Research report

Comparing the brain areas supporting nondeclarative categorization and recognition memory

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Abstract

Brain areas associated with both nondeclarative categorization and recognition memory were identified and contrasted using functional magnetic resonance imaging (fMRI) of healthy volunteers. Activity during dot-pattern categorization and recognition were compared with a control task (counting dots) in two separate groups of participants ($n=5$ each). The network of areas associated with nondeclarative categorization was found to include bilateral inferior prefrontal and parietal cortical areas that have been implicated in several other studies of categorization. During recognition, increased activity was found in posterior visual areas, the precuneus, posterior cingulate and right prefrontal cortex. Using the common control condition as a reference, recognition and categorization were contrasted and recognition was found to evoke more activity in posterior early visual cortex, the precuneus, right medial temporal lobe and right dorso-lateral prefrontal cortex. Previous research has implicated changes in visual representation in learning a category of dot-pattern [23,24] by comparing activity evoked by categorical and non-categorical stimuli. The current findings support those results and additionally identify brain areas active during categorization that are involved in expressing this category knowledge. © 2002 Elsevier Science B.V. All rights reserved.

Learning a visual category based on incidental study of a set of category exemplars has been shown to depend on nondeclarative memory [12,32]. This type of learning can occur without the participants having conscious memory of the exemplars studied when the category was learned. This is the case with amnesic patients, who learn a category of dot-patterns derived from an underlying prototype in spite of having impaired declarative memory for study items [12]. Intact learning in amnesic patients indicates that the medial temporal lobe memory system, which supports conscious declarative memory, is not crucial to this type of category learning. A study of dot-pattern categorization learning in patients with Parkinson's disease (PD) indi-

cated that this kind of learning also does not depend on the neostriatum [22], although some other categorization tasks do [22]. These neuropsychological studies were able to rule out contributions from two important memory systems in the brain, but do not indicate the areas that do support this kind of category memory.

Three reports have used functional magnetic resonance imaging (fMRI) to examine the brain areas involved in nondeclarative category learning for dot-patterns [1,23,24]. Reber et al. [23,24] compared brain activity for categorical and noncategorical patterns during a categorization test after participants had learned the category. Learning the category resulted in changes in visual processing for the dot-pattern stimuli so that subsequent processing of categorical stimuli was more fluent than processing of noncategorical stimuli, i.e., less activity was observed in early visual areas for categorical patterns compared with non-

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categorical patterns. Aizenstein et al. [1] also compared activity for categorical and noncategorical patterns, but did so during acquisition of the category. Reduced activity was once again observed for the categorical patterns compared with noncategorical patterns when the category was learned implicitly.

Together, these studies provide evidence that the neural basis of this visual category learning task is a form of perceptual learning that occurs outside awareness. The neuropsychological studies indicate that acquiring knowledge of the category does not depend on the medial temporal lobe or neostriatum being intact, while the functional imaging studies suggest that performance is associated with fluency for categorical stimuli. The fluency effect suggests a mechanism like priming, in which repeated presentation of visual stimuli results in less evoked activity than the original presentation did (see Ref. [29] for a review), except that this effect generalizes to novel category members. The existence of a nondeclarative category learning mechanism, independent from category learning based on conscious hypothesis testing [10], indicates that the multiple memory systems of the brain support multiple categorization processes.

As an alternate to the multiple memory systems view of category memory, Nosofsky and Zaki [15] suggested that differences in the cognitive processes involved in making a recognition or a categorization judgment may produce the apparent dissociation between nondeclarative category learning and recognition memory. Since recognition memory requires making a specific match between test stimuli and study items, it requires a different decision process to support a correct hit than a categorization judgment that is based on a general similarity to a collection of previously seen exemplars. In their model, Nosofsky and Zaki showed that a collection of weak memories (e.g., acquired by an amnesic patient) could support apparently normal categorization memory while recognition memory was impaired if the decision criteria differs for these tasks. This model suggests that the dissociation between categorization and recognition performance in amnesic patients could be accounted for with a single memory system. Discriminating between the model of Nosofsky and Zaki and the multiple memory systems view is extremely difficult to do if the brain is treated as a black box. However, the ability to collect information about the brain areas that are involved in categorization and recognition can provide a relatively direct test of whether there is a quantitative difference in the decision criteria used to make categorization and recognition judgments (as in Ref. [15]) or whether there are qualitatively distinct neural systems supporting these two processes. If the two types of memory depend on similar neural systems and representations then the networks of brain areas supporting these judgments should be similar. Evidence for distinct, separable networks supporting categorization and recognition would provide evidence that these two types of memory are supported by separate neural systems, as posited by the multiple memory systems theory.

Previous neuroimaging studies of dot-pattern categorization have not identified the network of areas involved in performing this categorization task. If the fluency effect is driving the ability to endorse categorical stimuli as category members, there must still be additional brain areas that are involved with using this information to behaviorally express knowledge of the category. In order to observe the fluency effect, the previous studies [23,24] compared activity in early visual areas during category judgments for categorical and noncategorical dot-patterns. This comparison does not identify changes in activity in areas that are active during the categorization process, since both conditions involve performing categorization. Comparing categorization to a control task will provide information about the brain areas involved in performing categorization and these can be directly contrasted with the brain areas that support recognition memory.

Several other studies have examined neural activity during category learning tasks in order to identify brain areas associated with category learning. These studies have used a variety of tasks and learning conditions and may depend on different cognitive processes even though they share some commonality in requiring categorization judgments. The role of multiple brain areas in different categorization tasks can be seen in the double dissociation shown with the probabilistic classification task (typically presented as 'weather prediction'). Amnesic patients exhibit normal learning on the probabilistic classification task [13], indicating that intact function of the MTL is not critical for this task. In contrast, patients with Parkinson's disease (PD) are impaired at learning this task [11], indicating that normal function of neostriatum is necessary for normal performance. The dot-pattern categorization task is learned at a normal rate by patients with PD [22] suggesting that although these two tasks require learning categorical information, different neural systems support them. One potentially important difference in the administration of the two tasks is that the probabilistic classification task is administered with feedback on each performance trial and without a separate study phase. Typically the dot-pattern categorization task is administered with an incidental study phase (no mention of the category is made at study) followed by a surprise categorization test without feedback. The differing task demands of administering categorization tasks in these two methods may evoke different cognitive processing strategies that depend on different neural systems.

