Neural Correlates of Rule-Based and Information-Integration Visual Category Learning

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An emerging theory of the neurobiology of category learning postulates that there are separate neural systems supporting the learning of categories based on verbalizeable rules (RB) or through implicit information integration (II). The medial temporal lobe (MTL) is thought to play a crucial role in successful RB categorization, whereas the posterior regions of the caudate are hypothesized to support II categorization. Functional neuroimaging was used to assess activity in these systems during category-learning tasks with category structures designed to afford either RB or II learning. Successful RB categorization was associated with relatively increased activity in the anterior MTL. Successful II categorization was associated with increased activity in the caudate body. The dissociation observed with neuroimaging is consistent with the roles of these systems in memory and dissociations reported in patient populations. Convergent evidence from these approaches consistently reinforces the idea of multiple neural systems supporting category learning.

Keywords: category learning, caudate, explicit, fMRI, implicit, medial temporal lobe

Introduction

Humans are remarkably adept at identifying categories, reacting similarly to distinct objects in the environment with common features, even when differences in features between category members are very subtle (e.g., faces). Learning a novel visual category depends on developing new representations of category membership, a process thought to involve both major types of memory: declarative (explicit) and nondeclarative (implicit) (e.g., Reber and others 2003). Declarative memory, supported by the medial temporal lobe system (MTL, containing the hippocampus), aids in both storage and conscious recollection of previous examples, supporting heuristic evaluation of category membership. The role of nondeclarative memory is seen in the nonconscious abstraction of a category prototype (Knowlton and Squire 1993) based on changes in sensory cortex (Reber and others 1998a, 1998b, 2003) or the gradual acquisition of the category definition via feedback supported by the basal ganglia (Knowlton and others 1996; Seger and Cincotta 2005).

The existence of multiple brain systems for category learning does not answer the critical question of what factors determine how categories will be learned. One factor that is likely to be very important (although there are likely to be others) is that the information structure of the category may determine what neural system will support learning (Ashby and Ell 2001; Maddox and others 2003). A category defined by a verbalizeable rule, for example, a criterion applied to a single stimulus dimension, can be learned by an explicit, rule-based (RB) system. In contrast, a highly similar category structure that requires information integration (II) of 2 or more stimulus dimensions (Ashby and Gott 1998) cannot be described by a simple verbalizeable rule (Ashby and others 1998) and is hypothesized to be learned by a separate neural system.

One multiple-systems theory of the neurobiology of category learning that incorporates the information structure of the categories is the COVIS (Competition between Verbal and Implicit Systems) model proposed by Ashby and others (1998). In this model, 2 learning systems compete: an explicit, RB system that depends on working memory and attention, and an implicit, procedural learning system. A new addition to the COVIS model is the MTL (Ashby and Valentin forthcoming). In this system, the MTL acts together with prefrontal cortex (PFC) structures and the head of the caudate to identify verbalizable rules for categorization. Within COVIS, implicit learning is hypothesized to depend on connections between visual cortical areas and posterior regions of the caudate (e.g., posterior body and tail of the caudate). These connections may serve to facilitate the development of new representations in the cortex through feedback signals available in the basal ganglia.

This multiple-system model of category learning can be tested with functional neuroimaging (fMRI) of RB and II categorization tasks. Closely matched RB and II categorization tasks were created by modifying the structure of the categories, although stimuli in both tasks are extremely similar and the stimulus dimensions are identical (e.g., Maddox and others 2003). The stimuli here were sine-wave gratings that varied in components of frequency and orientation (Fig. 1). For the RB task, the frequency of the grating determined category membership. For the II task, participants were required to integrate frequency and orientation information to determine membership. The discriminability between categories was adjusted to roughly match the 2 tasks in overall difficulty. fMRI data were collected from participants in both groups while learning to categorize over four 80-trial runs. Feedback after each trial enabled the participants to learn the categories throughout scanning.

