

Recognition memory is modulated by visual similarity

Elena Yago and Alomit Ishai*

Institute of Neuroradiology, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland

Received 19 September 2005; revised 25 November 2005; accepted 15 December 2005

Available online 3 February 2006

We used event-related fMRI to test whether recognition memory depends on visual similarity between familiar prototypes and novel exemplars. Subjects memorized portraits, landscapes, and abstract compositions by six painters with a unique style, and later performed a memory recognition task. The prototypes were presented with new exemplars that were either visually similar or dissimilar. Behaviorally, novel, dissimilar items were detected faster and more accurately. We found activation in a distributed cortical network that included face- and object-selective regions in the visual cortex, where familiar prototypes evoked stronger responses than new exemplars; attention-related regions in parietal cortex, where responses elicited by new exemplars were reduced with decreased similarity to the prototypes; and the hippocampus and memory-related regions in parietal and prefrontal cortices, where stronger responses were evoked by the dissimilar exemplars. Our findings suggest that recognition memory is mediated by classification of novel exemplars as a match or a mismatch, based on their visual similarity to familiar prototypes.

© 2005 Elsevier Inc. All rights reserved.

Keywords: Category learning; Encoding; Faces; fMRI; Prototypes; Retrieval

Introduction

Learning about a new category of stimuli requires experience with multiple instances that define that category. It has been suggested that category knowledge emerges implicitly by acquiring information about prototypes (Posner and Keele, 1968; Fried and Holyoak, 1984), or explicitly by memory of the training items (Medin and Schaffer, 1978; Nosofsky, 1984; Hintzman, 1986). Intriguingly, amnesic patients who have impaired declarative memory, correctly classify test stimuli as categorical based on their similarity to learned stimuli, despite their inability to recognize these items. It therefore seems that category learning is independent of the medial temporal lobe structures implicated in declarative memory (Knowlton and Squire, 1993; Squire and

Knowlton, 1995). Nevertheless, it has been shown that amnesic patients are impaired in verbal category learning that requires the extraction of meaning from training exemplars, a process that depends on explicit memory (Kitchener and Squire, 2000). It therefore seems that the category learning ability of amnesic patients is limited to visually presented items, when the visual similarity between exemplars emerges instantaneously.

Inspired by the dissociation between the implicit acquisition of category knowledge and the explicit declarative memory for categorical instances, Reber and colleagues conducted a series of fMRI studies (Reber et al., 1998a,b, 2002, 2003) in which subjects viewed dot patterns that were distortions of an underlying prototype, then judged whether new dot patterns belong to that category. Behaviorally, subjects endorsed new items as categorical based on their similarity to the prototypes. Two patterns of brain activity were correlated with categorical items: reduced activation in occipital cortex and increased activation in prefrontal cortex, reflecting priming and memory retrieval, respectively (Reber et al., 1998a). A subsequent report showed that activation in occipital cortex was task-dependent: while implicit categorization was associated with reduced activity, explicit recognition memory resulted in increased activity (Reber et al., 1998b). Additionally, when the two tasks were contrasted, recognition evoked more activation than categorization in the precuneus and dorsolateral prefrontal cortex (Reber et al., 2002). Finally, implicit learning was compared with explicit learning of prototypes and the later was associated with increased activity in the hippocampus, precuneus, and regions in prefrontal cortex (Reber et al., 2003). In all these studies, the same low-level stimuli were presented during training and the test session begun a couple of minutes later. Subjects therefore relied on their short-term memory and had no time for consolidation. In these and other studies that used the dot patterns to investigate category learning (e.g., Vogels et al., 2002; Little et al., 2004), both low- and high-distortions of the prototypes were included in the test, however the new items were grouped in a block design and the activation evoked by different stimulus types was not analyzed. It is therefore unclear to what extent activation evoked by new exemplars depends on their visual similarity to familiar prototypes. Finally, despite the apparent dissociation between tasks (categorization versus recognition) and learning strategy (implicit versus explicit), inspection of the statistical maps

* Corresponding author. Fax: +41 44 6353449.

E-mail address: ishai@hifo.unizh.ch (A. Ishai).

Available online on ScienceDirect (www.sciencedirect.com).

reveals activation in very similar cortical regions, suggesting that common neural substrates mediate category learning and recognition memory, consistent with previous predictions from behavioral studies (Nosofsky, 1991).

As category learning and recognition memory require matching novel items with stored ones, we hypothesized that both are mediated by activation in a distributed cortical network, and used event-related fMRI to test whether matching between novel exemplars and familiar prototypes depends on their visual similarity. Our experimental approach combined explicit category learning with a recognition memory task, and an original set of stimuli, namely portraits, landscapes, and abstract compositions by 6 painters with a unique style (e.g., faces with long neck by Modigliani, see Fig. 1). In the training session, subjects were told that paintings from each artist belonged to a category of paintings with a characteristic signature and were instructed to learn and memorize these prototypes. Four days later, in the test session, subjects were presented with the familiar prototypes and with new exemplars and indicated whether they had seen these pictures before. The new exemplars were either visually similar to the prototypes, somewhat similar (ambiguous), or different (Fig. 1). We predicted fast and accurate responses to the new, dissimilar exemplars, and slower, less accurate responses to the new, similar and ambiguous exemplars, due to their visual resemblance to the prototypes. Moreover, we predicted that activation in the visual cortex and in parietal and prefrontal regions would be modulated by the degree of visual similarity and expected reduced activity with decreased visual similarity between the new exemplars and the familiar prototypes.

Our results show that, on average, 72% of the prototypes were correctly recognized and that responses to the novel items were faster and more accurate with decreased similarity to the prototypes. In the visual cortex, the paintings evoked activation in face- and object-selective regions, where familiar prototypes

elicited stronger activation than the new exemplars. Consistent with our hypothesis, in the intraparietal sulcus and superior parietal lobule, responses evoked by new exemplars were reduced with decreased similarity to the prototypes. In memory-related areas, two patterns of activation were observed: in the caudate, insula, and anterior cingulate cortex, the familiar prototypes elicited stronger activation than the new items, whereas in the precuneus, superior temporal and superior frontal gyri the new, visually different exemplars evoked stronger activation. Finally, in the hippocampus, the similar items evoked weaker activation than the other novel exemplars. Our findings suggest that recognition memory is mediated by activation in a cortical network that includes regions in visual cortex where stimulus-specific representations are stored, attention-related areas where visual similarity to familiar prototypes is detected, and memory-related areas where new items are classified as a match or a mismatch based on their similarity to familiar prototypes.

Methods

Subjects

Fourteen normal, right-handed subjects (7 males, mean age 25 ± 4 years) with normal vision participated in the study. All subjects gave informed written consent for the procedure in accordance with protocols approved by the University Hospital. All subjects were unfamiliar with the stimuli and reported visiting art museums once a year or less.

Stimuli and tasks

Stimuli were displayed using Presentation (www.neurobs.com, version 9.13) and were projected with a magnetically shielded

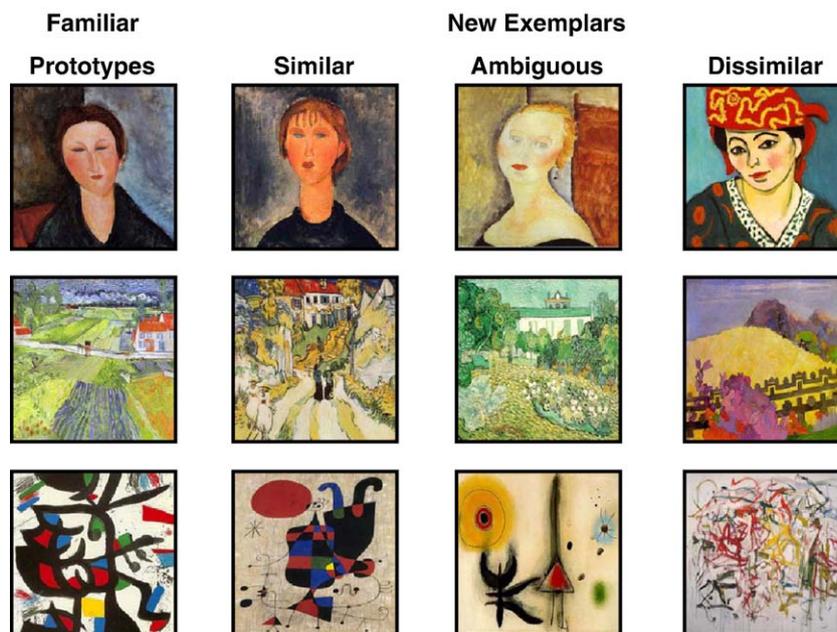


Fig. 1. Stimuli used in the experiment. Subjects memorized prototypes of portraits, landscapes and abstract paintings taken from six painters (shown from top to bottom are examples from Modigliani, Van Gogh and Miro). Four days later, in the memory retrieval session, the familiar prototypes were mixed with new exemplars that were visually similar, ambiguous or dissimilar, and subjects indicated whether they had seen each picture before. The degree of visual similarity between the prototypes and the new exemplars was assessed in a separate behavioral pilot (see Methods).

