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**Behavioral/Systems/Cognitive**

**Dissociable Prototype Learning Systems: Evidence from Brain Imaging and Behavior**

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**The neural underpinnings of prototype learning are not well understood. Amajor source of confusionisthattwo versions ofthe prototype learning task have been used interchangeably in the literature; one where participants learn to categorize exemplars derived from two prototypes (A/B task), and one where participants learn to categorize exemplars derived from one prototype and noncategorical exem plars (A/non-A). We report results from an fMRI study of A/B and A/non-A prototype learning that allows for a direct contrast of the two learning methods. Accuracy in the two tasks did not correlate within subject despite equivalent average difficulty. The fMRI results revealed neural activation in a network of regions consistent with episodic memory retrieval for the A/B task while greater activation of a nondeclarative learning network was observed for the A/non-A task. The results demonstrate that learning in these two tasks is mediated by different neural systems and that recruitment of each system is dictated by the context of learning rather than the actual category structure.**

***Key words:*category learning; declarative memory; functional MRI; medial temporal lobe; perceptual learning; striatum**

**Introduction**

Category learning is an essential cognitive function. Evidence suggests that different forms of category learning are supported by different memory systems (Poldrack and Foerde, 2008) with each memory system being associated with different neural cir cuits (Schacter, 1987; Squire, 1992; Poldrack and Packard, 2003). For instance, rule-based learning relies on prefrontal cortex mediated working memory while information integration relies on striatum-mediated procedural learning (Ashby and O’Brien, 2005; Nomura et al., 2007).

An important form of category learning is prototype learn ing—prototypes provide the abstract representation for many natural categories (Rosch, 1973; Rosch and Mervis, 1975) and form the basis of much categorization in young children (Strauss, 1979; Ross, 1980). However, the neural underpinnings of proto type learning remain unclear and contradictory findings exist, with an ongoing debate over whether prototype learning relies on declarative or nondeclarative memory systems (cf. Knowlton and Squire, 1993; Palmeri and Flannery, 1999). Ashby and colleagues (Ashby and Maddox, 2005; Ashby and O’Brien, 2005) suggest that the lack of clarity may be due to the use of two different tasks to study prototype learning: an A/B task and an A/non-A task. In the A/B task, participants learn to categorize exemplars derived from two prototypes. In the A/non-A task, participants learn to

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categorize exemplars derived from one prototype against noncat egorical exemplars.

When task type is taken into account, the neural basis of pro totype learning may be clearer. A/non-A prototype learning is intact in patients with Parkinson’s disease (Reber and Squire, 1999), schizophrenia (Ke´ri et al., 2001b), and amnesia and Alz heimer’s disease (Knowlton and Squire, 1993; Bozoki et al., 2006). Neuroimaging studies with the A/non-A task report learning-related activity reductions in occipital cortex for cate gory A exemplars compared with noncategorical exemplar (Aizenstein et al., 2000; Reber et al., 1998a,b), although the acti vation pattern also depends on the intentionality of learning (Reber et al., 2003). The results suggest that the perceptual rep resentation memory system (Schacter, 1990) might mediate A/non-A learning.

In contrast, the A/B task is impaired in Alzheimer’s disease and amnesia (Zaki et al., 2003). Neuroimaging studies with the A/B task primarily report learning-related changes in prefrontal and parietal cortices (Seger et al., 2000), when comparing task activation to that of fixation baseline. Vogels et al. (2002) used a hybrid A/B/neither task and found prefrontal and parietal activa tion, but also orbitofrontal and neostriatal activation with no task-related changes in occipital cortex. These findings suggest that explicit reasoning and/or declarative memory processes might mediate A/B prototype learning.

Firm conclusions regarding the neural basis of A/non-A and A/B prototype learning are complicated by the methodological differences between the two tasks and by the different fMRI con trasts typically used. To date, no neuroimaging study has exam ined A/non-A and A/B prototype learning using the same stimuli, participants, and fMRI contrasts. The overriding goal of this study is to address this significant shortcoming and examine the

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although the training phases differed across

tasks, the test phases were identical.