For each condition, activity evoked by correct categorization was compared with that evoked by incorrect categorization to identify brain areas associated with successful categorization. This approach has the advantage of not just identifying activity associated with making a categorization judgment but identifying when knowledge of the category is being successfully applied. In addition, this contrast captures the process of learning over the course of the experiment as more successful categorization judgments are made later in the session when the category has been more effectively learned. By identifying the brain regions associated with successful categorization, we
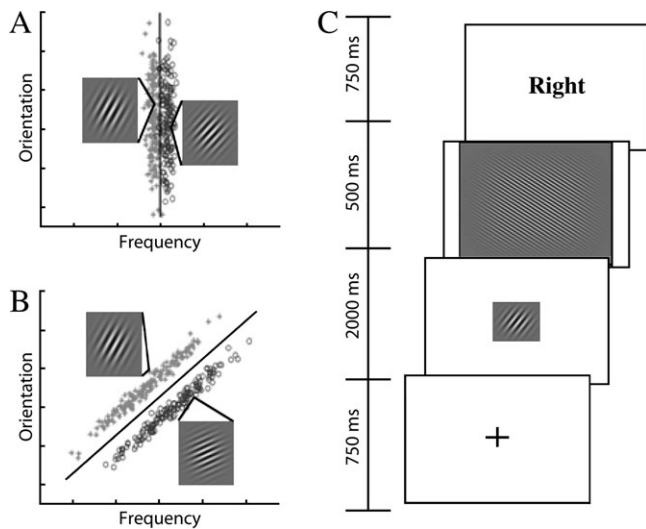
Figure 1. RB (*A*) and II stimuli (*B*). Each point represents a distinct Gabor patch (sine-wave) stimulus defined by orientation (tilt) and frequency (thickness of lines). In both stimulus sets, there are 2 categories (crosses and open circles points). RB categories are defined by a vertical boundary (only frequency is relevant for categorization), whereas II categories are defined by a diagonal boundary (both orientation and frequency are relevant). In both RB and II stimuli there are examples of a stimulus from each category. (*C*) Schematic of a single trial. A fixation point is followed by the to-be-categorized-stimulus (either RB or II depending on the subject), then a short visual mask that is followed by the feedback. The subject responded "category A" or "category B" during the 2 s the stimulus was on the screen using handheld buttons. The length of the intertrial interval was pseudorandom and based on between zero and five 4-s "fixation-only" trial periods arranged to maximize the separability of the measured hemodynamic response to stimulus trials.

hypothesized that the different neural networks that support RB and II category learning could be distinguished.

We predicted that successful RB categorization would be associated with increased activity in the MTL, reflecting explicit knowledge of the category. In contrast, successful II categorization would be associated with increased activity in the posterior caudate, reflecting the critical role of this area in feedback-oriented implicit category learning. Because our prior hypotheses focused on the MTL and caudate as key components of the 2 memory systems thought to participate in category learning, anatomical regions of interest (ROIs) were defined for these areas. For additional sensitivity, the ROI alignment (ROI-AL) (Stark and Okado 2003) alignment technique was used to coregister these anatomical structures directly to assess differences in evoked activity for the RB and II groups within the MTL and caudate.

Materials and Methods

Participants

Thirty-four healthy, native English-speaking, right-handed adults (15 males, 19 females) of mean age 23 (range, 18–30) were recruited from the Northwestern University community for participation in this study. All participants gave informed consent according to procedures approved by the Northwestern University Institutional Review Board and were compensated for their time. Participants were randomly assigned to either the RB (*N* = 17) or II (*N* = 17) group. One RB participant was eliminated due to poor quality echo-planar imaging (EPI) data and 8 participants (4 RB, 4 II) were eliminated due to an inability to learn the categories (failing to meet a performance criterion of 60% correct on the final block).

Materials

Stimuli were circular sine-wave gratings (Gabor patches; see Fig. 1) that varied in spatial frequency (thickness of lines) and orientation (tilt of lines) as in Maddox and others (2003). Participants were instructed to place each stimulus into one of two categories and to try to learn these categories over time based on the feedback given after each trial. The only difference between the RB and II groups was in the boundary that defined the categories. The stimulus space for both the RB and II groups can be thought of in 2 dimensions, spatial frequency on the *x* axis and orientation on the *y* axis. For the RB group, the stimuli were divided into categories based on a vertical decision boundary such that category membership depended only on the spatial frequency of the sine-wave grating (Fig. 1*A*). For the II group, the categories were defined by a diagonal decision boundary that required integration of spatial frequency and orientation information (Fig. 1*B*).

Procedure

On each trial, a fixation cross was presented for 750 ms followed by a single stimulus that was presented for 2 s and during this time, participants indicated to which category they judged the stimulus belonged. Stimulus offset was followed by a 500-ms visual mask and feedback for the participant's choice ("Right," "Wrong") was shown for 750 ms. Participants were warned ("Time") if they had not made a response during the 2 s the stimulus was on the screen (see Fig. 1*C*). A total of 320 categorization trials were performed by each participant in 4 runs of 80 trials each. An equal number of fixation-only trials were pseudorandomly interspersed between stimulus trials to maximize the separability of the measured hemodynamic response.

