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Dissociation of pathways for object and spatial vision: a PET study in humans

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A positron emission tomography (PET) study was conducted to determine which brain regions are differentially involved in visual object identification and object localization. Subjects engaged in a spatial task in which they matched the location of common objects, and an object task in which they matched the identity of common objects. In both tasks the stimulus arrangements used were of the same kind. Regional cerebral blood flow data showed that a right-sided region in the inferior parietal lobule was more activated during spatial than during object matching. In contrast, bilateral occipitotemporal regions, with the left more predominant, were more activated during object than spatial matching. These results provide support for Ungerleider and Mishkin's dual pathway model of vision and indicate important patterns of lateralization in the human visual system.

Key words: Object vision; Spatial vision; Temporal cortex; Parietal cortex; Positron emission tomography; Human, Visual pathways

Introduction

Visual processing in primates involves a large number of subcortical and cortical regions.[1] Ungerleider and Mishkin[2] proposed that the cortical regions implicated in vision in rhesus monkeys are organized into two functionally specialized pathways. The occipitotemporal or 'ventral pathway', which includes inferior temporal cortex is implicated in visual object identification. In contrast, the occipitoparietal or 'dorsal pathway', which includes posterior parietal cortex is implicated in visual localization of objects. Functional brain imaging techniques used in conjunction with appropriate cognitive tasks provide a tool to investigate whether the visual cortex of humans is similarly organized. At present, support for Ungerleider and Mishkin's dual pathway model in humans has been obtained from a positron emission tomography (PET) study in which brain activity during a face matching task was compared with brain activity during a matching task for spatial locations.[3] However, the model has not yet been tested in humans with objects other than faces. It is well documented that patients with lesions restricted to occipitotemporal cortex can exhibit deficits in face recognition while being unimpaired in object recognition.[4] The reverse pattern of impairments has been observed in agnosic patients who are impaired at recognizing common objects in the visual modality.[4,5] Thus, there is evidence to suggest that the identification of faces and common objects is carried out by at least partially distinct subsystems of visual cortex. Consequently, it is important to evaluate whether Ungerleider and Mishkin's model holds similarly for visual object identification and object localization when common objects rather than faces are processed. Our PET study addressed this issue directly by comparing the brain activity associated with a spatial task in which subjects matched the location of line drawings of common objects, and an object task in which they matched their identity. To control for possible confounding effects of different stimulus variables across tasks, the same kind of stimulus arrangements were used in both tasks.

Materials and Methods

PET measurements of regional cerebral blood flow (rCBF) were obtained while 12 young healthy right-handed males engaged in two different tasks as illustrated in Figure 1: an object matching task and a spatial matching task. In both tasks, subjects compared two consecutively presented computer displays and decided whether these were identical or different. Each display consisted of representational line drawings[6] of three unique common objects arranged in a unique spatial configuration. Within a

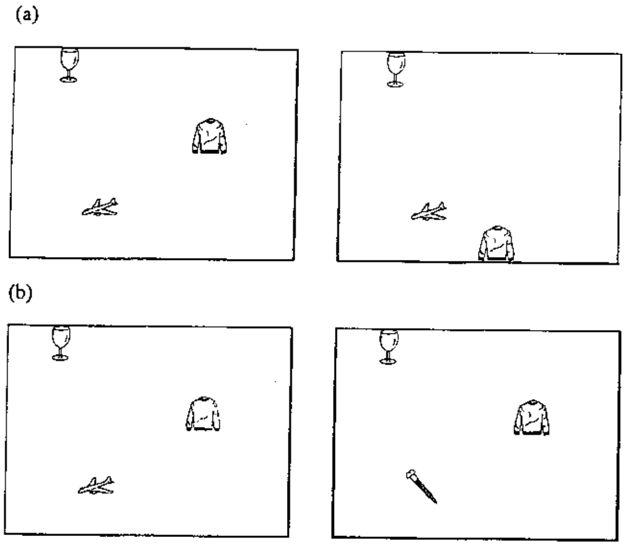

FIG. 1. Examples of pairs of displays used in 'different' trials of the spatial matching task (a) and the object matching task (b).

trial, two displays were presented for 1 s each with a 0.75 s interdisplay interval and a subsequent response interval of 2.25 s. Subjects reported their responses manually. In 'identical' trials of both tasks, displays were identical in every respect. In 'different' trials of the spatial matching task (Fig. 1a), displays differed only with respect to the spatial location of one of the objects. In 'different' trials of the object matching task (Fig. 1b), displays differed only with respect to the identity of one of the objects. Subjects undertook two blocks (scans) of each task in a counterbalanced order.