LCD video projector onto a translucent screen placed at the feet of the subject. During the encoding session, subjects were instructed to learn and memorize paintings (portraits by Modigliani and Renoir, landscapes by Pissarro and Van Gogh, abstract paintings by Kandinsky and Miro) and were explicitly told that the prototypes from each painter belong to a category of paintings with a unique style. Each run included prototypes from one painter and the order of the 6 runs was randomized across subjects. Each picture was presented on the center of the screen for 5 s and was repeated 4 times to enable deep encoding. Four days later, subjects performed a memory retrieval task in the MR scanner. In an event-related design, the 15 familiar prototypes from each painter were randomly presented with 45 new exemplars. The new pictures were either visually similar to the familiar prototypes, ambiguous, or dissimilar (Fig. 1). Each picture was presented for 3 s and subjects pressed a response button to indicate whether they had seen it before (“Yes” for the prototypes, “No” for the new exemplars).

The degree of visual similarity between the new exemplars and the prototypes was assessed in a separate behavioral pilot. Seven subjects (who did not participate in the fMRI experiment) rated the new pictures as visually similar, ambiguous, or dissimilar using a scale (0 = Dissimilar, 1 = Somewhat similar; 2 = Similar; 3 = Very similar). The mean ratings were: similar portraits: 2.29 ± 0.5 ; similar landscapes: 2.2 ± 0.5 ; similar abstract paintings: 2.1 ± 0.53 ; ambiguous portraits: 1.1 ± 0.65 ; ambiguous landscapes: 1.4 ± 0.8 ; ambiguous abstract paintings: 1.3 ± 0.6 ; dissimilar portraits: 0.27 ± 0.4 ; dissimilar landscapes: 0.47 ± 0.46 ; dissimilar abstract paintings: 0.26 ± 0.23 .

Each fMRI session included 6 recognition memory runs (one for each painter) and a visual baseline run in which subjects viewed portraits, landscapes and abstract paintings by various painters, and pressed a response button when a new picture appeared.

Data acquisition

Data were collected using a 3T Philips Intera whole body MR scanner (Philips Medical Systems, Best, The Netherlands). Changes in blood-oxygenation level-dependent MRI signal were measured by using sensitivity encoded gradient-echo echoplanar sequence (SENSE, Pruessmann et al., 1999) with 35 axial slices, TR = 3 s, TE = 35 ms, flip angle = 82° , field of view = 220 mm, acquisition matrix = 80×80 , reconstructed voxel size = $1.72 \times 1.72 \times 4$ mm, and SENSE acceleration factor $R = 2$.

High-resolution spoiled gradient recalled echo structural images were collected in the same session for all the subjects (180 axial slices, TR = 20 ms, TE = 2.3 ms, field of view = 220 mm, acquisition matrix = 224×224 , reconstructed voxel size = $0.9 \times 0.9 \times 0.75$ mm). These high-resolution anatomical images provided detailed anatomical information for the region-of-interest (ROI) analysis and were used for 3D normalization to the Talairach and Tournoux atlas (1998).

Data analysis

Accuracies and reaction times were computed for each subject, object category (portraits, landscapes, abstract paintings), and stimulus type (familiar prototype (P), and the new, similar (S), ambiguous (A) and dissimilar (D) exemplars). As familiar prototypes and new exemplars were presented with different probabilities (25% and 75%, respectively), we tested

whether subjects had any response biases by calculating the d' , a measure of sensitivity [$Z(\text{hit rate}) - Z(\text{false alarm rate})$, Macmillan and Creelman, 1991]. To calculate the d' for the familiar prototypes, the hit rate was computed as the proportion of trials in which familiar prototypes were correctly identified as “old”, and the false alarm rate was computed as the proportion of trials in which new exemplars were identified as “old”. The d' for the new exemplars was calculated by computing the hit rate for each type (S, A, D), namely the proportion of trials in which new exemplars were correctly identified as “new”. The false alarm rate was computed as the proportion of trials in which familiar prototypes were incorrectly identified as “new” and was therefore identical for the three types of new exemplars (S, A, D).

Pair-wise t tests were used to compare between correct recognition of prototypes of portraits, landscapes, abstract paintings. Additionally, to compare between correct recognition of the prototypes and the new exemplars, repeated-measures ANOVA was computed separately for portraits, landscapes and abstract paintings with stimulus type (P, S, A, or D) as factor.

Functional MRI data were analyzed in BrainVoyager QX Version 1.3 (Brain Innovation, Maastricht, The Netherlands). All volumes were realigned to the first volume, corrected for motion artefacts and spatially smoothed using a 5-mm FWHM Gaussian filter. Face- and object-selective responses in the visual cortex were analyzed using multiple regression (Friston et al., 1995) with the contrasts: portraits versus landscapes; portraits versus abstract paintings; and landscapes versus abstract paintings. Based on these contrasts, a set of ROIs was anatomically defined for each subject with clusters that showed a significant object category effect ($P < 0.01$, uncorrected). These regions included bilateral face-selective regions in the inferior occipital gyrus (IOG), lateral fusiform gyrus (LFG), and the superior temporal sulcus (STS); landscape-selective regions in posterior and medial fusiform gyri (PFG and MFG), the parahippocampal gyrus (PPA), and dorsal occipital cortex (DOC); and regions that responded more to abstract paintings in the inferior occipital gyrus (IOG), PFG and DOC.

To compare responses evoked by the familiar prototypes with responses evoked by the new exemplars, a general linear model was constructed with the four stimulus types (P, S, A, and D) as predictors. To test our hypothesis that recognition memory is modulated by the degree of visual similarity, we contrasted activation evoked by the prototypes and the new, similar exemplars with activation evoked by the new ambiguous and dissimilar items (P + S versus A + D). Based on this contrast, a set of ROIs was anatomically defined for each subject with clusters that showed a significant effect ($P < 0.01$, uncorrected), which included the precuneus, superior temporal gyrus (STG), intraparietal sulcus (IPS), superior parietal lobule (SPL), caudate, anterior cingulate cortex (ACC), insula, inferior frontal gyrus (IFG), and superior frontal gyrus (SFG). Additionally, the hippocampus was anatomically defined in subjects who showed significant activation ($P < 0.05$, uncorrected) when the response to the new, similar exemplars was contrasted with the response to the dissimilar ones (S versus D).

In each subject and each ROI, the mean parameter estimates were calculated separately for each stimulus type (P, S, A and D) in all correct trials and were used for between-subjects random-effects analyses. Separate repeated measures ANOVAs analyzed the effect of stimulus type in each region and each hemisphere.

Results

Behavioral data

While in the scanner, subjects were presented with the familiar prototypes and novel exemplars, and indicated whether they had seen each picture before (correct responses were YES for the prototypes and NO for the novel exemplars). Prototypes of portraits were recognized more accurately (89%) and faster (mean reaction time 1070 ms) than landscapes (65%, $t_{13} = -8.1$, $P < 0.00001$; 1384 ms, $t_{13} = 12.3$; $P < 0.0000001$) and abstract paintings (59%, $t_{13} = 11.3$; $P < 0.0000001$; 1433 ms, $t_{13} = -9.1$; $P < 0.000001$), but the differences between landscapes and abstract paintings were not statistically significant (Table 1). Fig. 2 shows the behavioral responses to the familiar prototypes and the novel exemplars. Subjects responded more accurately and faster to the new, dissimilar exemplars than to the familiar prototypes (portraits: $F_{1,13} = 14.4$, $P < 0.01$, $F_{1,13} = 28.9$, $P < 0.001$; landscapes: $F_{1,13} = 44.6$, $P < 0.0001$, $F_{1,13} = 23.9$, $P < 0.001$; abstract paintings: $F_{1,13} = 157.5$, $P < 0.0000001$, $F_{1,13} = 54.9$, $P < 0.00001$, for accuracy and reaction time, respectively). Similarly, subjects responded more accurately to the new, ambiguous exemplars than to the familiar prototypes (portraits: $F_{1,13} = 11.6$, $P < 0.01$; landscapes: $F_{1,13} = 24.2$, $P < 0.001$, abstract paintings: $F_{1,13} = 137.2$, $P < 0.0000001$). Additionally, the response to the new, ambiguous abstract paintings was significantly faster than the response to the familiar ones ($F_{1,13} = 10.3$, $P < 0.01$). Interestingly, there were no differences in terms of accuracy between the familiar portraits and the novel, similar ones, however the response to these similar exemplars was significantly slower ($F_{1,13} = 9.7$, $P < 0.01$). For both landscapes and abstract paintings, subjects responded to the new, similar items more accurately than to the familiar prototypes ($F_{1,13} = 18.8$, $P < 0.001$; $F_{1,13} = 35.4$, $P < 0.0001$, respectively), however the difference in reaction times was not statistically significant.