Imaging

fMRI data were collected using a Siemens TRIO 3.0 T MRI scanner equipped with a transit/receive head coil while participants performed the categorization task. Whole-brain, gradient-recalled EPI (35 axial, 3-mm slices, 0 gap) were collected every 2 s (time repetition = 2000; echo time = 25 ms; flip angle = 78°; 22 cm field of view; 64 × 64 acquisition matrix; resulting voxel size = 3.44 × 3.44 × 3 mm) for 330 volumes in each of 4 scans. For anatomical localization, high-resolution, 3D MP-RAGE T_1-weighted scans (voxel size = 0.859 mm × 0.859 × 1 mm; 160 axial slices) were collected for each participant following the functional runs.

Data Analysis

The functional images were first coregistered through time to correct for motion using a 3D alignment algorithm (Cox 1996). Voxels with low signal (<100 units, 30% of mean signal) or excessive sudden signal change were eliminated (>30% in 2 s) and the EPI data were smoothed (6.9 mm full-width half maximum Gaussian kernel). Data were transformed to standard stereotactic space (Montreal Neurological Institute 305; Collins and others 1994). Estimates of trial-locked evoked activity were made for the period of 4–12 s after stimulus onset to account for hemodynamic delay with overlapping responses deconvolved via a general linear model. Brain regions in which activity was associated with successful categorization were identified by comparing activity during correct and incorrect trials for each participant. Within each group, brain regions that exhibited consistently greater activity during successful categorization was identified by a second-pass random effects analysis. Monte Carlo simulation identified a reliability threshold of $t > 4.5$ ($P < 0.01$ uncorrected) for all voxels in clusters of at least 300 mm^3. This method estimates the false-positive rate for the study by creating random noise data that matches the mean and standard deviation of each voxel for each participant, maintaining the spatial structure of the data. The noise data is then subjected to exactly the same analysis as the real data (including spatial smoothing and the 2-pass random effects model), and a statistical threshold is identified for which fewer than 0.05 false-positive clusters are identified anywhere in the brain for the study.

In addition to the whole-brain analysis, the ability to identify anatomical boundaries for 2 critical regions hypothesized a priori to be important for category memory enabled a specific ROI analysis in the hippocampus and the caudate. For each participant, ROIs were drawn following anatomical boundaries that are visible on structural MRI. The

MTL ROIs were drawn using boundaries that are described elsewhere (Insausti and others 1998; Reber and others 2002). The caudate ROIs were drawn according to known neuroanatomical boundaries separating the caudate from the surrounding white matter and ventricles. Each individual's ROIs were then aligned using the ROI-AL method described in Stark and Okada (2003). This method optimizes regional alignment at the expense of whole-brain alignment allowing for more precise localization and enhanced statistical power. Of particular interest was to test whether these 2 regions play different roles in RB and II categorization, that is, whether there was significantly different activity associated with successful categorization in the RB and II groups. Separate reliability thresholds for contrasts between the participant groups within the ROIs were identified by additional Monte Carlo simulations (the MTL ROI volume was 21 500 mm^3 and the caudate ROI was 11 000 mm^3; note that this method matches the shape as well as providing a "small volume" correction for the ROI volumes). Within the targeted ROIs, an alpha level of 0.05 is met by requiring clusters for which each voxel exhibited $t_{24} > 2.0$ to be at least 700 mm^3 in volume for the MTL and 600 mm^3 for the caudate.

Results

For both groups of participants who learned the task, performance was above chance in all runs, and the groups demonstrated similar learning curves (Fig. 2). Learning across runs was reflected in a significant linear trend ($F_{1,23} = 111.6$, $P < 0.05$). Mean accuracy averaged across all 4 runs for the RB group was 70.8% (standard error [SE] = 1.83), and for the II group it was 74.9% (SE = 3.03). RB and II accuracy was not significantly different across all 4 runs ($F_{1,23} = 1.25$, not significant), thus one cannot attribute differences observed in functional activity to task difficulty.

