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ScienceDirect
Progress in Natural Science 19 (2009) 1553–1559
Progress in Natural Science
www.elsevier.com/locate/pnsc

Functional dissociation of the left ventral occipito-temporal cortex in the direct and indirect retrieval of color features

Yan Wang[a,b,*], Jinghui Zhao[b], Jiongjiong Yang[c], Lin Ma[d], Sheng He[e], Xuchu Weng[b]

[a] *Beijing Key Laboratory for Learning and Cognition, Department of Psychology, Capital Normal University, Beijing 100048, China*
[b] *Institute of Psychology, Chinese Academy of Sciences, Beijing 100101, China*
[c] *Department of Psychology, Peking University, Beijing 100871, China*
[d] *PLA General Hospitals, Department of Radiology, Beijing 100853, China*
[e] *Department of Psychology, University of Minnesota, Minneapolis, USA*

Received 20 November 2008; received in revised form 19 December 2008; accepted 2 June 2009

Abstract

Previous studies suggest that the storage/retrieval of object features is related to brain regions that are involved in the processing of these features. However, it remains unclear whether, and under what conditions, retrieving information about a feature reactivates the same region that specifically supports that feature's perception. In this functional magnetic resonance imaging (fMRI) study, we compared brain activation in the left ventral occipito-temporal cortex during subjects performing a color perception task, and direct and indirect color retrieval tasks. After performing the color perception task to localize the regions responsible for color perception, subjects were intensively trained (outside of the scanner) to remember associations between colors and motion directions, and associations between colors and letters. Then, they were asked to perform two color retrieval tasks in the scanner, with stationary and gray scaled images as control stimuli. The results showed that the bilateral posterior occipito-temporal cortex was activated during the color perception task. When color information was retrieved by direct cues (motion direction), the same bilateral occipito-temporal region was activated. When color information was retrieved indirectly (judging whether a motion direction matched a letter by their associated colors), a region anterior to the color perception region in the left ventral occipito-temporal cortex was additionally activated. Our results provided evidence for the functional dissociation in the two subregions of the ventral occipito-temporal cortex during retrieval of color features: the posterior area might relate to perceptual features of color, while the anterior region might relate to the knowledge of associations with color.

Keywords: Occipito-temporal cortex; Color perception; Reactivation; Retrieval; fMRI

1. Introduction

During our daily lives, we see numerous objects and remember a lot about them. For example, when we see an apple or just see the word "apple", we can retrieve its knowledge, such as it is round, red, edible, sweet, and so on. One of the central questions in neuroscience is how object concepts are stored and retrieved in the brain.

Findings of functional magnetic resonance imaging (fMRI) studies for normal subjects and brain lesioned patients indicate that information about the properties of an object is composed of its perceptual features, for example, what it looks like (its shape or color), how it moves, and what its functional features are [1]. The storage and retrieval of these object features are related to brain regions that are involved in the processing of these features [2–6]. For instance, when words representing the actions of the face, arm, or leg (e.g., to lick, pick, or kick) are presented, areas along the motor cortex are activated differentially,

* Corresponding author.
E-mail address: wyfmri@126.com (Y. Wang).

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doi:10.1016/j.pnsc.2009.06.007

which are either directly adjacent to or overlapped with areas activated by actual movements of the tongue, fingers, or feet [3,7]. In these studies, it was found that the regions for storage/retrieval of concept knowledge are overlapped with those in perceptual processing of the same objects [2,3,5]. For example, Simmons et al. [5] reported that when subjects verify whether a named color is appropriate for an object (e.g., TAXI-yellow), a region of the left fusiform gyrus, which is highly responsive during color perception tasks (e.g., judging color hues), is also activated. The results indicate that retrieval of an object's concept is related to the perceptual features of that object (such as its color features) [8,9]. But other studies reported that the regions for storage/retrieval of the concept is not overlapped with, but close to the perception regions, e.g., retrieving of color information activates a region in the ventral temporal cortex that is anterior to the color perception area [2,6,10]. It implies that the anterior region of the ventral occipito-temporal cortex is recruited in the processing of knowledge of association, which is different from the processing of the perceptual features [1].