The role of the neostriatum in performing the probabilistic classification task was reinforced by a neuroimaging study by Poldrack et al. [18]. In this study, brain activity (assessed with fMRI) during category learning with feedback on each trial was compared with a control task requiring counting the number of stimuli presented. During category learning, increased activity was observed in the

neostriatum, as predicted, as well as in prefrontal and posterior visual areas bilaterally. Because the comparison in this study examined the process of making a categorization judgment (and learning) with a control task, these areas reflect parts of a network supporting categorization in this task. However, since the study of PD patients has already shown differences in the role of the neostriatum in this task compared with dot-pattern categorization, the question of whether there are brain areas that are consistently involved in categorization is left open.

Seger et al. [30] examined category learning using an abstract visual category derived from an underlying prototype, again having participants learn during task performance with feedback on each trial. Brain activity (measured with fMRI) elicited by the categorization task was compared with a control task in which participants saw a checkerboard and pressed the response keys randomly (measured using fMRI). In this task, increased activity was associated with categorization in prefrontal, parietal and posterior occipital cortical areas. Activity was not observed in the neostriatum or the medial temporal lobe and since this task has not been studied with neuropsychological populations, it is not possible to conclude whether either of these brain systems was involved in learning this task. Seger et al. [30] reported that left inferior prefrontal cortex (PFC) exhibited increased activity with increasing performance, suggesting that this area is involved with acquiring expertise in the task while the other active areas may support general performance.

Two additional recent reports have compared item and rule-driven category learning using functional neuroimaging. In both of these studies, it seems likely that participants were using a conscious, declarative strategy to guide their categorization decision. While a conscious strategy would likely use separate categorical representations than a nonconscious categorization task, the similarity in task demands in judging category membership might evoke similar activations in prefrontal cortex.

Smith et al. [31] compared activity associated with performing a categorization task when the category had been previously learned either by explicitly learning the categorization rule or by memorization of a set of exemplars. The stimuli for this task were novel animal-like stimuli that were classified into two types. During rule-driven categorization (measured with PET), increased activity was observed in posterior occipital, inferior parietal areas, the precuneus, and right dorsolateral prefrontal cortex (DLPFC). Categorization driven by memorization of the exemplars activated a subset of these areas.

Fletcher et al. [8] examined category learning in which letter strings that conformed to a set of rules were classified as correctly following the rules or not. Rule and item memory were assessed separately by giving participants multiple trials of practice with the same stimuli with feedback on each trial. During the task, increases in activity were observed bilaterally in dorso-lateral and inferior PFC, the anterior cingulate, precuneus, and posterior visual areas. Activity in the precuneus was particularly associated with item-based learning while left inferior PFC was associated with rule learning.

Across these studies, several brain areas have been implicated in categorization with some consistency. Left inferior PFC was associated with categorization performance in Seger et al. [30], Fletcher et al. [8], Poldrack et al. [18] and the explicit categorization task in Aizenstein et al. [1]. Right DLPFC exhibited increased activity during categorization in Poldrack et al. [18], Seger et al. [30], Smith et al. [31] and Fletcher et al. [8]. However, in Fletcher et al. [8], the right DLPFC activity is hypothesized to be related to explicit retrieval processes that could support conscious categorization. This interpretation might also be applied to the consistent increase in activity in the precuneus seen across each of the studies. Increased activity in the precuneus has been associated with retrieval processes, particularly those supported by mental imagery [9]. Increased activity was also noted in parietal cortex on both left and right sides (although not in every study) for categorization tasks [18,30,31]. Across these studies of different categorization tasks, these areas emerge as possible candidates for neural systems that might play a general role in categorization processes (or cognitive subprocesses that support categorization).

Both the Smith et al. [31] and the Fletcher et al. [8] studies used tasks that are similar in principle to nondeclarative memory tasks (e.g., Refs. [27,20]). However, in both of those protocols, the healthy participants were encouraged to learn the categorization rules consciously and explicitly apply them to the test. In the dot-pattern categorization task used in neuropsychological studies, participants are often unaware of the category that has been learned. The use of conscious recognition memory or a conscious categorization strategy changes the neural systems that are involved in categorization [1,21,24]. Thus, the brain areas implicated in these studies may reflect more conscious categorization processing rather than categorization processing that depends on nonconscious category knowledge.

In order to identify the network of brain areas supporting nonconscious category learning, brain-wide activity during performance of the categorization task will be examined and contrasted with activity during a similar recognition memory task. This network can then be compared to networks that have been shown to support other nondeclarative category learning tasks, e.g., Poldrack et al. [18] (although this task depends more on the basal ganglia than the dot-pattern task). Comparisons can also be made to other studies of categorization to identify common areas of the brain involved in categorization decisions. The approach used here of comparing task-based activity is not expected to examine the changes in representation identified in previous studies that found stimulus-based changes in activity [1,23,24], it will identify the network of

areas necessary to drive behavior based on this representation of category knowledge.

1. Methods

1.1. Subjects

Ten healthy, right-handed volunteers (three women, seven men) gave written informed consent prior to participating in the study. Five participants received the categorization protocol and the other five received the recognition protocol.

Both the study and test portions of the behavioral paradigm were performed in the MRI scanner, but fMRI data were collected only during the test phase. A mirror was placed so that stimuli could be back-projected onto a viewing screen 3.5 m from the subject's head. The material on the screen subtended a visual angle of 5–7°. All responses were made via a fiber-optic button box in the participant's right hand.

1.2. Category learning

Participants ($n=5$) studied 40 dot-patterns one at a time (Fig. 1A). Each pattern was composed of nine white dots, constructed from an underlying prototype dot-pattern as described previously [12,19]. Specifically, each dot-pattern was a 'high distortion' of a single underlying prototype dot-pattern. Patterns were presented for 5 s, and volunteers imagined pointing to the center dot in the pattern in order to guarantee attention. Volunteers were not informed of the existence of a prototype.

After a short delay (~2 min), volunteers were told that the patterns had all belonged to a single category of patterns in the same sense that, if a series of dogs had been presented, they would all belong to the category 'dog.' Scanning then occurred while a categorization test consisting of 84 novel dot-patterns was presented. The test stimuli included four presentations of the prototype dot-pattern (P), 20 low-distortions of the prototype dot-pattern (L), 20 high-distortion dot-patterns (H), and 40 random patterns (R).