In Figure 3, activity evoked by correct categorization was compared with that evoked by incorrect categorization to identify brain areas associated with successful categorization. The normalized atlas coordinates of the center of each of these clusters for the RB and II groups are listed in Table 1. In the RB group (Fig. 3, top) successful categorization was associated with activity bilaterally in the MTL, body of the right caudate, anterior cingulate, and medial frontal gyrus. In the II group (Fig. 3, bottom), activity was observed bilaterally in the body and tail of the caudate for successful categorization.

There was a great deal of common activity between the groups that performed RB and II categorization. No differences were observed in total trial-locked activity (for all trials) between the groups, and there were no global differences in total activity for correct categorization trials alone at a corrected
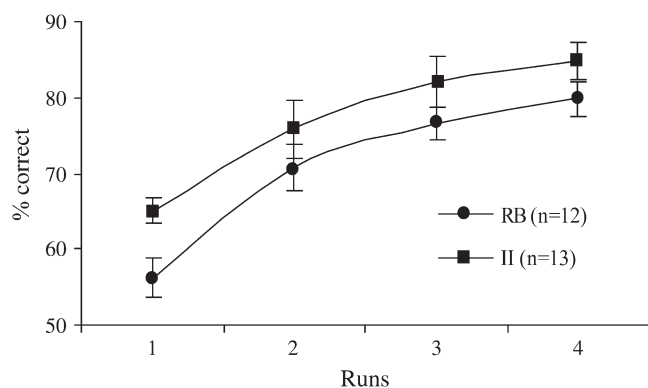
threshold across the whole brain. The involvement of the MTL and caudate in RB and II categorization was examined with targeted anatomical ROI analysis of these structures to improve sensitivity to group differences in these crucial regions in which we had prior hypotheses about differential activity.

Within the MTL ROI, the effect of successful categorization was significantly larger for the RB than the II group in the left anterior hippocampus. Correct RB responses evoked relatively greater activity than incorrect RB responses, whereas the II responses did not vary with success. It should be noted that the general profile of activity in the anterior hippocampus was a negative deflection that occurred for all stimuli (see Fig. 4C), whether the trial reflected correct or incorrect categorization. The RB success effect was an increase that effectively reduced the size of this deactivation. This type of trial-locked deactivation has been reported previously and interpreted as a familiarity signal during recognition memory (Henson and others 2003) or as an indication that MTL activity may be elevated during "easy" or rest baseline conditions (Law and others 2005), for example, during the fixation periods interspersed among trials here. Although it is tempting to suggest that assessing the familiarity of stimuli is involved in RB categorization, the size of this deactivation was not reliably different for RB and II categorization (although success did not affect MTL activity for II categorization), and further speculation should await a better understanding of the conditions under which trial-locked deactivations occur during memory tasks in the MTL. Regardless of the reason for the deactivation, the MTL activity was found to be correlated with RB success, implying a role for the MTL memory system during the RB task.

In contrast, successful II categorization was associated with greater differential activity in the right body of the caudate compared with successful RB categorization (Fig. 4B). In this region, increased activity was identified on all trials (Fig. 4D), particularly correct trials, but the differential activity to successful categorization was reliably larger for II participants, suggesting that caudate activity is correlated with successful II categorization. Both targeted ROIs exhibit some commonality in the overall pattern of activity, possibly reflecting the competition between 2 simultaneously active categorization systems. However, the difference between activity on correct and incorrect trials indicates that the MTL activity is associated with successful RB categorization while the body of the caudate is associated with successful II categorization.

Discussion

Participants learning to categorize simple visual stimuli based on an underlying structure that either afforded a RB or II approach exhibited dissociable patterns of neural activity. For the participants performing RB categorization, the MTL was associated with successful categorization responses. In contrast, participants performing II categorization exhibited activity in the caudate associated with success. The localization of these differences further supports the idea from memory systems research that RB categorization depends on declarative, explicit memory, whereas II categorization may depend more on the basal ganglia and nondeclarative memory mechanisms.