To test whether subjects had any response biases, we calculated the d' (see Methods). As shown in Fig. 2, the discriminability of the prototypes was different from the discriminability of the new exemplars. New, dissimilar portraits, landscapes and abstract paintings had the highest d' values ($t_{13} = -6.6$, $P < 0.0001$; $t_{13} = -4.6$, $P < 0.001$; $t_{13} = -8.01$, $P < 0.0001$, respectively), confirming our hypothesis that detection of these visually different items would be very accurate. Moreover, the d' values of the ambiguous exemplars of portraits and abstract paintings were higher than those of the prototypes ($t_{13} = -4.4$, $P < 0.001$; $t_{13} = -4.8$, $P < 0.001$, respectively). Interestingly, the d' values of new, similar landscapes and abstract paintings did not differ from those of the prototypes, but the similar portraits had lower d' values than the prototypes ($t_{13} = 2.38$, $P < 0.05$). Taken together, these differential responses suggest that our subjects did not have a general response bias for the more frequent new exemplars, but, rather,

that recognition memory was modulated by the degree of visual similarity.

Imaging data

Activation in the visual cortex

To identify face- and object-selective regions in the visual cortex, we contrasted activation evoked by portraits with activation evoked by landscapes or abstract paintings, and landscapes with abstract paintings. Portraits activated bilaterally face-selective regions in the inferior occipital gyrus (IOG), lateral fusiform gyrus (LFG) and the superior temporal sulcus (STS). Landscapes activated bilaterally 'house'- and 'place'-selective regions in posterior and medial fusiform gyri (PFG and MFG), the parahippocampal gyrus (PPA), and dorsal occipital cortex (DOC). Abstract paintings evoked activation bilaterally in PFG, DOC, and in the left IOG (Table 2).

Fig. 3 shows the differential activation evoked by portraits in the LFG, landscapes in the DOC and MFG, and abstract paintings in the PFG. In the LFG, the familiar prototypes of portraits evoked stronger activation than the new exemplars ($F_{1,10} = 19.54$, $P < 0.001$). In both the MFG and the PPA, similar activation was evoked by the familiar prototypes and the new exemplars of landscapes and the differences between the stimulus types were not statistically significant. In the PFG, the familiar prototypes of abstract paintings evoked stronger activation as compared with the novel exemplars ($F_{1,11} = 8.3$, $P < 0.05$). Finally, significant clusters of activation were found in dorsal occipital cortex, where both landscapes and abstract paintings showed stronger responses than portraits. In the DOC the familiar prototypes of abstract paintings elicited stronger activation than the novel exemplars ($F_{1,6} = 6.34$, $P < 0.05$), but no differences were found between prototypes and the new exemplars of landscapes.

Task-related activation

To test whether recognition memory is modulated by the degree of visual similarity between the new exemplars and the familiar prototypes, we contrasted activation evoked by the prototypes and the new, visually similar exemplars with activation evoked by the ambiguous and dissimilar exemplars (P + S versus A + D). This contrast revealed significant activation in multiple regions, including the intraparietal sulcus (IPS), superior parietal lobule (SPL), insula, anterior cingulate cortex (ACC), caudate, precuneus, superior temporal gyrus (STG), inferior and superior frontal gyri (IFG and SFG), and the hippocampus (Table 3). We grouped together regions that showed similar patterns of activation to the different stimulus types.

Activation in attention-related regions

Consistent with our hypothesis, in the IPS and the SPL, regions implicated in many attention tasks, we found decreased activation

Table 1
Recognition of familiar prototypes

	Modigliani	Renoir	Pissarro	Van Gogh	Kandinsky	Miro
Accuracy (%)	92 ± 2.7	87 ± 3.4	67 ± 4.5	63 ± 5.6	52 ± 4.7	69 ± 3.1
RT (ms)	1036 ± 32.9	1103 ± 38.1	1407 ± 44.9	1360 ± 51.9	1493 ± 68.3	1373 ± 59.2

Accuracy and reaction times (mean ± SEM) were averaged across all subjects. Prototypes of portraits (Modigliani and Renoir) were recognized more accurately and faster than prototypes of landscapes (Pissarro and Van Gogh) and abstract paintings (Kandinsky and Miro).

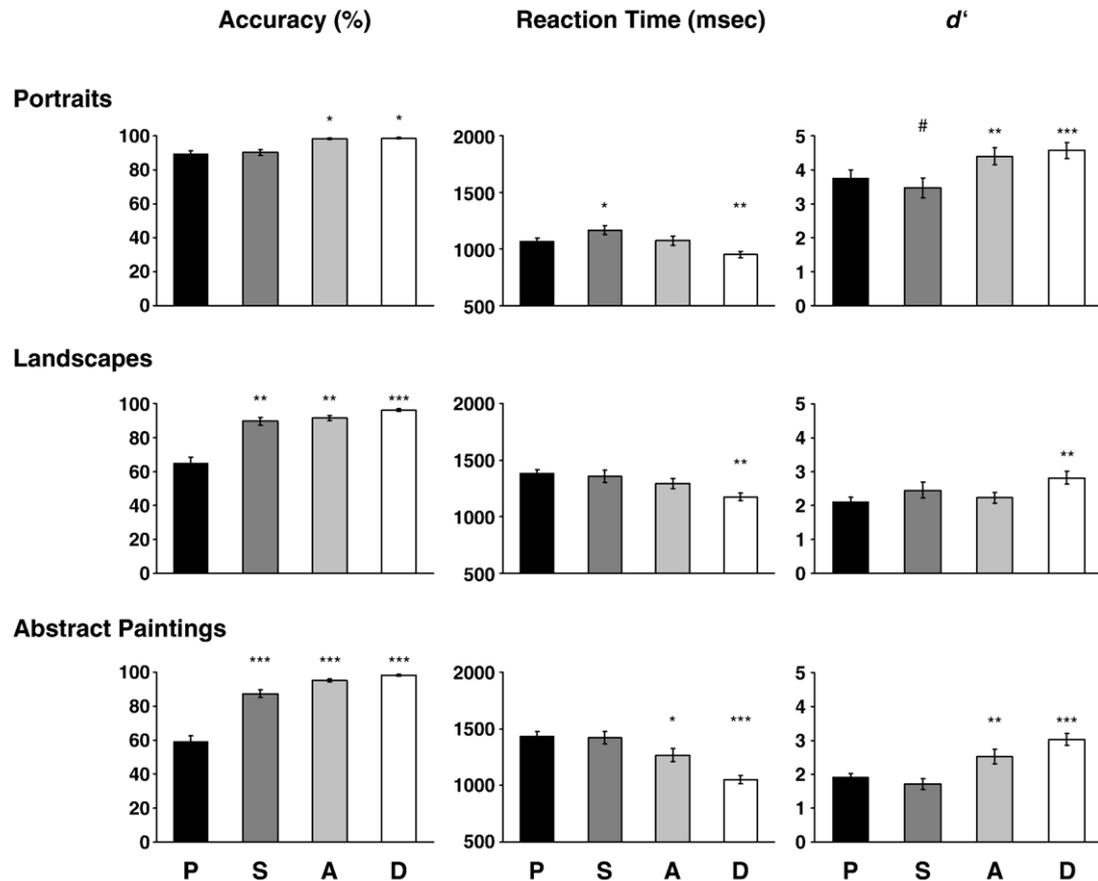


Fig. 2. Behavioral data. Mean accuracies (left), reaction times (middle), and d' values (right) averaged across all subjects. Accuracies and reaction times are shown for correct trials only. P = familiar Prototypes, S = new, Similar, A = new, Ambiguous, D = new, Dissimilar exemplars. Asterisks show the level of significance between responses to the familiar prototypes and the new exemplars ($^{\#}P < 0.05$; $*P < 0.01$; $**P < 0.001$; $***P < 0.0001$). In this and subsequent figures, error bars indicate standard error of the mean (SEM).