For each pattern, volunteers judged whether or not it came from the same category as the training patterns (a 'yes' response was correct for the P, L and H patterns; a 'no' response was correct for the random patterns). Each pattern was presented for 3.5 s. with a 500-ms inter-item interval. At the top of the display, a single word instruction 'Categorical?' was presented to remind the participants of the task (since the categorization task alternated with the Counting task described below). The categorization task
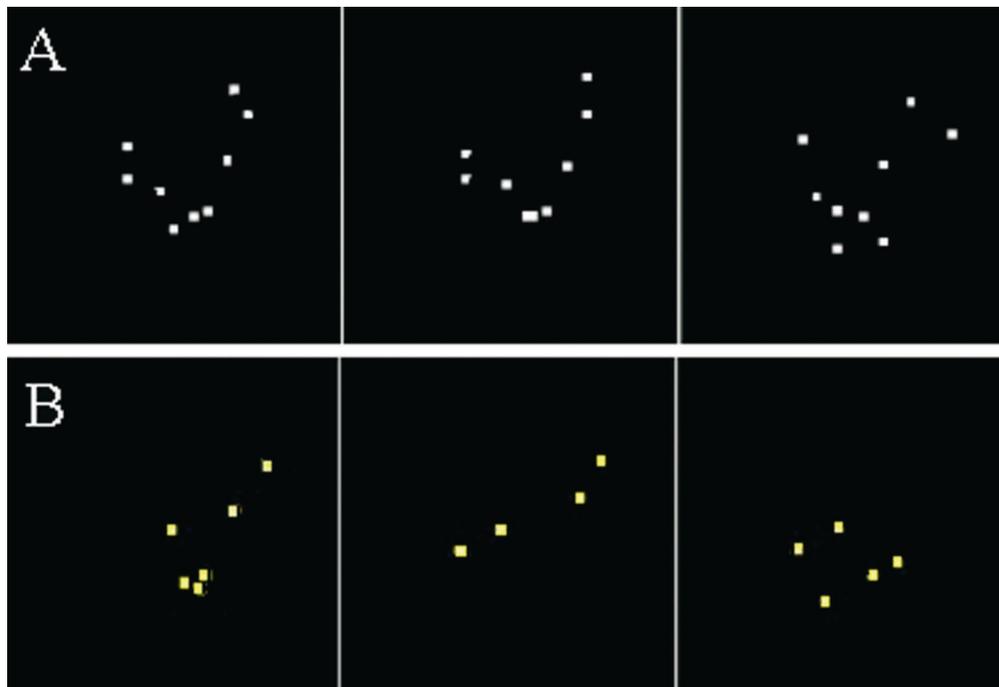

Fig. 1. Dot-pattern stimuli. (A) Example dot-patterns from the categorization task. The prototype pattern (P) that defines the category is shown at the left. At test low (L; middle) and high (H; right) distortions are shown as members of the category. The study phase consists of 40 high distortions. (B) Example pattern from the counting task. Participants are instructed to count the dots and indicate whether there is an odd or an even number of dots in the pattern. Yellow dots are used for this task to assist the participants in remembering which task they are performing.

was administered in 12 blocks (seven stimuli/block) across three separate scanning runs with short breaks (1–2 min) between each run.

1.3. Recognition

Participants ($n=5$; separate group from categorization) studied 40 dot-patterns one at a time. The 40 patterns consisted of eight repetitions of each of five target items. Each pattern contained nine white dots on a black background. In all other respects, this study phase was identical to the categorization test. After a short (~2 min) delay, scanning occurred while volunteers took an 84-item recognition memory test involving 42 novel patterns and 42 target patterns (each of the five dot-patterns that had been presented during study occurred either eight or nine times). Each pattern was presented for 3.5 s with a 500-ms inter-item interval. Volunteers were instructed to use the button box to respond 'yes' if the presented pattern had been seen during study and 'no' if the pattern was novel. A single word instruction was shown at the top of the screen 'Recognize?' to remind participants of the task (since it alternated with the Counting task described below). As in categorization, the recognition task was administered in 12 blocks (seven stimuli/block) across three separate scanning runs with short breaks (1–2 min) between each run.

1.4. Counting

As a control task, participants were shown patterns of four to seven dots and asked to count the dots and report 'yes'/'no' whether there was an odd number of dots shown. To identify this task separately from the categorization or recognition tasks, the dots were shown as yellow on the black background (instead of the white dots used in the other tasks, see Fig. 1). A single word instruction was shown at the top of the display, 'Odd?' to remind the participants to use the 'yes' response button for odd numbers of dots. Fifteen blocks of the counting task (seven stimuli/block) were performed across the three scanning runs.

1.5. Functional imaging

Imaging was performed on a GE 1.5T SIGNA clinical MRI scanner fitted with a high performance local head gradient and RF coils [36,37]. Functional T2*-weighted images were acquired using an echoplanar single-shot pulse sequence with a matrix size of 64×64, echo time (TE) of 40 ms, flip angle of 90°, and in-plane resolution of 3.75×3.75 mm. For each scanning run, 74 images were acquired for each of 20–22, 6-mm sagittal slices in an interleaved fashion with a repetition time (TR) of 3.5 s. The first two images from each slice were discarded to assure that the MR signal had reached equilibrium on each

slice. For anatomical localization, a whole-brain, T1-weighted, 3D MP-RAGE sequence (developed in-house for the GE scanner) was acquired (flip angle=10°, FOV=24 cm, $256\times256\times128$ acquisition matrix, coronal slices, thickness=1.3–1.4 mm).

Images were first corrected for distortion due to field inhomogeneity [25] and were co-registered through time using a 2D registration algorithm [6]. Each slice was spatially smoothed using a 2D (in-plane) Gaussian kernel, FWHM=7.5 mm. Linear drift in the overall magnitude of the MR signal over the course of the entire scan was eliminated in each voxel. Within each run, voxels were eliminated if their mean signal level was below a threshold defined by the inherent noise in the data acquisition or if the signal magnitude changed more than 10% between two samples (3.5 s). Voxels exhibiting sudden large signal magnitude changes were taken as indicative of motion and were eliminated. Runs in which more than 7% of the voxels with signal were eliminated were judged to be motion-contaminated and eliminated from further analysis (four of 30 total runs). One additional scanning run was lost due to operator error. The remaining 25 runs were transformed to conform to the atlas of Talairach and Tournoux (1988) with a final voxel size of 2.5 mm³ (MNI_autoreg; [5]).