*Training design (not scanned).* Participants

were in the scanner, but no fMRI was recorded

during the training phase of each run. During

training for the A/B task, participants were

asked to categorize 10 A and 10 B items (pre

sented one by one in a random order) with cor

rective feedback. On each trial, 2 s after stimulus

onset, the participant was prompted to give an

A or B response. After each response, the par

ticipant was informed whether they were cor

rect or wrong. Within each category, 2 training

stimuli differed from the category prototype on

1 feature, 3 differed on 2 features, 3 differed on

3 features, and 2 differed on 4 features. Across

all 10 stimuli within each category, the category

**Figure 1.** Example stimuli from one stimulus set. The leftmost stimulus represents the prototype of category A, stimuli to the right ofthe prototyperepresent examples ofstimuli with increasing distances fromthe A prototype. Therightmoststimulus isthe category B prototype. Stimuli with distance 0 – 4 from prototype A were considered category A members, stimuli with distance 6 –10 were considered category B (non-A) members.

neural underpinnings of A/B and A/non-A prototype learning

typical features were presented 7 or 8 times and the opposite category typical features were pre sented 2 or 3 times. Neither prototype was pre sented. The training stimuli were presented in a random order, different for each of the four runs, but identical across participants.

Before A/non-A training, participants were informed that they will need to learn to dis

using a well controlled paradigm.

**Materials and Methods**

*Participants.* Twenty-seven young adult volunteers (age 18 –30; 13 fe males) participated in the study. Data from 3 participants (1 female) were excluded due to excessive head motion, leaving 24 participants for anal ysis. Each participant provided signed informed consent to participate in the study and all procedures were approved by the IRB of The University of Texas, Austin. Volunteers received $50 compensation fora2h session.

*Stimuli.* The stimuli were cartoon animals that varied along 10 binary dimensions, such as body shape (round or square), head position (facing forward or upward), tail shape (feathery or pointy), etc. (Fig. 1), adapted from a prototype learning study of Bozoki et al. (2006). For each run, one stimulus served as the category A prototype with all 10 of its feature values being referred to as prototypical features. All other stimuli can be defined relative to the prototype and can differ on 1–10 of the prototyp ical feature values. The stimulus with all 10 nonprototypical features is the B prototype (in the A/B task) and the anti-prototype (in the A/non-A task). The number of nonprototypical features in each stimulus deter mines its distance from the prototype (see Fig. 1). Category A stimuli were defined as those with a distance of 0 – 4 from the A prototype and category B (or non-A) stimuli were defined as those with a distance of 6 –10 from the A prototype. Stimuli equidistant from the two prototypes were excluded from the study.

A second set of cartoon animal stimuli with different dimensions were also generated, and each prototype learning task was tested with both sets of stimuli. Note that in this study, unlike in a typical A/non-A experi ment, all non-A stimuli were internally consistent and constructed from a fixed prototype. Thus, the only difference between the A/non-A and A/B tasks was in the stimuli presented during training (only A stimuli in the A/non-A task, and A and B stimuli in the A/B task), and the category labels used during the testing phase. Critically, the same stimuli were used in the test phase for both the A/non-A and A/B tasks. Thus, any differences observed in the A/non-A and A/B brain activations cannot be attributed to differences between the structures of non-A versus B cate gory, nor to any stimulus-specific differences.

*Experimental design.* A within subject design was used. Each run con sisted of a training phase and a test phase, with functional MRI scans acquired during the testing phase of each run. Each participant com pleted two A/B runs (one run with stimulus set 1 and one run with stimulus set 2), a 10 min structural scan, and two A/non-A runs (again one run with each stimulus set). The order of stimulus sets and the order of the tasks were counterbalanced between participants. Importantly,

criminate members of category A from nonmembers (non-A). Dur ing A/non-A training, participants were shown stimuli from category A only. Twenty training stimuli from category A were passively viewed one by one for a minimum of 2 s, after which a prompt asked a participant to press any button to proceed to a next example of a category member. There were 5 training stimuli that differed from the A prototype on one feature, 5 differed on two features, 5 differed on three features, and 5 differed on four features. Across all 20 stimuli, the prototypical value on each dimension was presented 15 times and the nonprototypical value on each dimension was presented 5 times.