with decreased visual similarity between the prototypes and the novel exemplars (Fig. 4). In the IPS, the familiar prototypes of portraits, landscapes and abstract paintings elicited stronger activation as compared with the novel, similar ($F_{1,4} = 79.1$, $P < 0.001$), ambiguous ($F_{1,4} = 190.8$, $P < 0.001$) and dissimilar exemplars ($F_{1,4} = 70.3$, $P < 0.01$) in both hemispheres. Moreover, the new, similar exemplars evoked stronger activation than the ambiguous ($F_{1,4} = 6.3$, $P < 0.05$) and dissimilar exemplars ($F_{1,4} = 29.1$, $P < 0.01$). Similar patterns of activation were observed in the SPL. In both hemispheres, familiar prototypes evoked stronger activation than new, similar ($F_{1,10} = 60.8$, $P < 0.0001$), ambiguous ($F_{1,10} = 272.9$, $P < 0.0000001$) and dissimilar ($F_{1,10} = 190.1$, $P < 0.0000001$) exemplars. Reduced activation with decreased visual similarity between the prototypes and the new exemplars was also significant (similar vs. ambiguous: $F_{1,10} = 18.1$, $P < 0.01$; ambiguous vs. dissimilar: $F_{1,10} = 7.7$, $P < 0.05$; similar vs. dissimilar: $F_{1,10} = 56.4$, $P < 0.0001$).

Activation in memory-related regions

Contrasting the response to familiar prototypes and new similar exemplars with the response to ambiguous and dissimilar ones (P + S vs. A + D) revealed two patterns of activation in memory-related regions. In the caudate, insula and ACC, stronger activation was evoked by the prototypes as compared with the new exemplars, whereas in the precuneus, STG and SFG, stronger responses were

elicited by the new, visually different exemplars, namely the ambiguous and dissimilar ones.

In the caudate, insula and ACC, stronger activation was evoked by the familiar prototypes as compared with the new exemplars (Fig. 5). In the caudate, the prototypes evoked stronger activation than all new exemplars (prototypes vs. similar: $F_{1,6} = 171.9$; $P < 0.0001$; prototypes vs. ambiguous: $F_{1,6} = 327.3$; $P < 0.00001$; prototypes vs. dissimilar: $F_{1,6} = 262.9$; $P < 0.00001$) in both hemispheres. Similarly, in the insula, the prototypes evoked significantly stronger activation than the similar ($F_{1,4} = 135.3$, $P < 0.001$), ambiguous ($F_{1,4} = 122.7$, $P < 0.001$), and dissimilar exemplars ($F_{1,4} = 413.7$, $P < 0.0001$) in both hemispheres. Finally, in the ACC, stronger activation was elicited by the prototypes as compared with the similar ($F_{1,7} = 45.9$, $P < 0.001$), ambiguous ($F_{1,7} = 314.8$, $P < 0.000001$) and dissimilar ($F_{1,7} = 102.1$, $P < 0.0001$) exemplars.

In the precuneus, STG and SFG, the novel, visually different exemplars evoked stronger activation than the prototypes and the new, similar exemplars (Fig. 6). In the precuneus, response to ambiguous and dissimilar exemplars was stronger than the response to the prototypes ($F_{1,5} = 167.6$, $P < 0.0001$; $F_{1,5} = 21.9$, $P < 0.01$; respectively) and the similar exemplars ($F_{1,5} = 8.5$, $P < 0.05$; $F_{1,5} = 34.2$, $P < 0.01$; respectively). Similarly, in the STG stronger activation was evoked by the ambiguous items than by the prototypes ($F_{1,2} = 42.5$; $P < 0.05$) and the similar exemplars

Table 2
Face- and object-selective responses in the visual cortex

Region	N	Volume (cm ³)	x	y	z
		Mean ± SEM	Mean ± SEM	Mean ± SEM	Mean ± SEM
<i>Portraits</i>					
L IOG	11	7.1 ± 1.0	-39 ± 1.0	-67 ± 2.1	-17 ± 1.2
R IOG	12	6.7 ± 1.0	39 ± 0.9	-69 ± 2.5	-12 ± 2.4
L LFG	12	6.9 ± 1.1	-36 ± 1.6	-49 ± 1.9	-18 ± 0.8
R LFG	13	7.3 ± 0.8	38 ± 1.1	-46 ± 1.4	-16 ± 2.6
L STS	6	4.8 ± 1.7	-45 ± 3.2	-49 ± 4.9	8 ± 2.7
R STS	7	1.8 ± 1.1	45 ± 1.5	-42 ± 2.6	12 ± 2.9
<i>Landscapes</i>					
L DOC	11	7.7 ± 1.4	-29 ± 1.4	-82 ± 1.1	8 ± 2.5
R DOC	10	9.6 ± 1.2	32 ± 1.2	-80 ± 1.3	11 ± 1.8
L PFG	13	8.9 ± 1.0	-19 ± 1.4	-76 ± 1.3	-16 ± 2.1
R PFG	14	9.8 ± 0.7	18 ± 1.5	-75 ± 1.3	-10 ± 2.8
L MFG	12	8.4 ± 0.9	-23 ± 1.6	-56 ± 2.1	-11 ± 1.4
R MFG	14	9.9 ± 0.5	25 ± 0.9	-54 ± 2.1	-9 ± 1.0
L PPA	10	4.9 ± 1.1	-21 ± 1.0	-42 ± 2.0	-9 ± 1.2
R PPA	12	6.1 ± 1.0	24 ± 1.3	-39 ± 1.0	-7 ± 1.1
<i>Abstract Paintings</i>					
L DOC	9	8.8 ± 1.1	-25 ± 1.6	-84 ± 1.8	6 ± 2.6
R DOC	8	9.2 ± 1.3	26 ± 2.5	-85 ± 2.4	7 ± 1.8
L PFG	12	9.2 ± 0.8	-19 ± 1.7	-77 ± 0.6	-14 ± 3.0
R PFG	14	9.1 ± 0.9	18 ± 1.5	-76 ± 1.0	-13 ± 1.5
L IOG	6	4.4 ± 1.6	-40 ± 1.0	-75 ± 2.0	-14 ± 3.4

Regions were identified by contrasting faces vs. landscapes, faces vs. abstract paintings, and landscapes vs. abstract paintings. Significant clusters ($P < 0.01$, uncorrected) were selected for each subject. N indicates the number of subjects who showed significant activation in each region. Volumes were calculated before spatial normalization. Coordinates are in the normalized space of the Talairach and Tournoux atlas. L: Left, R: Right.

(left hemisphere: $F_{1,6} = 17.9$, $P < 0.01$). Activation evoked by dissimilar exemplars was stronger than activation evoked by the prototypes ($F_{1,2} = 19.8$, $P < 0.05$) and by the similar exemplars ($F_{1,2} = 76.5$, $P < 0.05$). Finally, similar patterns of activation were found in the SFG, where ambiguous and dissimilar exemplars evoked stronger activation than the prototypes ($F_{1,3} = 63.7$, $P < 0.01$; $F_{1,3} = 59.7$, $P < 0.01$, respectively), and the similar exemplars ($F_{1,3} = 8.9$, $P < 0.05$; $F_{1,3} = 48.5$, $P < 0.01$, respectively).

In the hippocampus (Fig. 7), novel, similar exemplars evoked less activation than the familiar prototypes ($F_{1,4} = 40.6$, $P < 0.01$), ambiguous ($F_{1,4} = 17.8$, $P < 0.05$) and dissimilar exemplars ($F_{1,4} = 20.7$, $P < 0.05$) in both hemispheres.

Discussion

We investigated the neural correlates that mediate recognition memory of portraits, landscapes, and abstract paintings. The behavioral data showed that most of the familiar prototypes were correctly recognized and that responses to the new exemplars depended on their visual similarity to the prototypes. Consistent with our hypothesis, subjects responded faster and more accurately to the visually different exemplars, and longer latencies were associated with the novel, similar portraits, probably due to their visual resemblance to the prototypes. Moreover, we found activation in a distributed cortical network that included regions in visual, parietal and prefrontal cortices, where responses evoked

by new exemplars were modulated by their visual similarity to familiar prototypes.