Each run was first analyzed by comparing each voxel with a reference model reflecting the structure of the block design and accounting for an estimated 6 s delay in hemodynamic response to neural activity. The size of the signal change and correlation with the reference model was estimated in a general linear model (GLM) that also included models of low frequency structured noise (i.e., orthogonal polynomials up to order 3 to remove linear drift and other low frequency sources of noise). In the second stage of analysis, voxels were compared across the set of runs within each condition (treating each run from each participant as an independent sample) in order to identify consistent areas of significant change in activity. Each task was compared within-group to the counting control task and an additional 'double-subtraction' was performed across tasks in order to compare brain activity associated with recognition and categorization. The double-subtraction relies on the assumption that the level of activity evoked by the counting task was similar across groups, i.e., that there is no interaction between the counting task and the tasks of interest. This issue will be included in the discussion of those results below.

Statistical thresholds for identifying areas of significant change in activity were set for each analysis using monte-carlo simulations of normally distributed noise. While noise in fMRI data is not typically normally distributed, the bulk of the temporal autocorrelation comes from low frequency signal (i.e., the $1/f$ distribution described in [38]) and after removal of noise fit to a set of low-order orthogonal polynomials, normally distributed noise should

provide a reasonably good model for estimating false-positive rate. Noise data were matched to the observed mean and standard deviation in MR signal for each run of each subject in 10 full simulations of the data set. The noise data were analyzed using the same procedure as collected data (spatial smoothing, FWHM=7.5 mm, normalization to stereotactic space, etc.). By examining the rate of occurrence of clusters at various volumes given specific statistical thresholds, an estimation of the false positive (α) rate for one cluster at the specific threshold used across the dataset was obtained at a corrected P value of 0.01. The thresholds thus obtained were $t>5.00$ across a cluster of 390 mm^3 for the Categorization versus Counting and Recognition versus Counting analyses and $t>4.41$, across a cluster of at least 250 mm^3 for the double subtraction comparing Recognition and Categorization (which includes twice as many participants).

The cross-participants analysis model used here, in which each run is treated as an independent sample, improves slightly over traditional fixed effects analysis (in which each scan is treated as an independent sample) but still bears some risk that the group effects are driven disproportionately by a single subject and may not reflect consistent activity across all participants. To avoid limiting the generality of our findings, a third analysis stage was performed in which the regions exhibiting significant activity by the above thresholds were additionally examined in each participant within each group. For each participant, voxels within the regions identified in the group analysis were collapsed into a single time series, which was then re-analyzed using the GLM of the first stage of analysis and a single estimate of signal change was thus calculated for each participant for each region. If our results were driven by a subset of the participants within a group, the observed levels of activity in one or more of these regions would not be consistent across the five participants within each group by this random effects ROI analysis. This final analysis found that the regions identified in the first two-stage analysis reflected consistent activity across each group of participants and these results are reported below.

2. Results

2.1. Task performance

Behavioral data from one participant in the categorization condition was lost due to computer error. For the other four participants, categorization judgments were 64.2% ($\pm2.3\%$ S.E.) correct, significantly better than chance (50%; $t(3)=6.1$, $P<0.01$), indicating that the category was learned across the group. In the recognition condition, participants successfully identified old dot-patterns, performing 86.0% correct ($\pm4.7\%$ S.E.), also significantly better than chance (50%; $t(4)=7.6$, $P<0.01$). Performance

on the counting task was 96.0% ($\pm1.4\%$ S.E.) when alternating with recognition and 96.2% ($\pm1.5\%$ S.E.) when alternating with categorization. Neither accuracy nor reaction times (mean RT was 1706 ± 112 and 1820 ± 113 ms for the recognition and categorization groups, respectively) differed between the two groups on the counting task ($t(8)<0.8$)

During categorization judgments, participants took an average of 1551 ms (±61 ms S.E.) to make a response. Participants doing the recognition task took 1338 ms (±101 ms S.E.) for each response, non-significantly faster than the categorization decisions ($t(7)=1.71$, $P>0.13$). Across both groups, the counting task took longer to perform than the task of interest (combined across the recognition and categorization tasks), $t(8)=4.23$, $P<0.01$.

2.2. Categorization versus counting

Brain areas that exhibited significantly increased activity during categorization compared with the counting control task are shown in Fig. 2. The normalized atlas coordinates of the center of each of these clusters are listed in Table 1. Each of the 15 regions identified with the two-stage analysis additionally showed significantly increased activity in the random effects ROI analysis ($t(4)>3.76$, $P<0.02$) indicating that these regions exhibited consistent increases in activity across the group of five participants. Six areas were identified that exhibited increased activity during categorization compared with counting and also exhibited increased activity during recognition (see below). These areas likely reflect brain areas involved with processing the dot-patterns and making decisions about category or recognition memory. Since the reaction time to making counting decisions was generally longer than making a categorization decision, the extra activity observed in visual areas is not likely to be the result of longer visual processing, but additional cognitive processes engaged by the categorization (and recognition) tasks.

During categorization, additional activity was observed in nine areas that did not exhibit increased activity during recognition (also see the double-subtraction results below). In the frontal lobes, these areas included bilateral inferior prefrontal cortex, although the increased activity on the right side was of a much greater extent than the left (Table 1), as well as medial prefrontal cortex, and left frontopolar cortex. In addition, a left inferior parietal area exhibited increased activity, possibly the lateral match to the larger right inferior parietal cortical increase observed during both categorization and recognition. Two areas in left temporal cortex (middle and superior temporal gyri) also exhibited increased activity.