The role of the posterior regions of the caudate in II categorization supports the hypothesis first proposed in the COVIS model (Ashby and others 1998) and was later supported by neuropsychological research on patients with Parkinson disease
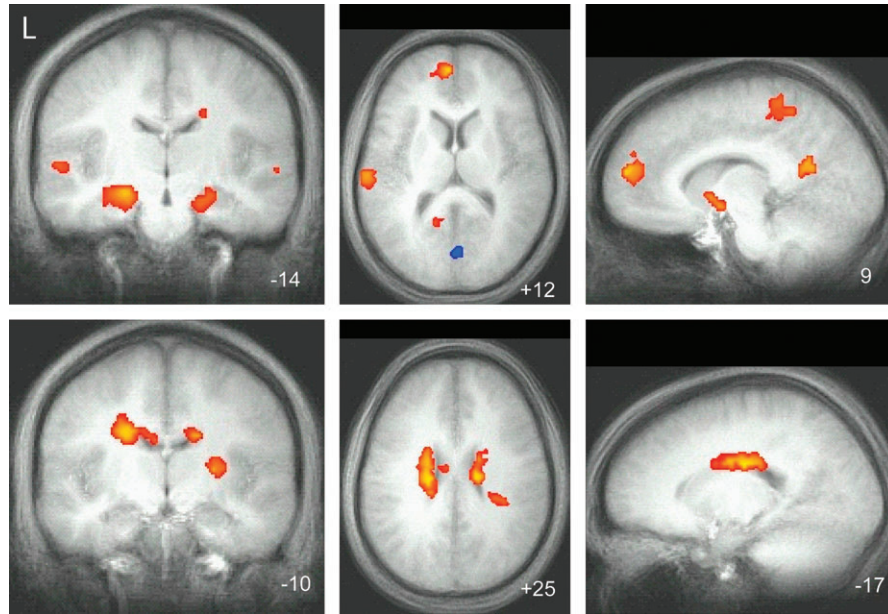

Figure 2. Accuracy of RB and II "learners" across 4 runs. Both groups performed above chance in all runs, and average accuracy did not differ between groups ($F_{1,24} = 1.25$, not significant). RB mean performance across runs was 70.8% (SE = 1.83) and II was 74.9% (SE = 3.03).

Figure 3. Top: a portion of the successful RB categorization network featuring the MTL ($t_{11} > 4.5$, cluster > 300 mm^3). Sagittal views are of the right hemisphere. Bottom: a portion of the successful II categorization network featuring the body of the caudate. $t_{12} > 4.5$, cluster > 300 mm^3).

Table 1

Volume-thresholded clusters of areas that activated differentially to correct versus incorrect categorization trials for the RB and II groups

Brain region	Brodmann area	Talairach coordinates (x, y, z)	Cluster size (mm^3)
RB group			
Correct > incorrect			
Left anterior hippocampus		−18, −8, −12	2172
Right anterior hippocampus		16, −5, −10	1781
Left superior frontal gyrus	8	−20, 17, 53	1688
Left medial frontal gyrus	10	−8, 53, 19	1203
Left transverse temporal gyrus	41	−59, −21, 10	1109
Right caudate body		18, −26, 28	1094
Left paracentral lobule	5	−8, −41, 56	1078
Right superior temporal gyrus	22	59, −8, −2	578
Left posterior cingulate	30	−11, −58, 17	531
Right precuneus	7	13, −47, 60	453
Right paracentral lobule	6	4, −34, 58	406
Right superior frontal gyrus	6	2, 2, 62	406
Incorrect > correct			
Right cuneus	18	2, −78, 5	719
Right supramargninal gyrus	40	55, −55, 37	578
II group			
Correct > incorrect			
Left caudate body		−20, −14, 29	2766
Left lentiform nucleus		24, −7, 3	1656
Right caudate body		17, −11, 28	969

(Knowlton and others 1996; Filoteo and others 2005). However, there is at least one additional way for the brain to acquire a novel visual category. Neuroimaging of prototype-based visual categories has implicated changes within visual cortical areas (Reber and others 1998a, 1998b, 2003). Learning this type of category does not appear to depend on the basal ganglia (Reber and Squire 1999), but those results differ from the II category learning studied here in several relevant ways. The categories are learned incidentally, without feedback, the category structure is based on a central prototype rather than a stimulus-space decision boundary and only a single category is learned.