Perception of portraits, landscapes and abstract paintings evoked activation in face- and object-selective regions in the visual cortex. In the lateral fusiform gyrus, a face-responsive region (Kanwisher et al., 1997), portraits elicited stronger activation than landscapes and abstract paintings. In the medial fusiform and parahippocampal gyri, regions that respond to houses and places, respectively (Aguirre et al., 1998; Epstein and Kanwisher, 1998), landscapes evoked stronger activation than portraits and abstract paintings. In the posterior fusiform gyrus, abstract paintings evoked stronger activation than portraits and landscapes, consistent with a report about the perception of beauty of various paintings (Kawabata and Zeki, 2004). Finally, landscapes and abstract paintings evoked stronger responses than portraits in dorsal occipital cortex. Previous findings have shown that man-made objects, but not faces, evoke activation in this region, presumably reflecting part-based processing, as the spatial arrangements of the parts of non-face objects are more variable (Ishai et al., 1999, 2000a). Within these face- and object-selective regions, familiar prototypes of portraits and abstract paintings evoked stronger responses than the new exemplars. Similar findings of increased activity in the visual cortex for categorical items were found when subjects performed recognition tasks (Reber et al., 1998b), however, categorization after implicit learning evoked decreased activity in the visual cortex, suggesting priming or “categorical fluency effect” (Reber et al., 1998a, 2003). It is of interest that enhanced responses to the prototypes were observed for portraits and abstract paintings, but not for landscapes. The landscapes contained scenes with multiple objects (e.g., houses, bridges, trees, flowers), and post-scanning debriefing revealed that subjects memorized the landscapes by focusing attention on one object within the scene, thus using a different encoding strategy. Taken together, the patterns of activation observed in the visual cortex indicate that explicit encoding of categorical paintings results in stimulus-specific representations. These findings are consistent with numerous visual imagery (Ishai et al., 2000b; Mechelli et al., 2004), working memory (Druzgal and D’Esposito, 2003) and associative memory retrieval (Ranganath et al., 2004) studies that showed stimulus-specific memory traces in the human visual ventral stream.

Activation in attention-related regions, namely the IPS and the SPL, revealed that stronger responses were evoked by the familiar prototypes than by the new exemplars of portraits, landscapes and abstract paintings. Moreover, confirming our hypothesis, activation within these regions was reduced with decreased similarity between the new exemplars and the prototypes. The IPS and the SPL, regions of the dorsal frontoparietal attention network, were implicated in many cognitive studies of attention. In particular, both regions were activated in target detection tasks (Corbetta et al., 2000; Shulman et al., 2001; Kincade et al., 2005). In our task, the familiar prototypes, for which the correct response was “Yes, I had seen these pictures before,” were mixed with new, never seen before exemplars. It is highly likely that subjects were searching for and detecting these familiar paintings as “targets”. We observed shorter reaction times and decreased amplitudes of the fMRI signal with decreased similarity to the prototypes. The enhanced activation evoked by the prototypes and the reduced activity elicited by the visually different exemplars suggest that the IPS and SPL process the segmentation of old from new items (Pollmann et al., 2003). Thus, recognition of familiar prototypes

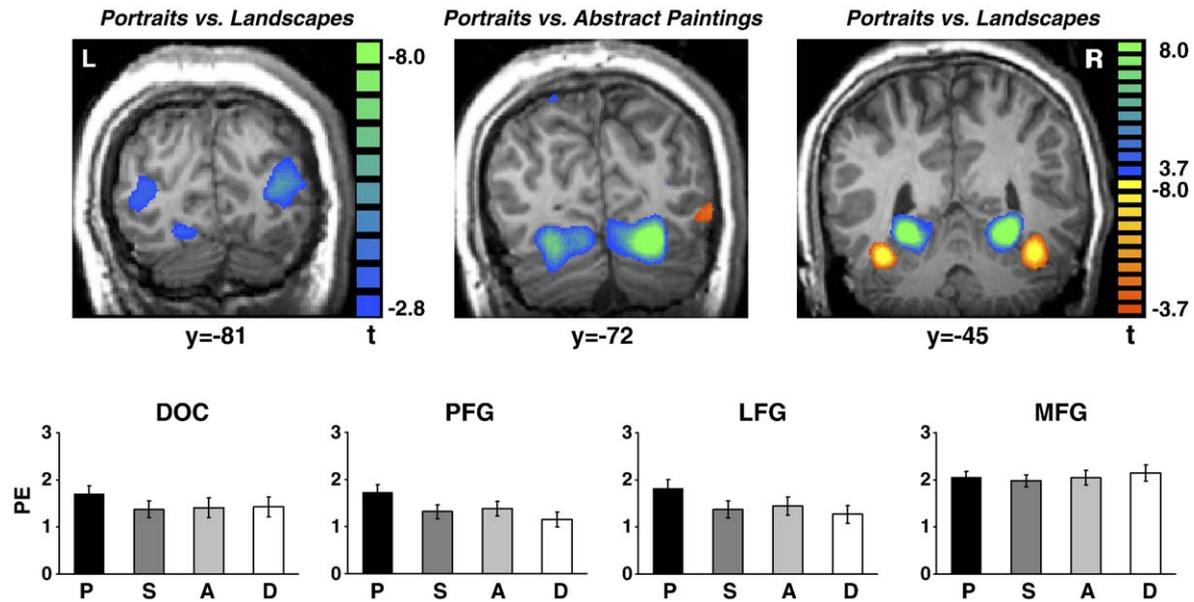


Fig. 3. Activation in the visual cortex evoked by portraits, landscapes and abstract paintings. Top: from left to right, coronal sections illustrating activation in DOC evoked by landscapes (slice taken from one subject, $P < 0.05$); activation in the PFG evoked by abstract paintings; activation in the LFG and MFG evoked by portraits and landscapes, respectively (group statistical map, $P < 0.00005$). Bottom: mean parameter estimates averaged across all subjects and both hemispheres. P = familiar Prototypes, S = Similar, A = Ambiguous, D = Dissimilar exemplars.

and target detection seem to be mediated by similar neural correlates within the attentional network. Numerous recognition memory studies have further shown that posterior parietal cortex does not merely ‘detect old items’ but, rather, mediates higher order cognitive processes associated with memory retrieval (Konishi et al., 2000; Wheeler and Buckner, 2003; Shannon and Buckner, 2004). Three hypotheses have been recently suggested to account for the role of posterior parietal cortex in memory retrieval:

attention to internal mnemonic representations; accumulation of sensory signals in order to reach a decision; and a memory buffer for stored information (see Wagner et al., 2005).

It has been suggested that category learning can be divided into rule-based, information-integration, and prototype-distortion tasks, each mediated by a specialized memory system (Ashby and O’Brien, 2005). Our task, namely explicit encoding and recognition of prototypes of paintings, revealed activation in

Table 3
Task-related activation

Region	N	Volume (cm ³)			
		Mean ± SEM	x Mean ± SEM	y Mean ± SEM	z Mean ± SEM
<i>Attention</i>					
L SPL	12	10.7 ± 0.7	-24 ± 1.9	-66 ± 2.3	49 ± 1.7
R SPL	11	8.3 ± 1.2	24 ± 1.7	-64 ± 1.6	48 ± 1.8
L IPS	9	9.7 ± 1.3	-30 ± 1.4	-52 ± 1.3	44 ± 2.7
R IPS	5	8.6 ± 1.7	32 ± 2.5	-50 ± 2.3	42 ± 3.6
<i>Memory</i>					
M Precuneus	6	5.1 ± 1.7	1 ± 1.8	-64 ± 2.0	24 ± 1.9
L STG	7	4.7 ± 1.2	-47 ± 1.4	-50 ± 2.4	13 ± 1.7
R STG	5	7.1 ± 2.1	46 ± 3.9	-52 ± 2.4	16 ± 2.9
L Hippocampus	7	38.6 ± 6.3	-26 ± 1.1	-18 ± 0.7	-12 ± 0.4
R Hippocampus	8	25.1 ± 1.3	27 ± 0.7	-18 ± 0.5	-8 ± 2.9
L Caudate	7	3.7 ± 0.9	-7 ± 0.5	5 ± 1.5	10 ± 1.3
R Caudate	8	4.8 ± 1.3	10 ± 0.5	7 ± 1.5	11 ± 1.3
L IFG	4	4.2 ± 0.6	-43 ± 2.3	11 ± 2.7	26 ± 3.1
L Insula	8	7.5 ± 0.9	-38 ± 2.2	17 ± 0.9	2 ± 1.5
R Insula	5	6.4 ± 1.9	38 ± 2.5	15 ± 0.7	2 ± 1.8
M ACC	8	7.6 ± 1.2	1 ± 1.1	22 ± 1.6	45 ± 1.1
L SFG	5	6.4 ± 1.8	-21 ± 2.2	41 ± 2.3	37 ± 1.8
R SFG	7	6.5 ± 1.8	16 ± 1.2	39 ± 1.2	43 ± 1.8

Significant clusters ($P < 0.01$, uncorrected) were selected for each subject based on the contrast between visually similar (P + S) and visually dissimilar (A + D) exemplars. The hippocampus was anatomically defined in subjects that showed significant activation ($P < 0.05$, uncorrected) when the response to similar and dissimilar (S vs. D) exemplars was compared. N indicates the number of subjects who showed significant activation in each region. Volumes were calculated before spatial normalization. Coordinates are in the normalized space of the Talairach and Tournoux atlas. L: Left, R: Right; M: Medial.