2.3. Recognition versus counting

Brain areas exhibiting significant increases in activity during recognition are shown in Figs. 3 and 4. The
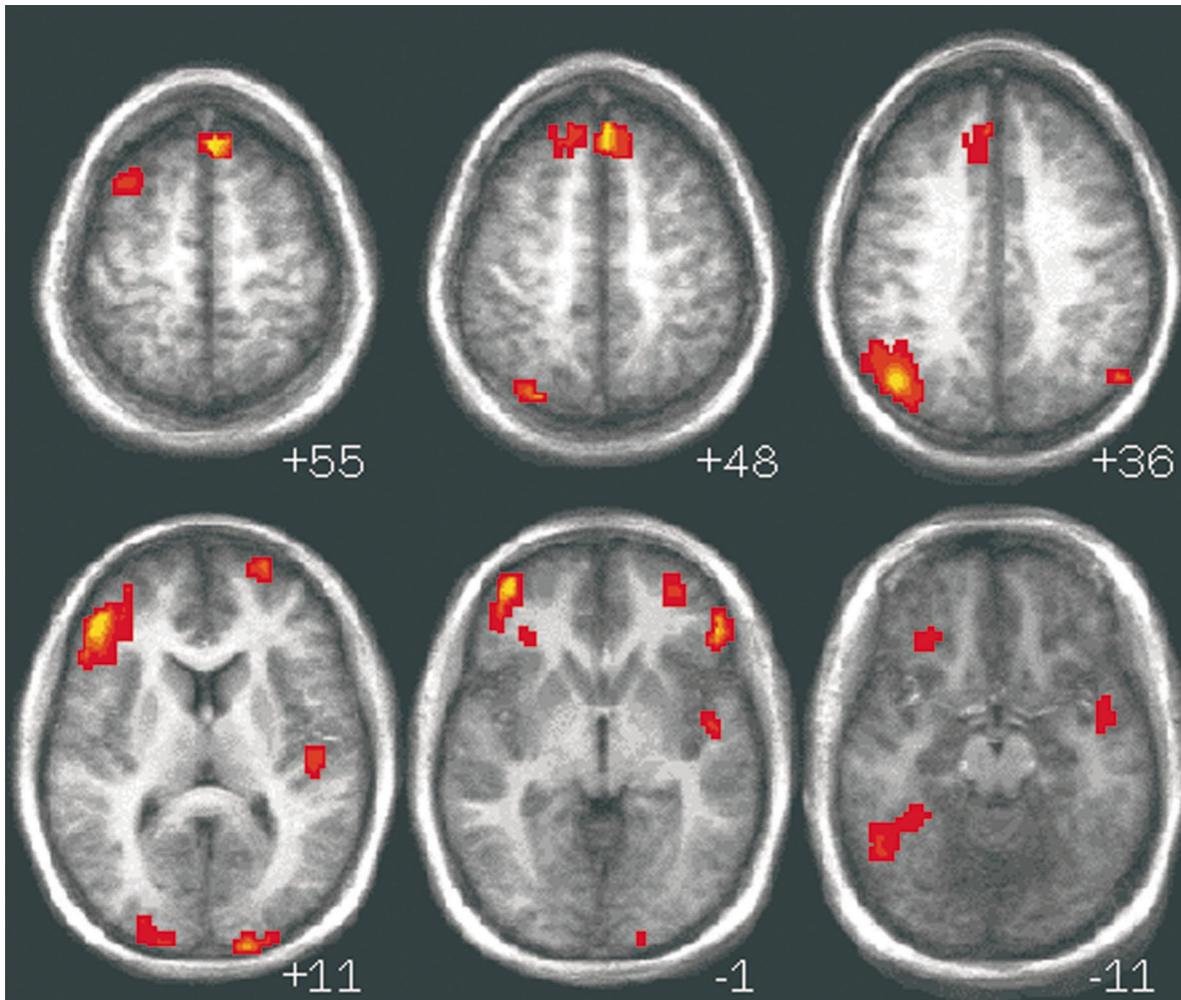
Fig. 2. Categorization>Counting. Areas that exhibited increased activity during categorization compared with counting are shown (see Table 2 for coordinates). Underlying anatomical images are axial images from high resolution structural images normalized to the Talairach atlas with the level (*z*) of each slice shown in the bottom right corner. Images are oriented according to the radiological convention with the right side of the brain on the left side of the image.

normalized atlas coordinates of the centers of these clusters are listed in Table 2. Each of the eight regions that were identified as exhibiting increase activity for recognition exhibited significantly increased activity across the five participants in the random effects ROI analysis ($t(4)>4.22$, $P<0.02$). As in categorization, increased activity was observed bilaterally in the inferior and middle occipital gyri (BA 18), in right inferior parietal cortex and in right ventral occipito-temporal cortex. Although the locations of these observed increases are similar, the extent of the BA 18 activations during recognition was considerably larger in recognition. In addition, during recognition extensive increases in activity were observed throughout the pre-cuneus bilaterally and the posterior cingulate. Two areas of increased activity were observed in the frontal lobes, in the right medial frontal gyrus and right dorsolateral prefrontal cortex (DLPFC).

2.4. Counting

A set of seven areas were identified that exhibited more activity during the counting task compared with categorization (listed in Table 3). No areas of significantly increased activity were observed during counting compared with recognition. The largest area of increased activity for counting compared with categorization included superior areas of pre-frontal cortex including the frontal eye fields (FEF). This increase in activity may be related to the eye movements involved with visual search through the pattern of dots in order to perform the count.

The areas associated with counting here probably indicate only a small fraction of the brain areas involved in this task since many areas may have exhibited increased activity in both the counting task and the alternating task of interest (categorization or recognition). The fact that the

Table 1
Talairach coordinates of areas exhibiting more activity during Categorization than counting

Brain area	Talairach coordinates (x, y, z)	Cluster size (mm³)
Areas in common with recognition of dot-patterns:		
Right parietal cortex BA 19/40	42, −69, 38	6484
Left middle occipital gyrus BA 18	−22, −98, 13	1906
Right middle occipital gyrus BA 18	18, −98, 15	922
Right superior frontal gyrus BA 6/8	33, 16, 57	969
Right precuneus	14, −60, 26	719
Right ventral occipito-temporal cortex BA 37	45, −51, −12	1812
Areas specific to categorization:		
Right inferior PFC BA 46	44, 43, 7	6406
Medial superior frontal gyrus BA 8	−5, 34, 51	2891
Medial middle frontal gyrus BA 8	10, 37, 43	2453
Left inferior PFC BA 47	−51, 39, −2	1641
Left fronto-polar cortex BA 10	−27, 61, 5	1406
Left middle temporal gyrus BA 21	−47, −2, −7	906
Left parietal cortex BA 19/40	−51, −69, 38	781
Left superior temporal gyrus BA 41	−47, −20, 10	516
Right inferior PFC BA 47	31, 33, −7	453

PFC, prefrontal cortex.

identified counting-related areas were different for categorization and recognition likely reflects different increases in activity during the tasks of interest rather than any specific differences in the activity associated with counting for the two groups.