*Test design (fMRI recorded).* The testing phase was identical for both tasks, with only the label of the second category (B versus non-A) differ ing between the tasks. Participants were presented with 42 stimuli, one at a time that included both prototypes and five stimuli selected from each distance from the prototype (except distance 5—ambiguous stimuli). None of the stimuli were previously used in the training phase. An event related design was used to examine the neural activity to specific trials during the testing phase. Four possible orders of A and B stimuli and their onsets including 30% of null time (to interject temporal jitter) were predetermined using the “optseq2” program. Each stimulus onset time and order was used in one experimental run. On each trial, a stimulus was presented for a maximum of 3.5 s, during which time the participant needed to indicate the category membership of the stimulus. No feed back was provided. A fixation cross was presented between each stimulus onset lasting 0.5, 2.5, or 4.5 s.

*MRI acquisition, processing, and analysis.* Functional and structural images were acquired using a 3T GE Signa MRI scanner with an 8-channel phased array head coil. Functional images were acquired dur ing the testing phase of each run, using a multiecho GRAPPA parallel imaging EPI sequence that reduces typical EPI distortions and suscepti bility artifacts. Images were collected using whole-head coverage with slice orientation to reduce artifact ( 20° off the AC-PC plane, TR 2 s, 3 shot, TE 30 ms, 35 axial slices oriented for best whole-head coverage, acquisition voxel size 3.125 3.125 3 mm with a 0.3 mm interslice gap). The first four EPI volumes were discarded to allow scans to reach equilibrium. Stimuli were viewed through a back projection screen and a mirror mounted on the top of the head coil. Responses were collected with an MR compatible button box that was placed under the right hand.

In addition to the EPI images collected during task performance, one or two high-resolution T1 SPGR scans that have been empirically opti mized for high contrast between gray matter (GM) and white matter (WM) and between GM and CSF were acquired. These images were acquired in the sagittal plane using a 1.3 mm slice thickness with 1 mm2 in-plane resolution.

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**Table 1. Regions commonly activated in both the A/B and A/non-A task**

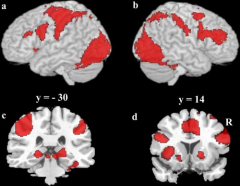
Brain region Volume Size Max*Zx y z*

Whole brain cluster corrected (*p*  0.05)

L lateral occipital (BA 19) 37,752 4719 6.93 36 86 4 R lateral occipital (BA 19) 27,096 3387 6.75 42 66 12 Calcarine (BA 17) 6456 807 3.59 10 72 6 L postcentral (BA 3/40) 29,640 3705 5.71 44 26 48 R inferior parietal (BA 7/40) 28,104 3513 5.69 36 54 46 R fusiform/inferior temporal (BA 37) 13,896 1737 6.83 40 54 20 L fusiform (BA 37) 7168 896 6.73 38 64 20 L inferior frontal (BA 44/48) 18,664 2333 6.1 48 6 28 Medial frontal (BA 24/32) 15,416 1927 5.79 4 8 46 R inferior frontal (BA 44) 13,920 1740 5.61 52 10 24 R middle frontal (BA 6) 3912 489 4.08 30 4 46 Small volume corrected (*p*  0.05)

R hippocampus 984 123 5.15 20 30 4 L hippocampus 672 84 4.56 20 30 8 R striatum 1040 130 4.35 16 16 2 L striatum 488 61 3.23 20 10 4

L, Left; R, right; BA, Brodmann area; Max, maximum. Volume is given in mm3, and size is given in voxels. Coordinates reflect standard MNI space.

the smoothness of the data estimated directly from the contrast im 

age. The determined minimal cluster size to satisfy cluster size prob

ability threshold of *p*  0.05 thus varied slightly from contrast to

contrast around 240 voxels (1920 mm 3).