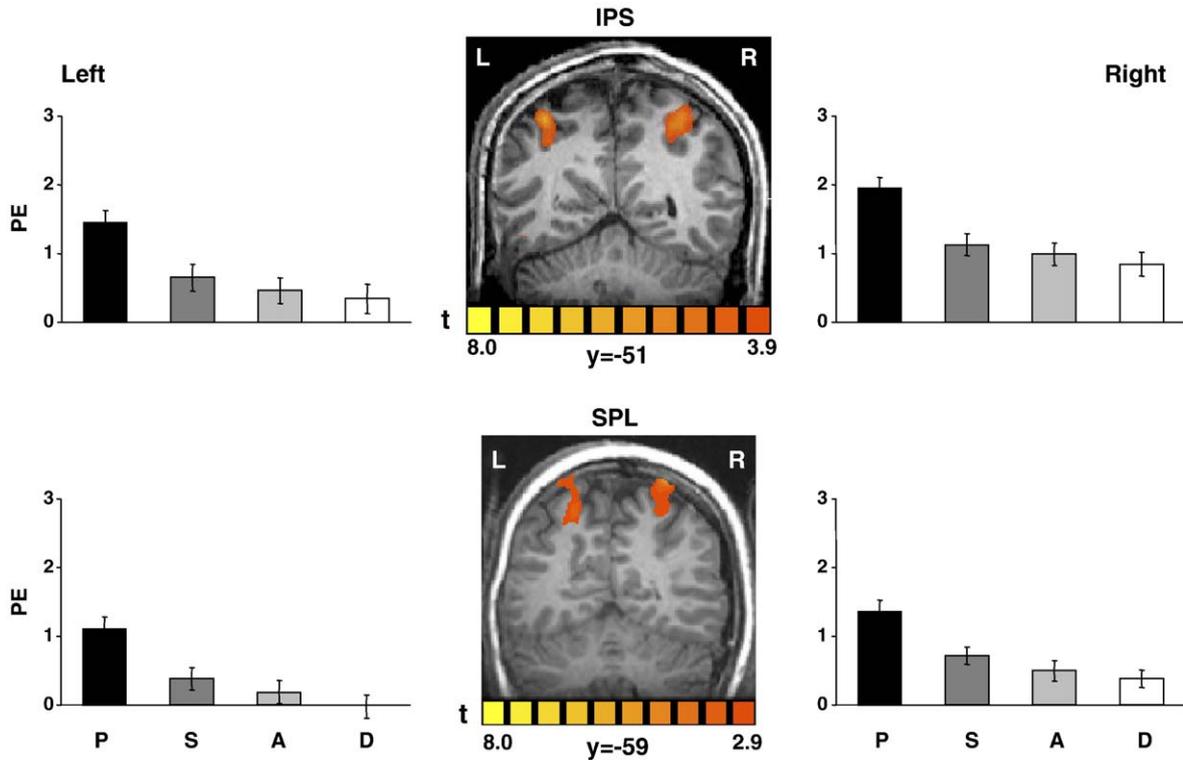


Fig. 4. Activation in attention-related areas. Coronal sections, taken from two individuals, illustrating stronger activation evoked by the prototypes and similar exemplars than by ambiguous and dissimilar exemplars in the IPS (top: $P < 0.0001$) and the SPL (bottom: $P < 0.005$). Mean parameter estimates for all stimulus types were averaged across all 6 runs (portraits, landscapes and abstract paintings) and all subjects.

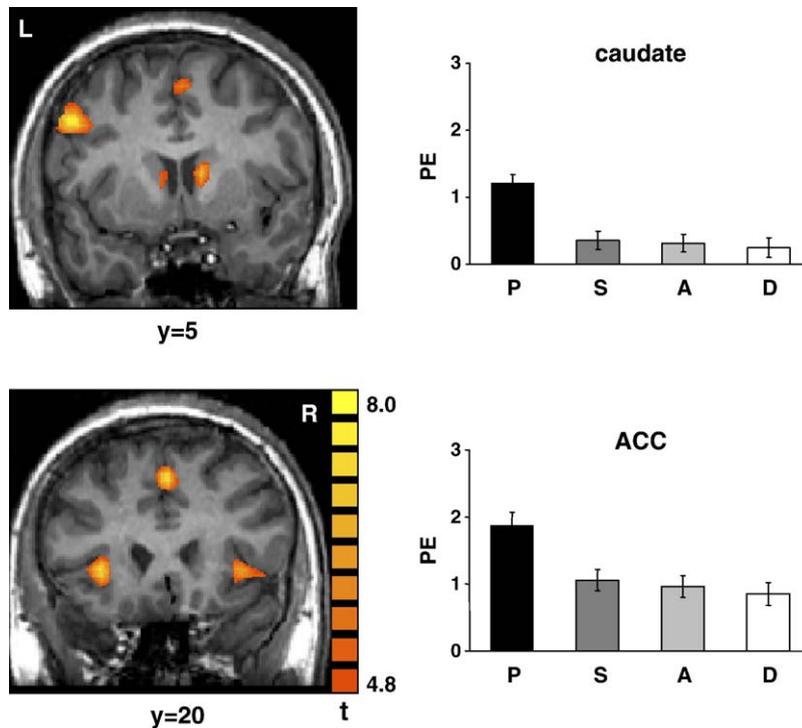


Fig. 5. Activation in memory-related regions. Group statistical maps showing stronger activation to familiar prototypes and similar exemplars than to ambiguous and dissimilar exemplars in the caudate (top), ACC and insula (bottom) ($P < 0.00005$). Mean parameter estimates for familiar prototypes (P), similar (S), ambiguous (A) and dissimilar exemplars (D) were averaged across portraits, landscapes and abstract paintings in both hemispheres.

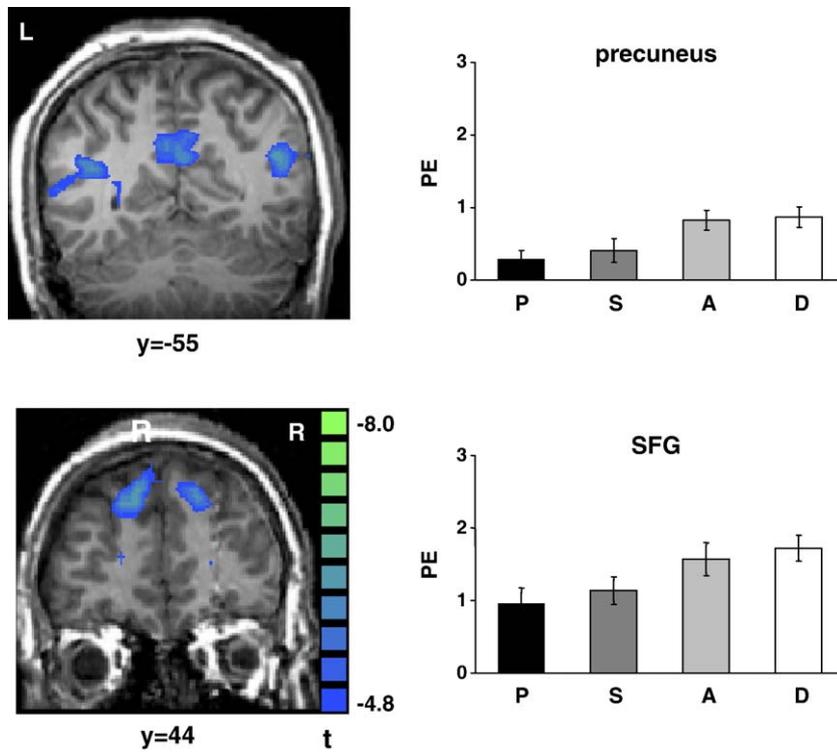


Fig. 6. Activation in memory-related regions. Group statistical maps showing stronger activation evoked by ambiguous and dissimilar exemplars than prototypes and similar exemplars in the precuneus and STG (top), and the SFG (bottom) ($P < 0.00005$). Mean parameter estimates were averaged across portraits, landscapes and abstract paintings in both hemispheres.

