hippocampal amnesia across the entire course of learning, whereas Knowlton et al. (1994) found significant impairment in subjects with amnesia that began after the first 50 trials. Aside from probabilistic classification tasks, the striatum and medial-temporal lobe are often activated simultaneously and noncompetitively (Voermans et al., 2004; Packard & Knowlton, 2002). Further research is needed to determine the conditions under which the striatal and hippocampal systems are cooperative or competitive.

Frontal Lobe Contributions

There were many common areas of activation in the ventrolateral, dorsolateral, and medial prefrontal cortex during both feedback and observational Learning. The dorsolateral prefrontal cortex is thought to involve manipulating and monitoring information in working memory (Curtis & D'Esposito, 2003; Duncan & Owen, 2000). In categorization tasks, greater dorsolateral prefrontal cortex activity has been found when comparing novel stimuli to previously learned categories (Vogels, Sary, Dupont, & Orban, 2002) and in comparisons of successful learners with nonlearners (Filoteo, Maddox, Simmons, et al., 2005; Seger et al., 2000). The ventrolateral prefrontal cortex is thought to be involved in the selection, comparison, and judgment of stimuli in long- and short-term memory (Elliot & Dolan, 1998). Previous category learning studies have found greater ventrolateral activity during categorization of category members in comparison with random stimuli (Reber, Stark, & Squire, 1998).

The medial prefrontal cortex is thought to be associated with the acquisition of stimulus–response associations through evaluating error (Volz, Schubotz, & von Cramon, 2003; Holroyd & Coles, 2002), and detecting uncertainty or response conflict (Ullsberger & von Cramon, 2003). The medial prefrontal cortex was active in both feedback and observational learning, even though observational learning involves little to no error, response conflict, or uncertainty. Our results support the view that the medial prefrontal cortex may generally respond to the acquisition of stimulus–response relationships, regardless of feedback.

Feedback and observational learning differed in activation of the superior frontal gyrus, anterior BA 8, with greater activation during feedback learning. This area is at the junction of the anterior supplementary motor area and the dorsolateral prefrontal cortex and includes the frontal eye fields. BA 8 is known to be an output target of the striatum, specifically from areas of the body and tail of the caudate and medial putamen that are associated with visual stimulus processing (Passingham, 1993). The anterior supplementary motor area is thought to subserve relatively more cognitive functions than the more posterior supplementary motor area, which subserves movement preparation (Pickard & Strick, 2001). In classification tasks, activity in this area has been associated with holding stimulus–response relations in working memory (Boettinger & D'Esposito, 2005) and perceptual decision making (Heekeren, Marrett, Bandettini, & Ungerleider, 2004). Greater BA 8 activity in feedback learning than observational learning may reflect greater working memory or perceptual decision-making demands during feedback learning. Alternatively, the BA 8 activation may be related to visual scanning, with greater amount of meaningful eye movements during feedback learning. Little, Klein, Shobat, McClure, and Thulborn (2004) found frontal eye field activation in an fMRI category learning study that utilized feedback. Eye movements have been found to play a functional role in visual learning such that the restriction of eye movements during learning has a negative effect on learning (Henderson, Williams, & Falk, 2005).

Behavioral Differences between Observational and Feedback Learning

Behavioral results showed robust category learning during both the observational and feedback tasks. In each task, accuracy was significantly above chance. Learning was similar in both observational and feedback learning. Accuracy rates did not differ significantly between observational test and feedback test blocks.

Ashby et al. (2002) found that subjects learned to categorize in both feedback and observational conditions, but that there was an advantage for the use of feedback. In Ashby et al., accuracy rates during test trials (transfer blocks) over the entire experiment were approximately

84% for feedback and approximately 77% for observational learning (Ashby et al., 2002; see note to Table 2 for details). In the current study, the accuracy rate of participants during feedback test blocks was 72%, and the accuracy rate for observe test blocks was 76%; they were not significantly different. We may not have found an advantage for feedback because the number of trials used in this study (200 training trials) was less than that used in the study of Ashby et al. (400 training trials). In Ashby et al., the advantage for feedback learning was not present in the first block, but emerged later in learning.

We did not obtain a monotonically increasing learning curve during observational test blocks: Participants' accuracy rate was high in the first quartile. We believe this high accuracy was due to irregularities in the randomization of the stimuli. A post hoc examination of the 10 first quartile stimuli in both the LA and DA stimulus sets found that each was either very similar to the prototype of the category, or had extreme values that made them very dissimilar from the prototype of the alternate category. These stimuli would have been much easier to categorize than stimuli with medial values.

Additionally, the behavioral models showed that subjects used similar strategies in both observational and feedback learning. In both, almost all subjects' performance was best fit by an information integration model. Only a few subjects used rule-based strategies, either unidimensional or conjunctive. However, it is important to note that subjects in the present study were in the early phases of learning, and may have been shifting strategies, or while using a rule-based strategy, shifting between particular rules. If so, the patterns of behavioral results might be best fit by the information integration model because the rule-based models only evaluate how well the data are fit by one rule strategy (unidimensional horizontal, unidimensional vertical, or conjunctive).

Conclusion

The current results contribute to the growing literature mapping the cognitive processes involved in categorization onto their functional neuroanatomical substrates. In particular, learning of associations between stimuli and categorization responses via both feedback and observation was linked to activity in the body and tail of the caudate and in the putamen. Processing feedback was linked to activity changes in the head of the caudate.

Acknowledgments

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