2.5. Recognition versus categorization

Under the assumption that the brain activity associated with counting should be similar across the two groups (as found in the behavioral performance), a double subtraction was performed to compare activity associated with recognition and categorization. Seven areas were identified that exhibited significantly more activity during recognition than categorization (Table 4). These include two regions in the medial aspect of the precuneus, two occipital cortical areas, two areas in the cerebellum and a region of the posterior, right hippocampus. Many, but not all, of these areas exhibited increased activity during the recognition minus counting contrast, reflecting the fact that a slight increase relative to counting during recognition and a decrease (or no difference) relative to counting during categorization can result in a measurable difference be-

tween recognition and categorization. No areas were identified by this analysis for which categorization produced significantly greater activity than recognition (compared with counting). Because of the relatively low power inherent in this double subtraction, it should not necessarily be concluded that there are no areas exhibiting greater activity for categorization than recognition although no such areas were identified here.

3. Discussion

During categorization, increased activity was observed in several prefrontal cortical areas, including inferior PFC bilaterally, superior and middle frontal gyrus and left fronto-polar cortex when contrasted with counting. Both left fronto-polar (BA 10) and right inferior PFC were found to exhibit increased activity in the categorical minus random patterns comparison reported in Reber et al. [23] (although the right inferior PFC activity reported there was approximately 2 cm more posterior than the region reported here). This comparison across studies tentatively suggests that these areas may be more involved in cate-
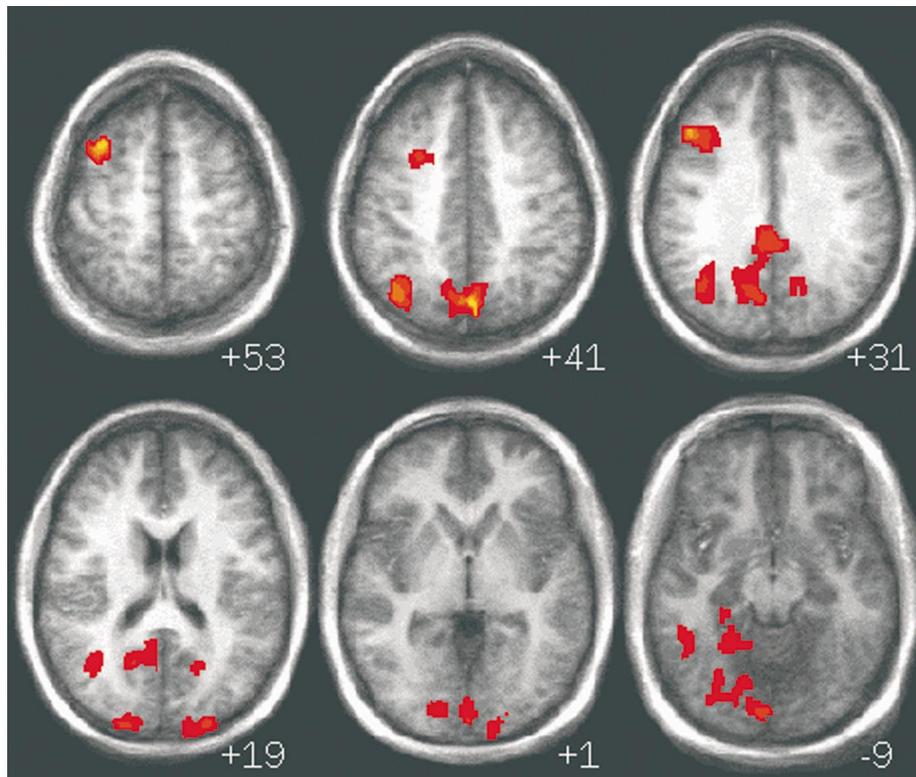
Fig. 3. Recognition>Counting. Areas that exhibited increased activity during recognition compared with counting are shown (see Table 3 for coordinates). Underlying anatomical images are axial images from high resolution structural images normalized to the Talairach atlas with the level (z) of each slice shown on the lower right of each image. Images are oriented according to the radiological convention with the right side of the brain on the left side of the image.

gorization success, since they were previously associated with increased activity for category members, while other areas may be more related to categorization effort. While this hypothesis would suggest more specific cognitive processes associated with these PFC areas in the network associated with categorization, an additional direct test is needed since (a) it is derived from an absence of increased activity in the other PFC areas in the Reber et al. [23] report and (b) Reber et al. [24] did not report any reliable increases in activity in PFC for categorical patterns compared with noncategorical patterns. Identification of brain areas associated with memory retrieval and success has been very effective in clarifying the role of PFC areas in the study of declarative memory. A similar approach may eventually be equally useful in understanding the role of PFC in nondeclarative memory.

The brain areas that exhibited increased activity for recognition compared with counting included several that generally showed increased activity in Reber et al. [24] in which recognition targets were compared with novel patterns. Although the previous report was more similar to previous reports examining retrieval success (e.g., Refs. [3,28]) while the current protocol identified brain areas associated with nonverbal retrieval, increased activity was observed in fairly early visual areas (R BA 18) and in higher-order visual areas (R BA 19/37) as well as right

DLPFC. The previous report identified a number of additional areas in PFC that exhibited increased activity for targets (retrieval success) that were not significantly activated here. The sizeable area of increased activity observed in the precuneus and posterior cingulate in the current report may have simply been approximately equally active for both recognition targets and new items in the previous report. Thus, the combination of the previous and current results provides a more complete picture of the brain areas associated with recognition of these nonverbal, abstract dot-patterns. Recognition of dot-patterns is supported by a network of brain areas including the precuneus, visual areas predominantly on the right side and right DLPFC. From Reber et al. [24], we can further suggest that when an old item is detected during recognition, additional areas of increased activity are observed, predominantly in the anterior PFC (BA 10).