Additionally to the whole-brain analysis, we defined two regions of

interest (ROI): medial temporal lobe (MTL) and striatum. We were

especially interested in area MTL because its involvement in proto

type learning has been controversial and in striatum because it has

been implicated in other kinds of category learning and is thought to

operate complementary to area MTL (Poldrack et al., 2001; Poldrack

and Packard, 2003). The MTL ROI was defined by combining the FSL

Harvard–Oxford atlas hippocampus and parahippocampal regions

for the left and right hemispheres. The striatum ROI consisted of the

combined putamen and caudate from the FSL Harvard–Oxford atlas,

again for both the left and right hemispheres. Activation in each ROI

was assessed using a small volume correction at *p*  0.05 based on

Monte Carlo simulation, accounting for both smoothness of the data

and the shape and size of each ROI. During each simulation, uniform

random numbers were assigned as activation *p* values to individual

**Figure 2.** Commonly activated regions in both tasks versus baseline. ***a***, ***b***, Whole-brain 3D rendering with cortical activation overlay. ***a***, Left hemisphere. ***b***, Right hemisphere.***c***, ***d***, Coro nal slices with activations overlays. ***c***, Bilateral hippocampus. ***d***, Bilateral striatum and medial frontal cortex. Activation maps were overlaid upon a canonical brain in standard MNI space using MRIcro software (www.sph.sc.edu/comd/rorden/mricro.html).

Preprocessing and data analysis were conducted using FEAT (FMRI Expert Analysis Tool) version 5.63, part of FSL (www.fmrib. ox.ac.uk/fsl) software. Preprocessing included motion correction us ing MCFLIRT (Jenkinson et al., 2002), non-brain removal using BET (Smith, 2002), high-pass temporal filtering with a 60 s cutoff, and spatial smoothing with a Gaussian kernel of 5 mm FWHM, and nor malization to a 2 mm resolution MNI template brain. Data from each run of each participant were analyzed separately at a first level of analysis. Category A and category B/non-A trials were modeled sep arately as two predictors. Each category stimulus time onsets were convolved with a canonical hemodynamic response function and to gether with their temporal derivatives were entered as predictors into a general linear model to estimate -weights. Data from all four runs from each participant were combined at a second level using a fixed effects analysis. Group level analysis combined data from each partic ipant in a random effects analysis using OLS. For all analyses, indi vidual voxels were considered active when reaching *Z*  2.3 and sur vived a whole-brain cluster-size threshold set at *p*  0.05 (Worsley, 2001). In the FSL implementation of random field theory, the mini mal cluster size is determined by both the set cluster size *p* value and

voxels in a mask of the same shape and size as the ROI of interest, representing a possible pattern of “activation” that could be recorded under the null hypothesis of no real activation in the region. The simulated voxel activations were then smoothed with the same kernel as the actual data and the maximal cluster size that occurred under the null hypothesis by chance was recorded for each simulation. Cluster size that occurred with probability 0.05 across 5000 simulations was then considered significant at the cluster-size threshold of *p*  0.05. The simulations were performed using “AlphaSim” tool in AFNI and determined a minimal required cluster size of 33 voxels (264 mm 3) in the normalized space for the MTL ROI and 30 voxels (240 mm 3) for the striatum ROI.

**Results**

**Behavioral performance**

For the main behavioral and fMRI analyses, test phase data were pooled across the two runs (the two stimulus sets) of each task. There were no differences between accuracies achieved on the two stimulus sets (A/B: 0.68 vs 0.71, *t*(23)  1.186, *p*  0.248; A/non-A: 0.67 vs 0.68, *t*(23)  0.441, *p*  0.664) and there was no difference between overall accuracy in the A/B task (mean 0.694, SE 0.018) and the A/non-A task (mean 0.673, SE 0.020; *t*(23)  0.644, *p*  0.526).