One problem in many previous studies is that brain activity was explored while subjects performed the perception tasks, or the retrieval tasks separately, rather than both tasks in the same subjects and in a single study [4,6,11]. This makes it unclear whether the regions activated during retrieval of a concept's feature is the same region as those specifically responding to that feature's perception. Although Simmons et al. [5] reported that there is an overlap in the neural basis of color perception and stored information about object-associated color, the region activated in their color perception task, which ranged from $y = -33$ to -38 in the left fusiform gyrus, is obviously anterior to the typical color areas ($y = -75$) reported in previous studies [11]. More importantly, few studies are reported on whether the activation in the perception region and the anterior region is related to different features of the objects. Based on the above issues, it is necessary to further explore whether retrieving information about a feature reactivates the same region that specifically supports that feature's perception, and whether the activation in the posterior and anterior regions relate to retrieval of different features of objects.

In this fMRI study, we asked subjects to perform two tasks for retrieving color information in the scanner. One was a direct retrieval task of color information with motion directions presented as cues. The other was an indirect retrieval task with motion directions and letters presented separately as cues. Before these tasks, subjects had learned the associations between colors and motion directions, and associations between colors and letters thoroughly. To avoid the interference of semantic information and prior knowledge, we used nonword materials, and asked subjects to make novel associations between them. We particularly performed a localization scan for color perception as the first scan run. Our hypothesis was that the posterior region in the occipito-temporal cortex relates to retrieval of perceptual features of color information, while the anterior region relates to processing of knowledge of associations among different features.

2. Materials and methods

2.1. Subjects

Eight healthy subjects (5 males, 3 females, age 21–31, mean 22 years old) participated in the study. None was achromatopsia. All had normal or corrected-to-normal vision, and no one reported neurological problems. All subjects were paid for their participation and gave written informed consent.

2.2. Experimental design

As shown in Fig. 1, experimental materials were eight kinds of stationary color dots, eight kinds of moving gray dots (10×10), and eight colored letters, with stationary and gray scaled dots as control stimuli. In order to locate the regions for color and motion perception, subjects were firstly required to press the key to the images of color and stationary dots, and images of moving and gray dots presented to them in the MR machine. Stimuli images were randomly presented, which lasted for 2 s.

Then, subjects were asked to remember two kinds of associations both related to color in the following 6 days. One was the arbitrary associations between eight kinds of color and eight kinds of motion direction with one kind of color corresponding with only one kind of motion direction; the other was the arbitrary associations between eight kinds of color and eight letters, with one kind of color corresponding with one letter exactly. Memory tests for the two associations following the training showed that the accuracy was 100%. Finally, during scanning, subjects were asked to do two recall tasks, one named the direct task, to vividly recall the color corresponding to the moving dots shown for 2 s; the other named the indirect task, to decide whether the letters and moving dots appeared successively with 1 s for each, matched with the same kind of color.

An event-related design was adopted with three sessions for each subject: perception location, direct retrieval, and indirect retrieval session, each lasting 328 s and consisting of 16 trials of 20 s, 18 s as the baseline (6 s before the stimulation image, 12 s after) and 2 s during which the stimuli were presented to ask the subjects to respond. At the beginning of each session, there were 8 s when baseline was presented and no response was required. The data of the first 8 s was removed from the data processing to ensure image quality. There were 16 trials in the perception session, with eight trials for color and eight for motion, respectively. Sixteen trials of motion in the direct retrieval session with the same motion trials were presented as those in the first session, but were presented twice. In order to match with the first session, we selected the first presented eight motion trials to do data analysis. In the indirect task, there were also