The comparison between brain activity observed during recognition and categorization identifies a number of brain areas commonly associated with memory retrieval that exhibited more activity during recognition than categorization. Although the region exhibiting increased activity in the right posterior hippocampus for recognition is small, the role of the medial temporal lobe (including the hippocampus) in recognition memory is well-established (e.g., Ref. [26]). Increased activity in the hippocampus
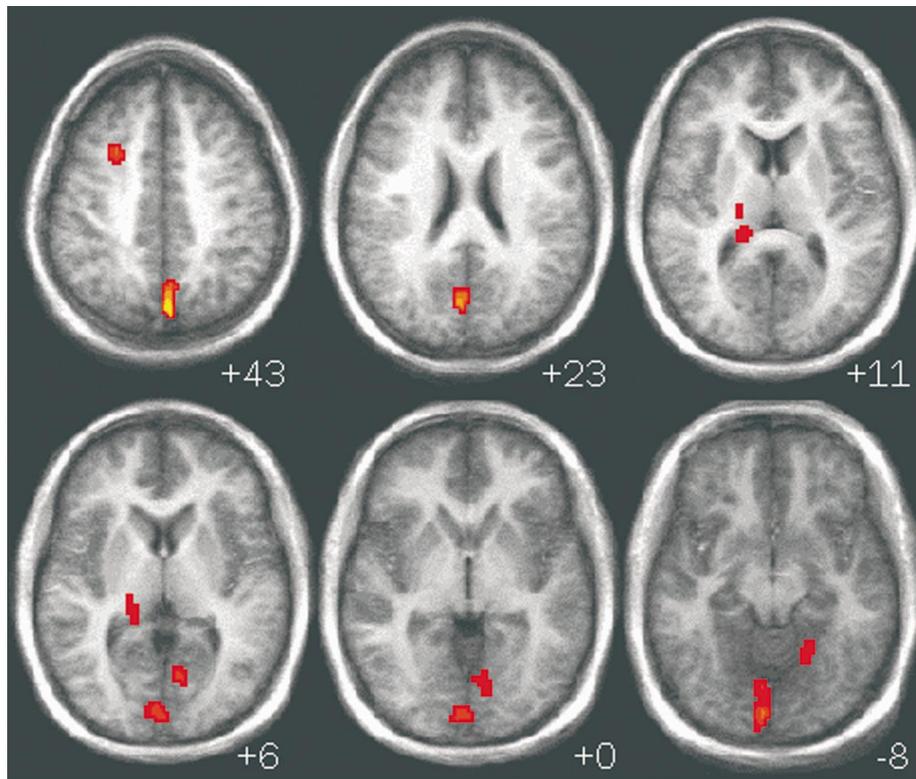
Fig. 4. Recognition>Categorization. Brain areas that exhibited increased activity for recognition compared with categorization by a double-subtraction analysis across the two groups of participants (under the assumption that counting activity was similar for the groups). The level of the axial image is noted at the lower right. Images are oriented according to the radiological convention with the right side of the brain on the left side of the image.

during retrieval has been reported in recent fMRI studies [7,33]. Several studies of memory retrieval have reported increased activity in the precuneus [9,14] suggesting that this area plays an important role in conscious retrieval processes. The role of the precuneus may be associated with imagery at retrieval [2,4,9,35]. However, a medial

Table 2
Talairach coordinates of areas exhibiting more activity during Recognition than counting

Brain area	Talairach coordinates	Cluster size (mm^3)
Large cluster spanning right precuneus, posterior cingulate (BA 31), posterior medial precuneus (BA 7) and left precuneus	15, −59, 20 (R pcu) 14, −62, 32 (R pcu) 3, −39, 32 (Post. cing.) 1, −74, 43 (M pcu) −10, −67, 35 (L pcu)	10 609
Right parietal cortex BA 19/40	37, −67, 40	4359
Right inferior/middle occipital gyrus BA 18	15, −83, −5	3438
Left inferior/middle occipital gyrus BA 18	−19, −98, 13	3406
Right parahippocampal gyrus BA 36	24, −46, −14	2328
Right medial frontal gyrus BA 6	34, 13, 50	1688
Right DLPFC BA 9/44	42, 21, 30	1391
Right inferior temporal gyrus BA 37	49, −46, −6	672

pcu, precuneus; Post. cing., posterior cingulate; DLPFC, dorsolateral prefrontal cortex; R, right; L, left; and M, medial.

Table 3

Talairach coordinates of areas exhibiting increased activity during counting compared with categorization

Brain area	Talairach coordinates (x, y, z)	Cluster size (mm^3)
Middle frontal gyrus BA 6/8	−8, 0, 61	7375
Left superior parietal cortex BA 7	−19, −55, 62	1875
Right caudate (tail)	18, −31, 22	938
Left middle frontal gyrus (DLPFC) BA 9	−34, 36, 33	719
Right caudate (tail)	16, −10, 27	531
Bilateral caudate	−1, 17, 8	469
Left middle frontal gyrus BA 6	−46, −5, 50	391

One area of increased activity during counting was observed during the recognition versus counting contrast but appeared to be within the left ventricle, suggesting it was an artifact of CSF or movement.

precuneus area, very close to the areas reported in Table 4, was found to exhibit increased activity [14] in retrieval tasks that did not require imagery at test. A network analysis of episodic retrieval [16] found that increased activity in occipital areas parallels increases in the precuneus. Whether in support of imagery specifically or more general retrieval processes, the increased precuneus and occipital cortical activity observed for recognition is likely to be part of the network supporting retrieval.