multiple memory-related areas, with two distinct patterns of response: stronger activation for the familiar prototypes in the caudate, ACC and the insula, and stronger activation for novel, visually different exemplars in the precuneus, STG and the SFG. Some of these regions were implicated in previous studies of category learning (e.g., Aizenstein et al., 2000; Reber et al., 2002; Vogels et al., 2002; Little et al., 2004), however this is the first report of differential activation within these regions as a function of visual similarity between the prototypes and new exemplars. In the caudate, ACC and insula, the familiar prototypes evoked stronger activation than all new exemplars, regardless of their visual similarity. These regions therefore likely mediate the correct classification of the prototypes, consistent with previous

reports about their role in memory retrieval, target detection and category learning (Poldrack et al., 1999; Seger and Cincotta, 2002, 2005). It is of interest that the pattern of activation in the caudate, ACC and insula resembles that of the face- and object-selective regions in the visual cortex, where the prototypes evoked stronger responses than the novel exemplars. The enhanced activation elicited by the prototypes is consistent with visual categorization studies in monkeys that revealed stronger responses to familiar prototypes in IT and PFC (Freedman et al., 2003).

In the monkey brain, a corticostriatal circuit was identified, suggesting that the basal ganglia modulates higher-level visual processes, such as object recognition and discrimination, in

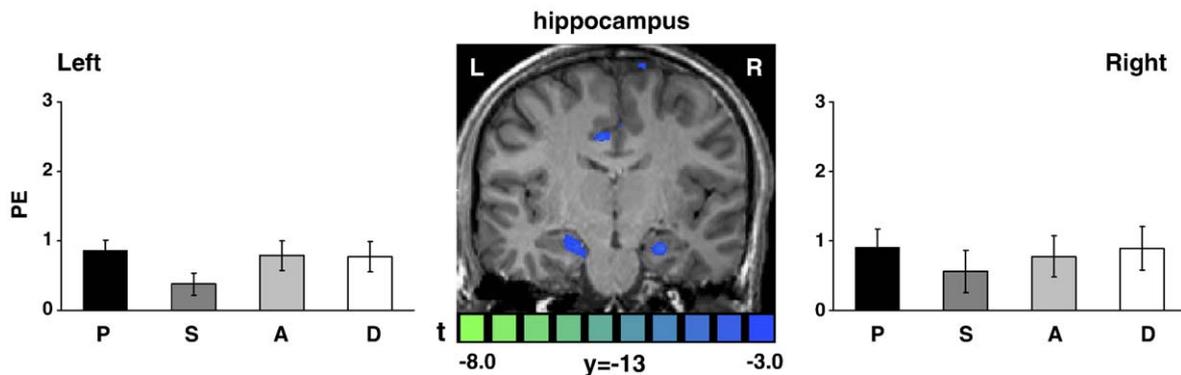


Fig. 7. Activation in the hippocampus. Coronal section taken from one subject illustrating stronger activation evoked by dissimilar than similar exemplars ($P < 0.0005$). Mean parameter estimates were averaged across portraits, landscapes and abstract paintings.

inferotemporal cortex (Middleton and Strick, 1996). A recent report has shown that during associative learning in monkeys, rapid learning-related responses in the caudate precedes slower responses in the PFC, further suggesting that output from the basal ganglia also modulates PFC activation during learning (Pasupathy and Miller, 2005). Interestingly, patients with Huntington's disease exhibit profound visual recognition impairments (Lawrence et al., 1998). A recent fMRI study in humans has further shown that the caudate has two functional roles in category learning: the body and tail mediate classification, whereas the head processes feedback during learning (Seger and Cincotta, 2005). It therefore seems that in addition to stimulus-specific representations stored in visual and prefrontal regions, recognition of familiar prototypes requires output signals from the striatum.

In the precuneus, STG and SFG, regions implicated in many studies of memory retrieval (e.g., Fletcher et al., 1995; Shannon and Buckner, 2004; Yonelinas et al., 2005), the new, visually different exemplars evoked stronger activation than the familiar prototypes and the new, visually similar exemplars. Behaviorally, the response to the new, visually different exemplars was faster and more accurate than the response to the visually similar ones. It is likely that the visually different, or mismatch items were classified as novel within these regions. Furthermore, we found that the visually similar exemplars evoked less activation than the prototypes and the visually different exemplars in the hippocampus. Activation in the hippocampus has been observed in various memory-related processes, including recognition memory (Stark and Squire, 2001), maintenance in working memory (Ranganath and D'Esposito, 2001), source memory (Davachi et al., 2003), generation of visual images from short-term memory (Ishai et al., 2002), and explicit categorization (Reber et al., 2003). Our recognition task revealed bilateral activation in the anterior hippocampus, where the novel, similar exemplars were associated with less activation. The behavioral response to these items was slower than the response to the novel, visually different exemplars, suggesting that although subjects responded correctly, they hesitated before pressing the button, presumably because the new, visually similar exemplars could have been mistaken for familiar prototypes. The reduced activity elicited by the similar items during correct recognition suggests that true and false memory traces can be dissociated within the hippocampus (Slotnick and Schacter, 2004).

In summary, our results show that recognition memory is mediated by a distributed cortical network where activation is modulated by the visual similarity between familiar prototypes and novel exemplars. Face- and object-selective regions in the visual system store stimulus-specific representations, attention-related regions in parietal cortex detect the familiar prototypes, and memory-related areas classify exemplars as a match or a mismatch. These findings could be applied to new simulation models of object recognition (Riesenhuber and Poggio, 2002) and classification learning (Fried and Holyoak, 1984; McClelland and Rumelhart, 1985) that need to integrate not only distributed representations of prototypes, but also the degree of visual similarity between familiar instances and new exemplars.

Acknowledgments

We thank Conny Schmidt for assistance with scanning and Andrea Mechelli for reading the manuscript. This study was

supported by the Swiss National Center for Competence in Research: Neural Plasticity and Repair.