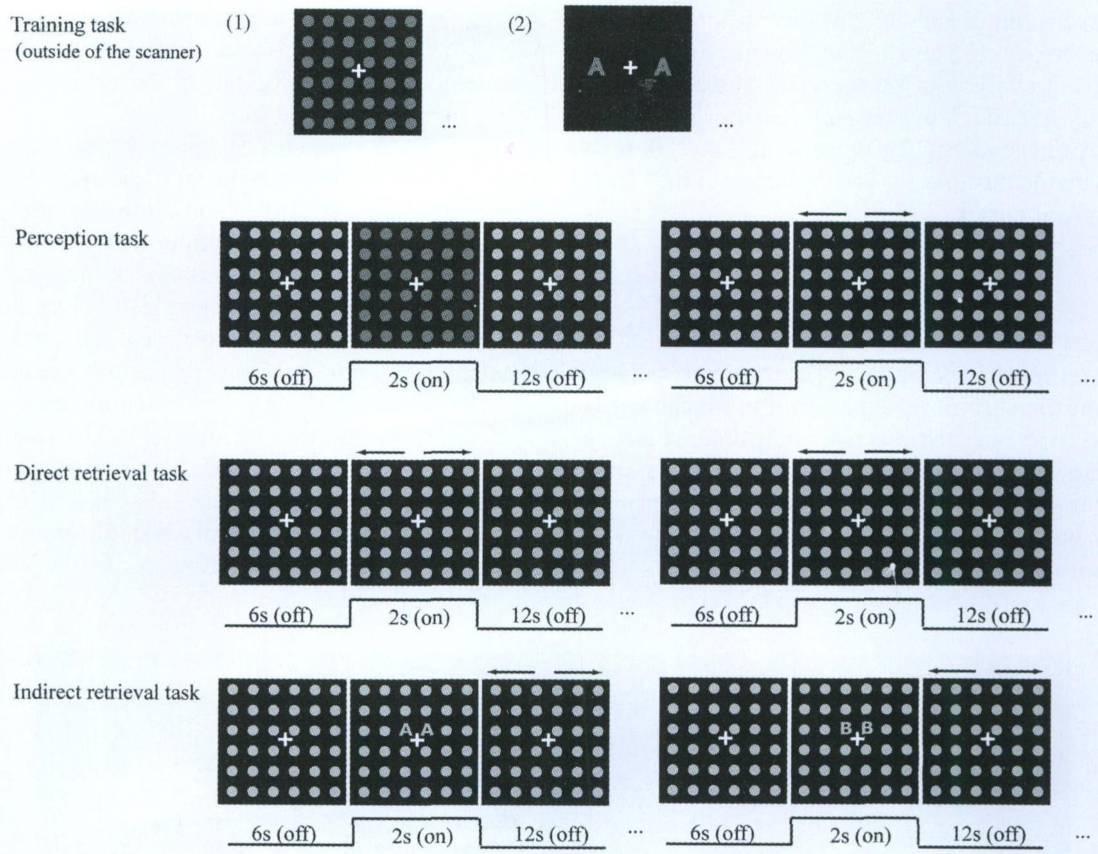

Fig. 1. The schema for the experimental design.

16 trials, with eight for the indirect retrieval task and another eight for the perceptual judging task (subjects were required to judge whether the motion and arrow matched with each other). As we focused on the issues with color knowledge, we did not discuss the results of the perceptual judging task.

2.3. MRI acquisition

Images were acquired on a 1.5 Tesla whole-body scanner (GE Medical Systems). A receive-only whole-head coil was used for signal reception. Earplugs were utilized to weaken scanner noise. Subjects lie supine in the scanner, looking at the picture shown on the screen through a mirror over their head at scan and were asked to fix their eyes onto the "+" in the centre of the pictures.

Structural images were acquired using a SE (spin echo, TR: 380 ms, TE: 9 ms, FOV: 24 cm, thickness: 6 mm, skip: 1 mm, matrix: 256 × 256), and whole brain sagittal SPGR (spoiled gradient recalled acquisition in steady state imaging) images (TR: 2.5 s, TR: 30 ms, TE: 6 ms, flip angle: 35°, thickness: 2.5 mm, FOV: 24 cm, matrix: 256 × 256) were collected for anatomical co-registration. A $T2^*$-weighted EPI sequence for functional imaging with parameters of TR 2 s, TE 55 ms, thickness 7.0 mm, slices 5, matrix 64 × 64, and FOV 24 cm was used to reduce inflow effects and maximize the blood oxygenation level dependent (BOLD) effect, acquiring 164 volumes during each session. Slices selected were coronal, which is perpendicular to the line connecting the anterior and posterior commeasures (AC–PC line), and covering the bilateral V4 and MT^+ area in the posterior of the brain.

2.4. Data analysis

Analysis of functional neuroimages (AFNI) (http://afni.nimh.nih.gov) was used for fMRI data analysis and images display. The first four EPI volumes were discarded because of data quality. The remaining 160 volumes were registered to the nearest volume close to anatomical images to correct subject's head movements, and then spatially realigned to the fourth volume. Sync interpolation was used to account for between-slice timing differences caused by differences in acquisition order, and the linear slope was removed on a voxel-by-voxel basis. And then volumes were interpolated and overlaid on each subject's anatomical scan after being spatially normalized into the system of reference of Talairach and Tournoux (1988) using AFNI (Cox, 1996) v 2.2. Normalized images were re-sampled to a voxel size of 3 × 3 × 3 mm for display purposes and then smoothed with a 4 mm FWHM Gaussian kernel.