Interestingly, A/B and A/non-A accuracy rates were moder ately negatively correlated (*r*  0.362, *p*  0.082), suggesting that distinct cognitive processes may underlie participants per formance in the two tasks. Unlike accuracy, mean reaction times

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**Table 2. Regions from whole-brain and region-of-interest (small volume corrected) analysis that activated differentially during the A/B task and the A/non-A task** Brain region Volume Size Max*Zx y z*

A/B A/non-A (whole brain cluster corrected)

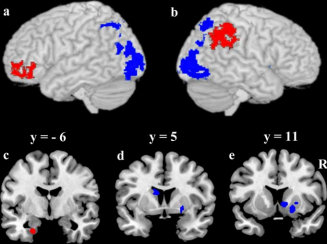
R inferior parietal (BA 40) 5968 746 3.79 58 38 46 L orbitofrontal (BA 47/11) 3048 381 3.9 36 54 16 A/B A/non-A (small volume corrected)

L parahippocampus (BA 36) 424 53 3.13 20 6 30 A/non-A A/B (whole brain cluster corrected)

L Inf lateral occipital (BA 18) 7912 989 4.88 20 94 0 R Inf lateral occipital (BA 19) 6208 776 4.37 38 82 2 L Sup parietal (BA 7) 3824 478 4.24 20 70 36 R Sup parietal (BA 7) 3608 451 3.74 22 64 48 A/non-A A/B (small volume corrected)

R putamen 328 41 3.47 20 10 8 R caudate head 264 33 3.24 10 10 2 L caudate body 256 32 4.27 10 6 18

L, Left; R, right; Inf, inferior; Sup, superior; BA, Brodmann area; Max, maximum. Volume is given in mm3, and size is given in voxels. Coordinates reflect standard MNI space.

as well as bilateral posterior hippocam 

pus (Fig. 2*c*) and bilateral striatum (Fig.

2*d*).

**Task differences**

The primary focus of this research was to

directly compare activity during the A/B

task and the A/non-A task within subject

using the same stimuli. On direct con

trast between test trials, a number of re

gions exhibited greater activity in one

task compared with the other. The list of

identified regions is provided in Table 2,

with corresponding statistical maps pro

vided in Figure 3.

The direct contrast revealed that the

A/B task involves to a greater degree fron

tal and parietal cortices and parahip

pocampus (Fig. 3, red overlay), areas that

have been previously implicated in explicit

episodic memory. In contrast, regions that

demonstrated greater activity in the

A/non-A task than the A/B task included

**Figure 3.** Regions from direct contrast of A/B task versus A/non-A task. In red, A/B A/non-A; in blue A/non-A A/B. ***a***, ***b***, Whole-brain cluster corrected contrasts overlaid on a 3D rendering of a canonical brain. ***a***, Left hemisphere. ***b***, Right hemisphere. ***c– e***, Coronal sections illustrating small volume corrected contrast maps in regions of interest. ***c***, Left parahippocampus. ***d***, Left caudate body.***e***, Right putamen and right caudate head. Statistical maps were overlaid upon a canonical brain in standard MNI space using MRIcro software (www.sph.sc.edu/comd/rorden/mricro.html).

differed between the two tasks by 0.2 s (A/B: mean 1.343 s,

primarily posterior cortices and striatum (Fig. 3, blue overlay), areas previously im plicated in nondeclarative perceptual (e.g., Slotnick and Schacter, 2006) and proce dural learning (e.g., Packard and Knowl ton, 2002; Poldrack and Packard, 2003). Because reaction times were not perfectly equated in the two tasks, it is possible that

SE 0.095; A/non-A: mean 1.545 s, SE 0.099; *t*(23)  3.566, *p*  0.002) and were positively correlated within subject (*r*  0.831, *p*  0.001).

**Common neural regions**

First, we identified regions that showed common activation in both the A/B task and the A/non-A task compared with the fixation baseline, using overlap masking of the two thresh olded *z*-maps. *Z* values for the common activation *z*-map (as reported in Table 1) are the minimum of the two tasks’ *z*-maps. A network of regions in which both tasks showed significantly greater activation compared with the fixation baseline (see Fig. 2, Table 1) included occipital and fusiform areas, inferior frontal cortex, and precentral gyrus (Fig. 2*a*,*b*),

some of the regions identified in the A/non-A A/B contrast may reflect longer processing times in the A/non-A task than in the A/B task. However, adding the reaction time differences as a covariate at the group level analysis did not eliminate the activa tion differences.