References

- Aguirre, G.K., Zarahn, E., D'Esposito, M., 1998. An area within human ventral cortex sensitive to "building" stimuli: evidence and implications. *Neuron* 21, 373–383.
- Aizenstein, H.J., MacDonald, A.W., Stenger, V.A., Nebes, R.D., Larson, J.K., Ursu, S., Carter, C.S., 2000. Complementary category learning systems identified using event-related functional MRI. *J. Cogn. Neurosci.* 12, 977–987.
- Ashby, F.G., O'Brien, J.B., 2005. Category learning and multiple memory systems. *Trends Cogn. Sci.* 9, 83–89.
- Corbetta, M., Kincade, J.M., Ollinger, J.M., McAvoy, M.P., Shulman, G.L., 2000. Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nat. Neurosci.* 3, 292–297.
- Davachi, L., Mitchell, J.P., Wagner, A.D., 2003. Multiple routes to memory: distinct medial temporal lobe processes build item and source memories. *Proc. Natl. Acad. Sci. U. S. A.* 100, 2157–2162.
- Druzgal, T.J., D'Esposito, M., 2003. Dissecting contributions of prefrontal cortex and fusiform face area to face working memory. *J. Cogn. Neurosci.* 15, 771–784.
- Epstein, R., Kanwisher, N., 1998. A cortical representation of the local visual environment. *Nature* 392, 598–601.
- Fletcher, P.C., Frith, C.D., Baker, S.C., Shallice, T., Frackowiak, R.S., Dolan, R.J., 1995. The mind's eye-precuneus activation in memory-related imagery. *NeuroImage* 2, 195–200.
- Freedman, D.J., Riesenhuber, M., Poggio, T., Miller, E.K., 2003. A comparison of primate prefrontal and inferior temporal cortices during visual categorization. *J. Neurosci.* 23, 5235–5246.
- Fried, L.S., Holyoak, K.J., 1984. Induction of category distributions: a framework for classification learning. *J. Exp. Psychol., Learn. Mem. Cogn.* 10, 234–257.
- Friston, K.J., Holmes, A.P., Poline, J.B., Grasby, P.J., Williams, S.C., Frackowiak, R.S., Turner, R., 1995. Analysis of fMRI time-series revisited. *NeuroImage* 2, 45–53.
- Hintzman, D., 1986. "Schema abstraction" in a multiple-trace memory model. *Psychol. Rev.* 93, 411–428.
- Ishai, A., Ungerleider, L.G., Martin, A., Schouten, J.L., Haxby, J.V., 1999. Distributed representation of objects in the human ventral visual pathway. *Proc. Natl. Acad. Sci. U. S. A.* 96, 9379–9384.
- Ishai, A., Ungerleider, L.G., Martin, A., Haxby, J.V., 2000a. The representation of objects in the human occipital and temporal cortex. *J. Cogn. Neurosci.* 12, 35–51.
- Ishai, A., Ungerleider, L.G., Haxby, J.V., 2000b. Distributed neural systems for the generation of visual images. *Neuron* 28, 979–990.
- Ishai, A., Haxby, J.V., Ungerleider, L.G., 2002. Visual imagery of famous faces: effects of memory and attention revealed by fMRI. *NeuroImage* 17, 1729–1741.
- Kanwisher, N., McDermott, J., Chun, M.M., 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J. Neurosci.* 17, 4302–4311.
- Kawabata, H., Zeki, S., 2004. Neural correlates of beauty. *J. Neurophysiol.* 91, 1699–1705.
- Kincade, J.M., Abrams, R.A., Astafiev, S.V., Shulman, G.L., Corbetta, M., 2005. An event-related functional magnetic resonance imaging study of voluntary and stimulus-driven orienting of attention. *J. Neurosci.* 25, 4593–4604.
- Kitchener, E.G., Squire, L.R., 2000. Impaired verbal category learning in amnesia. *Behav. Neurosci.* 114 (5), 907–911.
- Knowlton, B.J., Squire, L.R., 1993. The learning of categories: parallel brain systems for item memory and category knowledge. *Science* 262, 1747–1749.
- Konishi, S., Wheeler, M.E., Donaldson, D.I., Buckner, R.L., 2000.

- Neural correlates of episodic retrieval success. *NeuroImage* 12 (3), 276–286.
- Lawrence, A.D., Sahakian, B.J., Robbins, T.W., 1998. Cognitive functions and corticostriatal circuits: insights from Huntington's disease. *Trends Cogn. Sci.* 2, 379–388.
- Little, D.M., Klein, R., Shobat, D.M., McClure, E.D., Thulborn, K.R., 2004. Changing patterns of brain activation during category learning revealed by functional MRI. *Brain Res. Cogn. Brain Res.* 22, 84–93.
- Macmillan, N.A., Creelman, C.D., 1991. *Detection Theory: A User's Guide*. Cambridge Univ. Press, Cambridge, England.
- McClelland, J.L., Rumelhart, D.E., 1985. Distributed memory and the representation of general and specific information. *J. Exp. Psychol. Gen.* 114, 159–197.
- Mechelli, A., Price, C.J., Friston, K.J., Ishai, A., 2004. Where bottom-up meets top-down: neuronal interactions during perception and imagery. *Cereb. Cortex* 14, 1256–1265.
- Medin, D.L., Schaffer, M.M., 1978. A context theory of classification learning. *Psychol. Rev.* 85, 207–238.
- Middleton, F.A., Strick, P.L., 1996. The temporal lobe is a target of output from the basal ganglia. *Proc. Natl. Acad. Sci. U. S. A.* 93, 8683–8687.
- Nosofsky, R.M., 1984. Choice, similarity, and the context theory of classification. *J. Exp. Psychol., Learn. Mem. Cogn.* 10, 104–114.
- Nosofsky, R.M., 1991. Tests of an exemplar model for relating perceptual classification and recognition memory. *J. Exp. Psychol. Hum. Percept. Perform.* 17 (1), 3–27.
- Pasupathy, A., Miller, E.K., 2005. Different time courses of learning-related activity in the prefrontal cortex and striatum. *Nature* 433, 873–876.
- Poldrack, R.A., Prabhakaran, V., Seger, C.A., Gabrieli, J.D., 1999. Striatal activation during acquisition of a cognitive skill. *Neuropsychology* 13, 564–574.
- Pollmann, S., Weidner, R., Humphreys, G.W., Olivers, C.N., Muller, K., Lohmann, G., Wiggins, C.J., Watson, D.G., 2003. Separating distractor rejection and target detection in posterior parietal cortex—an event-related fMRI study of visual marking. *NeuroImage* 18, 310–323.
- Posner, M.I., Keele, S.W., 1968. On the genesis of abstract ideas. *J. Exp. Psychol.* 77, 353–363.
- Pruessmann, K.P., Weiger, M., Scheidegger, M.B., Boesiger, P., 1999. SENSE: sensitivity encoding for fast MRI. *Magn. Reson. Med.* 42, 952–962.
- Ranganath, C., D'Esposito, M., 2001. Medial temporal lobe activity associated with active maintenance of novel information. *Neuron* 31, 865–873.
- Ranganath, C., Cohen, M.X., Dam, C., D'Esposito, M., 2004. Inferior temporal, prefrontal, and hippocampal contributions to visual working memory maintenance and associative memory retrieval. *J. Neurosci.* 24, 3917–3925.
- Reber, P.J., Stark, C.E., Squire, L.R., 1998a. Cortical areas supporting category learning identified using functional MRI. *Proc. Natl. Acad. Sci. U. S. A.* 95, 747–750.
- Reber, P.J., Stark, C.E., Squire, L.R., 1998b. Contrasting cortical activity associated with category memory and recognition memory. *Learn. Mem.* 5, 420–428.
- Reber, P.J., Wong, E.C., Buxton, R.B., 2002. Comparing the brain areas supporting nondeclarative categorization and recognition memory. *Brain Res. Cogn. Brain Res.* 14, 245–257.
- Reber, P.J., Gitelman, D.R., Parrish, T.B., Mesulam, M.M., 2003. Dissociating explicit and implicit category knowledge with fMRI. *J. Cogn. Neurosci.* 15, 574–583.
- Riesenhuber, M., Poggio, T., 2002. Neural mechanisms of object recognition. *Curr. Opin. Neurobiol.* 12, 162–168.
- Seger, C.A., Cincotta, C.M., 2002. Striatal activity in concept learning. *Cogn. Affect. Behav. Neurosci.* 2, 149–161.
- Seger, C.A., Cincotta, C.M., 2005. The roles of the caudate nucleus in human classification learning. *J. Neurosci.* 25, 2941–2951.
- Shannon, B.J., Buckner, R.L., 2004. Functional–anatomic correlates of memory retrieval that suggest nontraditional processing roles for multiple distinct regions within posterior parietal cortex. *J. Neurosci.* 24, 10084–10092.
- Shulman, G.L., Ollinger, J.M., Linenweber, M., Petersen, S.E., Corbetta, M., 2001. Multiple neural correlates of detection in the human brain. *Proc. Natl. Acad. Sci. U. S. A.* 98, 313–318.
- Slotnick, S.D., Schacter, D.L., 2004. A sensory signature that distinguishes true from false memories. *Nat. Neurosci.* 7, 664–672.
- Squire, L.R., Knowlton, B.J., 1995. Learning about categories in the absence of memory. *Proc. Natl. Acad. Sci. U. S. A.* 92, 12470–12474.
- Stark, C.E., Squire, L.R., 2001. Simple and associative recognition memory in the hippocampal region. *Learn. Mem.* 8, 190–197.
- Talairach, J., Tournoux, P., 1998. *Co-Planar Stereotaxic Atlas of the Human Brain*. Thieme Medical, New York.
- Vogels, R., Sary, G., Dupont, P., Orban, G.A., 2002. Human brain regions involved in visual categorization. *NeuroImage* 16, 401–414.
- Wagner, A.D., Shannon, B.J., Kahn, I., Buckner, R.L., 2005. Parietal lobe contributions to episodic memory retrieval. *Trends Cogn. Sci.* 9 (9), 445–453.
- Wheeler, M.E., Buckner, R.L., 2003. Functional dissociation among components of remembering: control, perceived oldness, and content. *J. Neurosci.* 23 (9), 3869–3880.
- Yonelinas, A.P., Otten, L.J., Shaw, K.N., Rugg, M.D., 2005. Separating the brain regions involved in recollection and familiarity in recognition memory. *J. Neurosci.* 25, 3002–3008.