A voxel-wise deconvolution and multiple regressions were used to detect stimulus-related changes in the MR signals to acquire the average activation images through *t*-test analysis between stimuli and baseline (activation threshold: $p < 10^{-4}$, cluster size: 135 mm^3). The group activation map was gained from analysis of t-tests of the subjects, activation threshold: $p < 10^{-16}$, cluster size: 270 mm^3. Referencing from previous studies [12,13], we used $y = -60$ as the boundary to divide the anterior and posterior in the ventral occipito-temporal cortex.

3. Results

The subjects' accuracy was quite high in the direct and the indirect retrieval experiments. The response was not recorded in the direct retrieval experiment in which subjects were required to retrieve the corresponding color to the cue of motion. However, the test after the experiment showed that the accuracy was 100%. In the indirect experiment, the accuracy was 87.5 ± 11.2%, the reaction time was not recorded due to recording problems.

In the perception experiment, when color stimuli were shown, there was activation in the bilateral ventral occipito-temporal cortex for all of the subjects (the averaged coordinates of all subjects: left −22, −68, −9, right: 26, −73, −6), the region stretching from $y = -63$ to −82, which was overlapped with the regions of the classic color perception area [12,14]. When motion stimuli were shown, the bilateral motion perception area, MT^+ was activated for all subjects. These results are broadly consistent with findings from previous studies [15,16] (Fig. 2).

In the direct retrieval experiment, subjects retrieved the matched color to the cue of motion directions, and the results showed that the color perception area was also activated. Moreover, the coordinates of the two regions were very close (peak significance: color perception task: −22, −68, −9, direct retrieval task: −26, −74, −10), which demonstrated that the retrieval of color information reactivated the color perception area (Fig. 2). In the indirect experi-