*Behavioral relevance of differential neural regions*

For each of 10 clusters identified in the direct contrast, average time courses for each voxel and for each condition were com puted using a selective averaging technique (http://www. poldracklab.org/software). A mean activation (average of 4 –8 s after stimulus onset) was computed for each cluster and each participant, during the A/B task and during the A/non-A task, and were correlated with the participant’s performance in each task. For each task separately, we excluded participants

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**Table 3. Regions that exhibited greater activation during correct than incorrect trials**

Brain region Volume Size Max*Zx y z*

A/B task (whole brain cluster corrected)

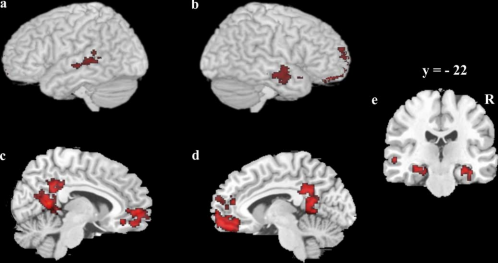
R middle temporal (BA 21/22) 2984 373 3.64 62 14 16 L middle temporal (BA 21/22) 2104 263 3.57 58 36 4 Posterior cingulate/ precuneus (BA

23) 12,608 1576 4.58 6 52 10 Orbitofrontal (BA 10/11) 11,440 1430 4.1 2 62 14 A/B task (small volume corrected)

R medial temporal (BA 20) 1904 238 4.18 30 22 16 L medial temporal (BA 20) 1608 201 3.69 32 22 14 A/non-A task (small volume corrected)

L putamen 1416 177 4.25 32 10 2 R anterior hippocampus 304 38 3.8 28 10 22

Regions are identified for each task separately. Volume is given in mm3, and size is given in voxels. Coordinates reflect standard MNI space.



**Figure 4.** Regions associated withsuccessful categorization during the A/B task. ***a***, ***b***, Lateral view of the left and right hemisphere 3D rendering with activation overlay.***c***, ***d***, Medial view of the left and right hemisphere.***e***, Coronal section showing medial temporal lobe activation.

who did perform at chance in both of the two runs of the given task. There were 3 participants excluded from A/B task corre lational analysis and four participants excluded from A/non-A correlational analysis. Neural activity in 2 out of 3 clusters identified in the A/B A/non-A contrast was predictive of behavioral performance in the A/B task—the left inferior or bital frontal cortex (*r*  0.432, *p*  0.050) and the left para hippocampus (*r*  0.443, *p*  0.044)—indicating that partic ipants who recruited these regions to a larger degree during the A/B task performed better in the A/B task. Neither of the regions predictive of performance in the A/B task was predic tive of performance during the A/non-A task. Out of the 7 regions identified in the A/non-A A/B contrast, none sig nificantly predicted accuracy in the A/non-A task (all *r*  0.30, *p*  0.19).

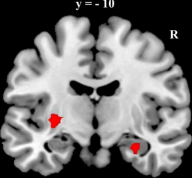
**Neural regions predictive of trial accuracy**

To identify brain areas predictive of successful categorization on an individual participant’s level, we compared activity evoked

during correct categorization trials with that evoked during in correct categorization trials, separately for each task. Identified regions that exhibited greater activation during correct than in correct trials are listed in Table 3 and are presented in Figures 4 and 5. No region exhibited greater activation for incorrect than correct trials in either task. The activation differences between correct and incorrect trials cannot be accounted for by reaction time differences. For both tasks, there were reaction time differ ences between correct and incorrect trials, but with longer incor rect than correct reaction times (A/B task: correct mean 1.39 s, SE 0.09 s, incorrect mean 1.51 s, SE 0.10 s, *t*(23)  3.03, *p*  0.006; A/non-A task: correct mean 1.59 s, SE 0.09 s, incorrect mean 1.70 s, SE 0.10, *t*(23)  3.83, *p*  0.001).