The role of the basal ganglia in categorization is becoming increasingly well supported by patient data (Knowlton and others 1994; Filoteo and others 2001, 2005; Shohamy and others 2004) as well as neuroimaging data (Poldrack and others 2001; Seger and Cincotta 2002, 2005). The neurobiology of the caudate has several notable features that suggest its effectiveness in visual category learning. The projections of visual cortical neurons in the TE area of the inferotemporal cortex onto the spiny neurons of the tail of the caudate are organized in a many-to-one fashion (Wilson 1995). This connection structure should be ideal for extracting commonalities across a range of stimuli and necessary to generalize to novel category exemplars. The basal ganglia receive widespread input from the cerebral cortex, and these pathways are topographically organized (e.g., McGeorge and Faull 1989). Specific cortical regions project to the dorsal and ventral striatum, and pallidal output from the basal ganglia loops back into these same cortical regions via various thalamic nuclei (Middleton and Strick 2000). It has been suggested that at least 5 parallel corticobasal ganglia loops exist, but of particular interest here is the inferotemporal-cortical loop through the posterior basal ganglia (Yeterian and Pandya 1995). This posterior loop would allow for the possibility of influencing cortical representations in the regions that project to the caudate during category learning. The convergent nature of these projections supports the idea that this region of the caudate should be particularly important for visual category learning, as found here during II category learning. Finally, the availability of reward signals via dopamine (Wickens 1990; Schultz 1992; Aron and others 2004) and dopamine's role in strengthening recently active synapses make feedback-driven learning highly likely to rely on the basal ganglia in general. Together, these features indicate the plausibility of the hypothesis that the caudate participates in visual category learning, and the neuroimaging data of participants performing II tasks now provide significant support for this hypothesis.

In contrast to the caudate, the neurobiology of the MTL has been proposed to be ideal for the information processing demands of explicit, declarative memory. McClelland and others (1995) provided an analysis of information processing in
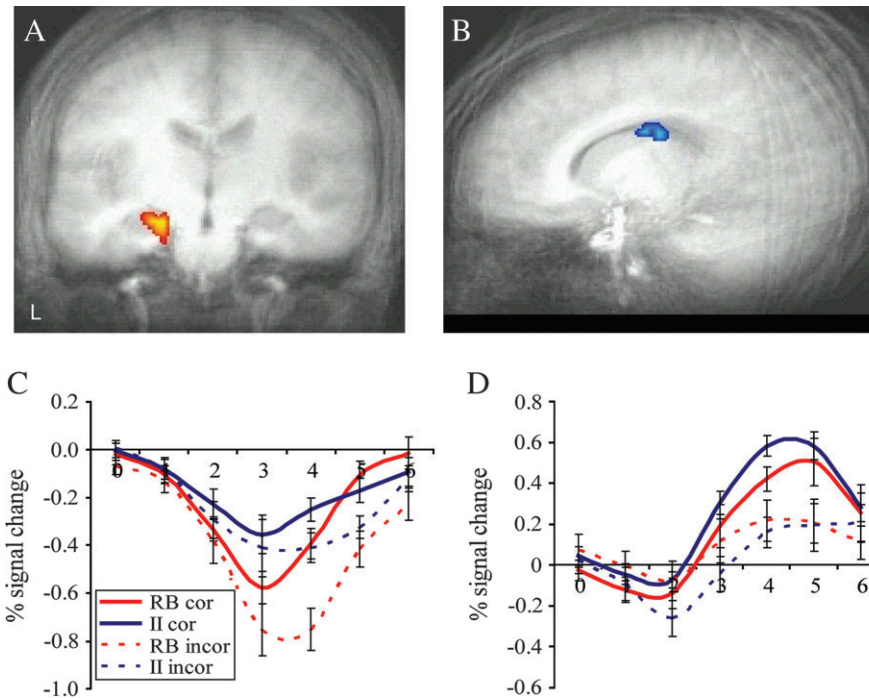
Figure 4. (*A*) RB categorization > II categorization in the left MTL (t_{24} > 2.0, cluster > 700 mm^3). (*B*) II categorization > RB categorization in the right body of the caudate (t_{24} > 2.0, cluster > 600 mm^3). ROI-AL methodology (Stark and Okada 2003) was used to align ROIs in both *A* and *B*. Note that cross-subject ROI-AL was improved at the cost of whole-brain alignment. (*C*) Peristimulus time (PST) course for the left MTL ROI. (*D*) PST course for the right caudate ROI.

distributed neural networks and demonstrated that the demands of rapid learning of distinct episodes requires specialized circuitry to avoid catastrophic interference. The hypothesized role of this system in categorization would be to learn the specific criterion (or rule) that distinguishes the categories. This may be accomplished through the creation of a representation of the boundary via exemplar stimuli that are very close to this boundary. Then, a comparison of the current stimulus with this boundary representation could be used to determine category membership. This approach would lend itself to RB tasks such as the one presented here in which a verbalizable rule (e.g., the relative spatial frequency of the Gabor pattern) clearly differentiates the categories. Amnesic patients attempting to learn an RB task are impaired (Kitchener and Squire 2000), indicating that the MTL plays a role in these tasks. Additionally, the known monosynaptic projections from hippocampus to PFC (Thierry and others 2000) as well as animal data of projections from hippocampus to the medial caudate via the fornix (Devan and White 1999) support the more recent COVIS model (Ashby and Valentin forthcoming) that includes the hippocampus.