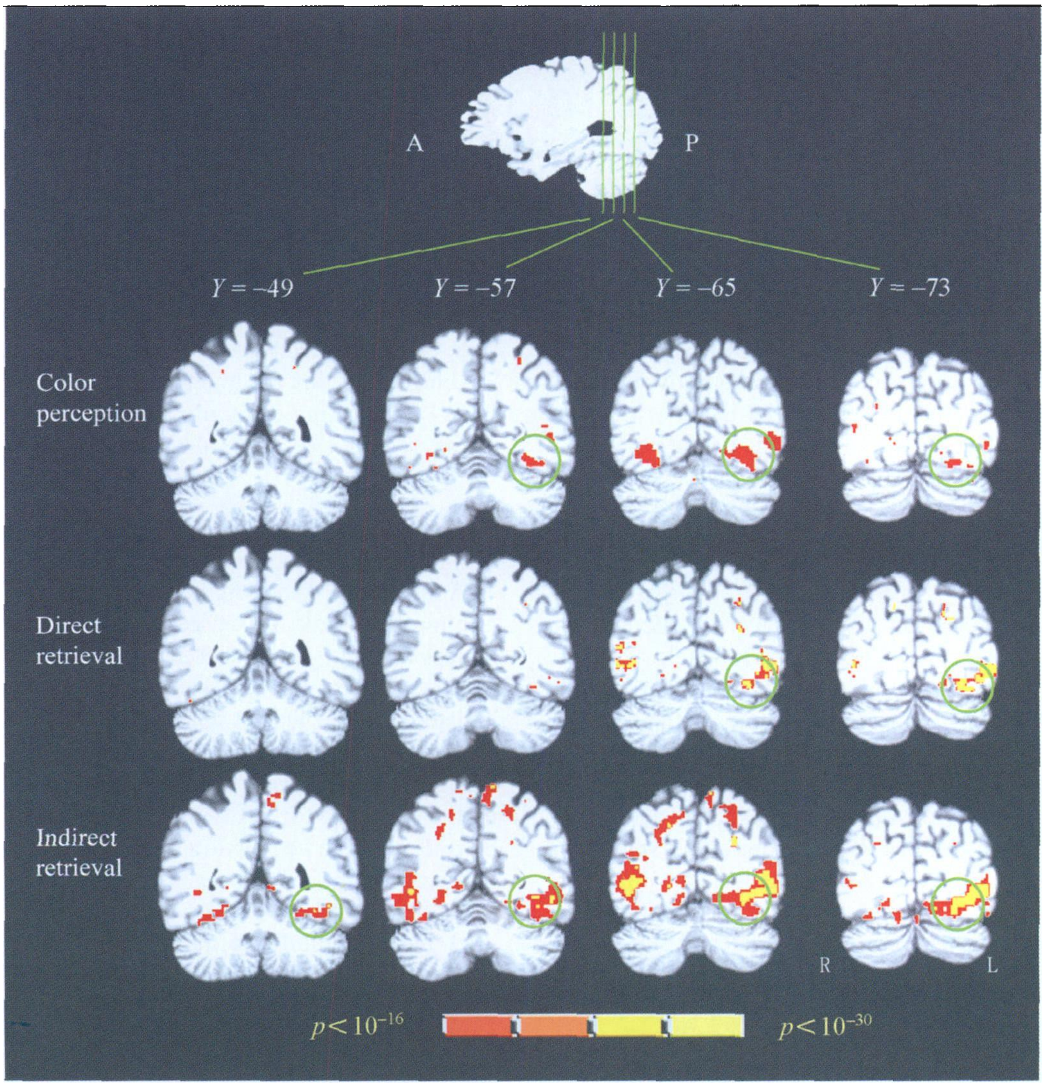

Fig. 2. An averaged significance map for the color perception location experiment, direct retrieval experiment and indirect retrieval experiments. The figure depicts coronal sections from the N27 template brain warped to Talairach space (template available in AFNI, http://afni.nimh.nih.gov/afni/). Obviously, the anterior area was activated in the indirect retrieval task only. A, anterior; P, posterior; R, right; and L, left.

ment, when subjects were required to use indirect cues to retrieve the color, that is, to judge whether the motion and the letter matched to the same color, two regions were activated in the ventral occipito-temporal cortex. The first region was in the posterior area (peak significance: −25, −71, −12) overlapped with the color perception area, and the other was in the anterior area (peak coordinate: −37, −51, −13 (Fig. 2)), with the left more activated than the right. It suggested that the anterior area was activated in the indirect retrieval task only, but not in the direct retrieval task.

There was the same activation pattern in single subject analysis (Fig. 3). In the perception task, all subjects showed the same activation pattern as that in the group analysis; seven out of eight subjects showed the same activation pattern as that of group analysis in the direct and indirect tasks. In the color perception experiment, the color perception area in the bilateral ventral occipito-temporal cortex was activated in all subjects, with the region stretching from $y = -63$ to -82. In the direct retrieval experiment, only the posterior areas in the occipito-temporal cortex were activated, with the region stretching from $y = -60$ to -78. While in the indirect retrieval task, two activation regions were found with the region stretching for the anterior one ($y = -48$ to -66), and the posterior one ($y = -61$ to -75).

4. Discussion

The novelty of our findings was the functional dissociation in the two subregions of the ventral occipito-temporal cortex during retrieval of color features in different retrieval conditions with nonverbal cues. By asking subjects to perform the color perception task and color information retrieval tasks, the current study showed that when retrieving color information by direct cues (moving direction), the