The fact that the contrast between recognition and categorization identifies activity in areas associated with conscious memory retrieval suggests that this cognitive process does not principally support the categorization task. The dot-pattern categorization task has been shown to depend on nonconscious, nondeclarative memory [12,32]. Because participants are frequently unaware of the category that has been learned, they are unlikely to be successfully consciously retrieving knowledge of the category in order to perform the task. Previous reports examining the representation of nondeclarative category knowledge using a stimulus-based contrast [23,24] indicate that category knowledge is associated with fluency in early visual areas for perception of category members. Here a

Table 4

Talairach coordinates of areas exhibiting more activity during Recognition than Categorization (double subtraction through the counting task)

Brain area	Talairach coordinates (x, y, z)	Cluster size (mm^3)
Medial precuneus	−4, −73, 43	1047
Medial occipital cortex BA 17	4, −87, 2	1000
Medial precuneus	4, −71, 22	656
Cerebellum	9, −68, −28	375
Left lingual gyrus BA 18	−9, −68, 4	344
Cerebellum	13, −52, −11	328
Right posterior hippocampus	17, −33, 9	297

broad network of areas was identified as active during categorization which represents the brain areas that are associated with evaluating dot-pattern stimuli, nonconsciously identifying category membership and translating this information into a yes/no response (even if this response seems to the participant to be made on the basis of a 'gut instinct'). The representation of category membership may be embedded in this fluency signal, but here we see the network of supporting areas required to perform the task.

While no difference in activity was observed in early visual areas during categorization compared with counting, the task-based contrast used here cannot identify the fluency effects reported earlier. The contrast with recognition provides indirect support for the fluency finding since recognition was associated with increased activity (compared with categorization) in the same early visual area that previously exhibited the fluency effect [23,24]. This difference likely reflects the lack of fluency effects observed in these early visual areas in [24] for both old and new items during recognition. If the categorical items are processed more fluently, then the average activity during categorization (fluent categorical patterns plus non-fluent random patterns; low activity+high activity) should be less than during recognition (non-fluent processing for both old and new patterns; high activity+high activity), as observed.

While the recognition versus counting subtraction alone did not identify increased activity in the MTL, the double subtraction between recognition and categorization suggested that the right posterior hippocampus is more active for recognition. This result suggests the possibility that there is a slight reduction in activity in the hippocampus during the categorization task, making the difference between recognition and categorization visible in spite of the relatively low power in this analysis. Reductions in hippocampal activity have been reported previously in a nondeclarative memory task based on categorization of sets of stimuli [18] and also in a nondeclarative skill-learning task [17]. The idea that reduced activity is observed in the MTL during a nondeclarative memory task compared with a baseline task suggests that there may be a process of disengaging the MTL during nondeclarative memory performance. A reduction in the role of the MTL during nondeclarative memory task is consistent with the neuropsychological findings that damage to this area of the brain does not impair these memory functions.

While the current results provide a contrast between the brain areas associated with nondeclarative category memory and conscious recognition, the activity associated with the categorization process is also comparable to a number of neuroimaging studies of categorization. Increased activity was observed here bilaterally in inferior PFC and similar increases were observed in Seger et al. [30], Poldrack et al. [18], Fletcher et al. [8] and the explicit learning condition in Aizenstein et al. [1]. Left inferior PFC has been

suggested to be associated with response selection within semantic memory [34], a process that may play an important role in making a difficult categorization decision. This left inferior PFC area has been reported as active in tasks of both conscious and nonconscious categorization tasks. While these tasks may differ critically in the representations that contribute to performance, there may also be common cognitive processes such as categorization-related decision making that are similar for both types of tasks. Other areas that may play a general role in categorization include bilateral inferior parietal cortex, which exhibited increased activity here and in the Seger et al. [30] study that also used abstract visual stimuli. Left fronto-polar cortex exhibited increased activity during categorization both here and in Poldrack et al. [18] and is another candidate area for processes that generally support categorization.

While increased activity is observed in several of the categorization studies in the precuneus and posterior visual areas, these increases are also highly associated with recognition memory. One of the challenges of imaging nondeclarative memory in healthy participants is the possibility that they may attempt to use conscious strategies during the testing phase, attempting to consciously remember study items or consciously learn during the test. However, conscious memory is unlikely to be contributing materially to task performance or else healthy participants would consistently outperform patients with memory disorders. If these conscious memory processes improved dot-pattern categorization performance, performance of healthy participants should reflect the contribution of both nondeclarative and declarative memory systems and be better than the performance of memory-impaired patients who must rely solely on nondeclarative memory. Here, the precuneus and posterior visual areas were found to be significantly more active during recognition than during categorization, suggesting that these areas may be more involved in conscious, declarative memory than nondeclarative categorization.

While previous neuroimaging studies have implicated fluency as an important mechanism supporting nondeclarative memory [23,24], the current results suggest that a network of inferior PFC and inferior parietal cortical areas are involved with expression of this categorization knowledge. Together these findings implicate a model in which changes in visual representations occur as a function of learning the category and the resultant processing changes are converted into behavioral task responses by a fronto-parietal network. Some elements of this fronto-parietal network appear to be involved in both conscious and nonconscious categorization decisions indicating that there may be some additional common cognitive components to categorization processing that are active for both types of categorization.

The dissociation between brain networks associated with dot-pattern categorization and recognition provides addi-

tional evidence that separate memory systems contribute to these tasks. Under the single system proposal of Nosofsky and Zaki [15], differences between these two processes should be limited to a small set of areas involved with setting decision criteria with the majority of other associated activity being similar. Instead, while there was a greater involvement of right DLPFC in recognition, there was also increased activity in posterior visual areas and the MTL, suggesting the greater involvement of the declarative medial temporal lobe memory system in recognition. The differential involvement of sensory cortical areas is consistent with the previous studies of dot-pattern categorization [1,23,24] that indicated different processing of stimuli during categorization and recognition. Together, these reports support the idea that there are separate neural systems with different types of processing supporting these two types of memory rather than the single system model proposed by Nosofsky and Zaki [15].

4. Conclusions

Previous reports have shown that nonconscious category knowledge is associated with fluency for perception of category members. The current study identifies a network of brain areas involved with performing categorization judgments that included bilateral inferior PFC and parietal cortex. A distinct network of brain areas was found to be associated for recognition judgments. Recognition judgments evoked increased activity in the medial temporal lobe, precuneus and posterior visual areas compared with categorization. Activity differences between the two tasks suggest that a declarative, conscious retrieval strategy supports the recognition of dot-patterns and that this strategy does not appear to be involved in performing the categorization task. The network of areas supporting categorization thus identifies brain areas involved with the expression of nonconscious memory, i.e., being able to successfully 'guess' category membership without conscious knowledge of what the category is. The differences in the patterns of brain activity associated with nondeclarative categorization and recognition support the idea that there are separate neural systems supporting these two kinds of memory rather than one system operating under different decision criteria.

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