The peristimulus time courses in Figure 4 suggest several hypotheses about the operation and interaction of these 2 category-learning systems. In the MTL, activity is deflected below baseline on each trial for all subjects. One potential explanation for this downward deflection is high baseline activity depressing the trial-locked activity (Law and others 2005). Another explanation is that this effect reflects familiarity with the stimuli (e.g., as in Henson and others 2003). In either case, the pattern of activity in the MTL suggests the operation of several opposing processes: 1) a tonic deactivation to each trial and 2) an increase in activity for correct trials during RB categorization, possibly reflecting successful recollection. Our data do not permit us to separate these effects although it is possible

that they reflect the neural correlates of the cognitive state (e.g., engaging in the general use of an RB strategy leads to deactivation on all trials) from trial-specific effects (e.g., a relative increase during a successful categorization event).

Activity in the caudate increases on each trial and the time course suggests the possibility that it may be related to the feedback given on each trial (although it's also possible that the delayed peak is simply a result of the hemodynamic response of this brain area). Behavioral studies have shown that feedback is particularly important for II but not RB category learning (Maddox and others 2003; Maddox, Ashby, and others 2004). Further, this pattern of activity has been observed previously (Seger and Cincotta 2005) in the body and tail of the caudate during successful categorization, thus emphasizing the importance of this structure in II category learning. As in the MTL, the caudate activity is similar for the RB and II groups, although the correct II trials evoke a reliably larger response. In both regions the greater involvement of the critical brain area is inferred from the greater observed response on correct trials as compared with incorrect trials.

The patterns of peristimulus activity observed here do not necessarily support the idea of direct competition between the 2 neural systems. In Poldrack and others (2001), opposing patterns of activity were observed in the MTL and caudate and interpreted as direct competition, that is, activity in one system downregulates the other system. Here, both tasks exhibited this cross-region activity, but successful categorization distinguished between the RB and II category-learning process. This could be interpreted as a form of competition in which 2 systems are engaged, but the system that "wins" is the one that has the greater probability of success. When studying the neural systems of healthy individuals, it is difficult to prevent them from using all available resources to learn a new skill,

particularly when one of these systems is hypothesized to operate implicitly. The similarities in overall activity observed here suggest that both types of learning may be active simultaneously in both conditions. Further, intermixing of strategies, especially early in the learning process, could reflect competition between the 2 categorization systems. The correlation of success-related activity in the MTL with RB categorization and in the posterior caudate with II categorization suggests that these regions play a crucial role in effective application of the associated categorization approach. Activity in the MTL during II categorization and in the posterior caudate during RB categorization may reflect activity in the system that loses in competition, resulting in that activity being unrelated to success.

Evidence from the cognitive neuroscience of category learning is consistently and convincingly demonstrating that there are multiple brain systems for category learning. Computational models have attempted to provide alternate accounts of behavioral and neuropsychological dissociations (Nosofsky and Zaki 1998; Nosofsky and Johansen 2000), but neuroimaging has found strong evidence for separable systems for category learning in the brain, in this as well as in previous studies (Poldrack and others 2001; Reber and others 2003; Seger and Cincotta 2005). In particular, we posit that the MTL and basal ganglia can function as independent memory systems in certain learning situations. One theory that attempts to characterize these independent systems is the COVIS model of category learning (Ashby and others 1998). The neuroimaging findings reported here provide significant support for this model and successfully bring together previously distinct theories of memory systems and category learning. Specifically, verbal, RB category learning relies upon the MTL-based explicit memory system (along with PFC structures), and nonverbal, implicit category learning relies upon the basal ganglia–based procedural learning system.

Human Research Statement

This experiment required the use of human subjects because we are interested in the higher cognitive process of learning. Before beginning the experiment, participants were required to read and sign the informed consent form. They were encouraged to ask any questions and had the option of leaving at any time with no adverse consequences. The informed consent forms are kept on record in the lab.

Notes

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