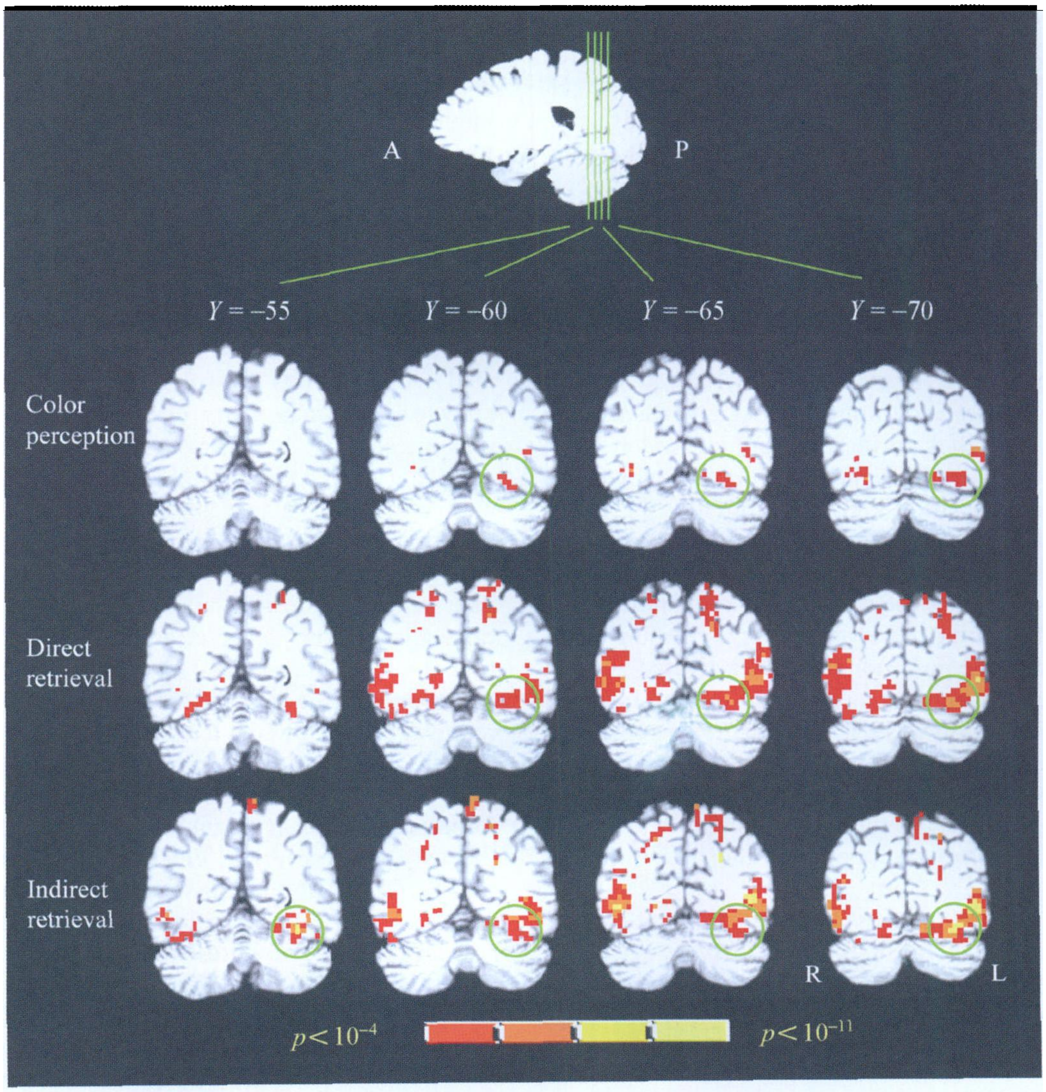

Fig. 3. The activation map from a standard subject for color perception, direct retrieval and indirect retrieval experiments. The figure depicts coronal sections from the N27 template brain warped to Talairach space (template available in AFNI, http://afni.nimh.nih.gov/afni/). Obviously, the anterior area was activated only in the indirect retrieval task. A, anterior; P, posterior; R, right; and L, left.

same bilateral occipito-temporal region was activated, which suggested that retrieving object concepts was related to their perceptual features [12,13,17]. When color information was retrieved indirectly, that is, subjects were asked to judge whether a moving direction matched a letter by their associated colors, a region anterior to the color perception area was additionally activated.

We found that the region posterior in the occipito-temporal gyrus was activated during the direct retrieval task, which was supported by previous studies [18,19]. For example, in the fMRI study by Wheeler et al. [18], subjects learned a set of picture and sound items and were then given the sound as a cue to retrieve the corresponding pictures. The results found that the area for pictures perception in the left occipito-temporal cortex (−14, −69, −6) was activated in naming pictures by sound cues. In Nunn et al.'s study on word-color synesthetes [19], the subjects experienced vivid color images on hearing noncolor words, it was observed that the color word synesthetic experience was associated with activity in the color perception area (−33, −66, −13) that was in the posterior occipito-temporal cortex. Based on these and our findings, we considered that the activation in the posterior region might be associated with retrieving perceptual features of knowledge.

While different from the posterior subregion, the anterior subregion was activated only in the indirect retrieval task. As Martin [1] proposed, this subregion may be related with some complex processing of knowledge of associations (e.g., between objects and color information) [1,6,17]. In the indirect task of the present study, subjects were asked to judge whether motion and letter were matched to each other or not. As subjects had learned the association between color and motion, and association between color and letter during the training session, both motion and letter were associated with color knowledge. Thus, when the association knowledge of color had to be retrieved to do the matching task, the anterior areas were correspondingly activated. In contrast, as subjects had learned the associations between color and motion, by motion cues they could retrieve the corresponding color information; thus, the posterior area was activated without the necessity of the anterior one. These results indicated that the posterior region was associated with the perceptual processing of color information, while the anterior region might be related to the associations between knowledge and features of different stimuli. This functional dissociation provides convincing support for the hypothesis by Martin [1].