Regions that were predictive of correct categorization dur ing the A/B task trials included bilateral middle temporal cor tices, posterior cingulate cortex, and orbitofrontal cortex, as well as bilateral medial temporal lobe spanning parts of both parahippocampus and hippocampus. Only two regions were predictive of correct categorization during the A/non-A task,

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an individual trial basis. These findings are consistent with the 

notion that A/B categorization tasks engage mechanisms that are

similar to other processes that rely on the MTL, such as declara

tive or associative memory.

Direct contrast of the tasks also revealed regions that were

preferentially recruited during the A/non-A categorization. This

included regions of lateral occipital cortex and striatum, with

regions of the striatum being predictive of correct responses on

individual trials during the A/non-A task. The striatum and pos

terior cortices have been implicated in multiple studies of non

declarative category learning (Poldrack et al., 2001; Seger and

Cincotta, 2002, 2005; Shohamy et al., 2004; Nomura et al., 2007)

and these findings are consistent with the idea that the A/non-A

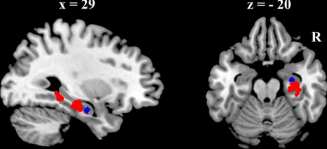
task is based to a larger degree on implicit, perceptual, and/or

procedural learning.

The preferential involvement of the posterior corticostria

tal loops was observed here even though the intentional learn

**Figure 5.** Regions associated with successful categorization during the A/non-A task. Coro nal section featuring left putamen and right hippocampal activation.



ing mode and within subject design could bias participants toward applying conscious, explicit strategies, and even though there was no external feedback

provided during test or training. Al

though individual differences in activa

tion of neither striatum nor posterior

cortical regions were predictive of par

ticipants’ accuracy, this could be ex

pected based on previous findings. Oc

cipital and temporal activity in

perceptual learning experiments is typi

cally not correlated with behavior

(Schacter et al., 2007). In addition, the

lack of correlation with striatal activity

may be due to the relatively small num

ber of trials used in the current experi

ment such that it may reflect the early

stages of learning in this system. For ex

**Figure 6.** Comparison of MTL regions implicated in the A/B task and the A/non-A task. Sagittal and horizontal section illus trating relative location of the regions of MTL that showed greater activation during correct than incorrect trials during the A/B task (red) and the A/non-A task (blue).

left putamen and right anterior hippocampus. The relative

ample, Seger and Cincotta (2005) found the striatum to be significantly involved throughout learning, but becoming pre dictive of accuracy only later in the learning, after 300 training trials,

location of the right hippocampal region identified in the A/non-A task and the right MTL region identified in the A/B task is presented in Figure 6. The A/non-A region was located anterior to the A/B region and there was minimal overlap between the regions (3 voxels).

**Discussion**

We conducted an fMRI prototype learning experiment that used equivalent stimuli, learning mode and a within subject design to examine the neural basis of A/non-A and A/B prototype learning. The results were consistent with the proposition that A/non-A and A/B prototype learning are based on dissociable processes, each with a corresponding neural system. First, there was a neg ative correlation between A/non-A and A/B task performance even when behavioral data on average showed comparable learn ing in both tasks. Second, brain regions were identified that were preferentially active during one task versus another. Most nota bly, the A/B task recruited to a larger degree parahippocampus and inferior parietal and orbitofrontal cortex. Moreover, individ ual differences in the activation of parahippocampus and orbito frontal cortex were predictive of participant’s accuracy in the A/B task, but not the A/non-A task. Hippocampal and parahip pocampal activation was also predictive of correct responses on

while each of our runs involved only 20 training trials. Com pared with the striatum, the hippocampal learning system comes online relatively quickly, being dominant early in learn ing (Poldrack et al., 2001), and providing the basis for the correlation with individual differences in accuracy observed here for the A/B task. The neuropsychological literature also supports the notion that the A/B task depends on MTL and declarative memory while the A/non-A task does not. For example, Knowlton and Squire (1993)found intact A/non-A prototype learn ing in patients with MTL lesion-based amnesia; Bozoki et al. (2006) and Ke´ri et al. (2001a) found intact A/non-A learning in patients with Alzheimer’s disease. In contrast, Zaki et al. (2003) found im paired learning in amnesic patients in the A/B prototype learning task, but not A/non-A task.