As previous studies indicated, the activation in the anterior region was related to the retrieval of object concepts [2,6,17]. For example, the anterior region (−46, −46, −12, and −52, −36, −16) is activated by asking subjects to generate color names for the achromatic objects or to name the color of the colored objects. And, in the study of Goldberg et al. [2], answering written questions concerning object-associated visual properties activated regions in the occipito-temporal regions involved in the color processing (−33, −36, −16). As these studies are all related to the retrieval of semantic information of concept knowledge, our study suggested that the cues, neither verbal nor nonverbal, are associated with the activation in anterior vs. posterior subregions. In the current study, instead of using verbal cues in previous studies to retrieve the long-term knowledge of associations [2,5,6,17], we used nonverbal cues which were difficult to name, and found the functional dissociations between anterior vs. posterior subregions. Our results indicated that one function of the anterior region might be to provide a neural substrate for acquiring new object-color associations and to represent those associations in the service of indirect retrieving.

Our results were not conflictive with those of Simmons et al. [5]. Their results indicated the overlap for color perception and feature retrieval about object-associated color, but the activation in their study was in the anterior region in the occipito-temporal cortex (−33, −36, −16), which is not the classic area for color perception. We consider the difference may be due to the task difference. In their study, they asked subjects to judge the hue of color, rather than a passive view of the color in the classic study [11], so the anterior region was activated [13]. The results further implied that the activation in the anterior area is related to more complex processing of color knowledge [1], such as judging the object-color association and indirect retrieval of color information.

Lesion studies shed light on our functional dissociation of perceptual features and knowledge of associations. For example, damage to more posterior ventral occipital color-selective areas (such as the lingual gyrus) is associated with difficulty in color vision. Interestingly, color knowledge in achromats often remains intact (such as grass-green) [20]. In contrast, color agnosia is impaired in retrieving color knowledge about objects (e.g., not knowing the color of bananas is yellow) due to lesions in the left temporal lobe, but the patients had spared color vision and intact knowledge of object form and functions [21]. These data indicate that the representation of the perceptual features and the knowledge of associations of color information could be dissociated.

It is interesting to note that the regions activated during retrieval tasks showed a tendency to be left lateralized, and similar results were reported in many other studies [2,5,6,10,19]. The activation in the right hemisphere was rather weak, which might indicate that the function of the two hemispheres is different in retrieving the color information of objects. It is also possible that the retrieval of concept processing of color association showed a left lateralization in the occipito-temporal cortex.

The data of response times for the retrieval tasks were missing in the present study. The possible difference in the response times, and hence task difficulty, between the two retrieval tasks might be confounded to influence the results, which we need to address in further studies. Nevertheless, we believe that this default will not affect our main conclusions for the following three reasons. First, the accuracy of memory tests reached 100% during the training of 6 days, which would largely reduce the influence of the task difficulty and mental load [13]. Second, the activation to task difficulty and mental load should be more extensive, while in our study the increment activation of the indirect task relative to the direct retrieval task was confined to the anterior area in the left ventral occipito-temporal cortex. Third, many other studies showed that the anterior region in the left ventral occipito-temporal cortex is related to the retrieval of semantic information [5,6,11,17]. Therefore, the activation in the anterior region in our study might be associated with the knowledge of associations with color.

In conclusion, in the present fMRI study, we compared brain activations in the left ventral occipito-temporal cortex during perception, direct and indirect retrieval of color information. The results showed that perception of color activated the bilateral posterior occipito-temporal cortex. When color information was retrieved directly, the same bilateral occipito-temporal region was activated. When color information was retrieved indirectly, a region anterior to the color perception area was additionally activated. Our results indicated that the posterior area might be associated with perceptual features of color, while the anterior region might be associated with the knowledge of associations with color. Our study provides the evidence for the functional dissociation in the two subregions of the ventral occipito-temporal cortex during retrieval of color features and sheds light on the mechanism of retrieving object knowledge in the brain.

Acknowledgements

This work was supported by the National Natural Science Foundation of China (Grant No. 30670674) and the Beijing Key Laboratory for Learning and Cognition.

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