Prototype learning is ubiquitous in everyday cognition. We hypothesized that prototype learning is not mediated by a single neural system, but rather that the system relevant to prototype learning depends critically upon the circumstances of learning— whether the task involves learning to discriminate a single cate gory from other stimuli (A/non-A task), or classification of stim uli into two separate categories (A/B task). In previous studies, the information about which prototype task was used was typi cally buried deep in the method section and conclusions derived

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from one version of the prototype task were readily generalized to the other version. However, there has been no empirical evidence that the two tasks recruit identical cognitive and neural processes and the differential demands of the two tasks suggest that they may not. In the A/non-A task, participants are likely to form a representation of a single prototype and then compare each test item to this single prototype. If the new stimulus is sufficiently similar to the prototype representation, it will be endorsed to the category; otherwise it will be categorized as a nonmember. Nov elty or familiarity signals from early processing areas may be used as a basis for successful categorization. In contrast, in the A/B task, participants are likely to form representations of two dis tinct categories centered on two prototypes. Each new stimulus is then weighed against each prototype and endorsed to the cate gory of the prototype that is closer to the current stimulus. Addi tionally, participants need to recollect details of learning and ex tract the appropriate verbal category label. In this case, familiarity or novelty signals are not sufficient for successful performance and additional processes need to be recruited to support learning. Thus, we expected that processes and neural structures support ing prototype learning should depend on the context of learn ing—whether a category is learned in isolation (as in the A/non-A task), or whether two categories are contrasted with each other (as in the A/B task).

Alternatively, some or all discrepancies in the prototype learn ing literature could be a by-product of the different learning modes typically adopted in the A/B task and the A/non-A task. The A/B task always involves intentional (conscious) learning where the participants are instructed to learn the characteristics of the categories based on corrective feedback or the provided category label (Little and Thulborn, 2006). The A/non-A task often involves incidental learning where participants passively view category exemplars first while being naive to the purpose of the experiment, with a later “surprise” test on discrimination of categorical from non-categorical exemplars (Reber et al., 1998a). Two fMRI studies compared neural activation in both incidental and intentional version of an A/non-A task (Aizenstein et al., 2000; Reber et al., 2003), showing differential pattern of activa tion for the two learning modes. However, the current experi ment may offer some clarification of this issue since the results presented here demonstrate that even when learning mode is equated, dissociable neural systems emerge that support the A/B task and the A/non-A task. Importantly, only the context of learning (A/non-A vs A/B) differed across the tasks in the current study and thus any differences in the neural signature must be due to context and not methodology, learning mode, or category structure differences.

Both prototype learning systems likely play an important and complementary role in concept acquisition, as everyday prototype learning experience contains elements of both tasks. Each system has its own strengths and limitations. The A/non-A prototype learning system has been shown to work automatically, supporting even incidental learning without supervision (Posner and Keele, 1968). Perceptual coherence of the category exemplars is a major factor in concept learnabil ity; concepts such as carrot or apple can be well learned by the A/non-A system. The A/B prototype learning system depends on supervision (Casale and Ashby, 2008), but allows one to form categories that are less perceptually coherent and make inferences that are not based solely on perceptual similarity. The concept of fruits and vegetables is better suited for the A/B system. While typically operating in parallel, these prototype learning sys tems are dissociable when demands of the task are tuned to suit one

system versus the other (as demonstrated here) or when damage to one system hinders learning of specific tasks versions (as sup ported by the neuropsychological literature). Importantly, rather than the category structure itself, theframing and context of the task, such as whether a category is learned in isolation or next to another category, play a crucial role in recruiting the complementary learn ing systems.

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