PET scans were obtained with a GEMS-Scanditronix PC2048-15B head scanner using bolus injections of 40 mCi (1.48 GBq) of [^{15}O]H_2O and 60 s data acquisition scans. To determine the brain regions implicated differentially in the two matching tasks, we analysed the PET data using the latest version of the Statistical Parametric Mapping (SPM) technique[7,8] with software provided by the Wellcome Department of Cognitive Neurology, London, UK. This software was implemented in Matlab (Mathworks Inc. Sherborn MA, USA). The analysis involved the following steps: the different images from each subject were realigned to the first image, using a rigid body transformation. These realigned images from each subject were then transformed into a standard space[9] by matching them to a reference image that already conforms to the standard space. The images were subsequently smoothed using an isotropic Gaussian kernel with a filter width of 15 mm in all dimensions. The effects of the cognitive tasks on regional cerebral blood flow at each voxel were then estimated using a general linear model. Changes in global blood flow were accounted for by proportional rescaling. The effects of each comparison were estimated using weighted contrasts which yielded a t-statistic for each comparison at each voxel. This t-statistic was subsequently converted into a Z-score. In this study, a change was accepted as significant only if the voxels of a spatially contiguous set were all independently significant at a level of $p < 0.001$ (which corresponds to a Z-score of 3.1). Such a method of analysis has empirically been shown to guard against the excessive occurrence of false-positive errors.[10]

The data reported here are part of a larger study on visual perception and memory.

Results

At the behavioural level, response accuracy was >93% in both tasks indicating that the brain activity being measured was associated with highly successful perceptual processing. In order to determine which brain regions were differentially activated during spatial matching and object matching, we subtracted the PET images obtained in one task from the images obtained in the other. The only region which was significantly more activated during spatial matching than object matching was highly circumscribed and located in the right inferior parietal lobule at the border to superior temporal gyrus (Brodmann's area [BA]39; Table 1). Following the logic of the experimental design, activity in this dorsal region is specifically associated with matching of spatial location because brain activity related to other aspects of visual processing, in particular those

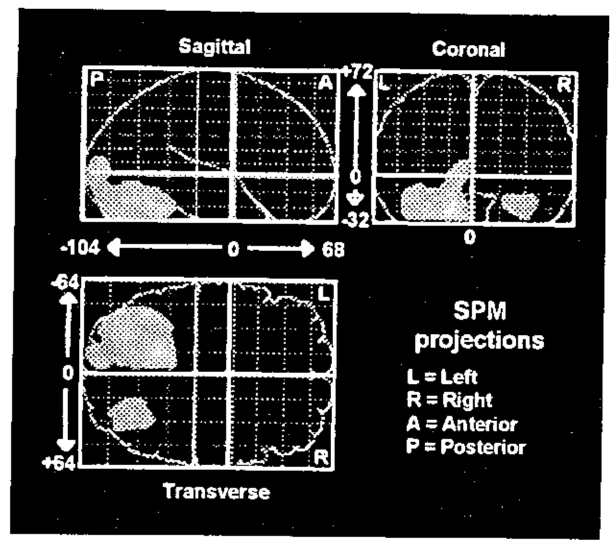

FIG. 2. Cerebral regions which show significant increases in rCBF ($p < 0.001$) in the comparison object matching minus spatial matching. Activations are presented in a standard format for displaying SPM results as a maximum intensity projection viewed from the back, the right hand side, and the top of the brain. The anatomical space corresponds to the atlas of Talairach and Tournoux.[9] Refer to Table 1 for coordinates of representative peak activations.

Table 1. Brain regions manifesting significant changes in rCBF

Region	Brodmann area	Talairach and Tournoux Coordinates			Z-score
		x	y	z	
Spatial Matching minus Object Matching					
Right Inferior Parietal					
supramarg./sup. temp. gyrus	39	44	−54	20	3.52
Object Matching minus Spatial Matching					
Left Ventral Posterior					
fusiform gyrus	37	−40	−60	−16	5.13
lingual gyrus	18	−14	−96	−4	4.16
lingual gyrus/cuneus	17	−8	−90	4	4.79
lateral cerebellum		−14	−48	−24	5.71
Right Ventral Posterior					
fusiform/lingual gyrus	18	28	−86	−16	3.16
lateral cerebellum		26	−64	−16	4.37

Coordinates of representative peak activations with Z-scores > 3.1 (corresponding to $p < 0.001$) are listed in mm according to the atlas of Talairach and Tournoux[9] along left-right (x), anterior-posterior (y), and superior-inferior (z) axes. Designation of region names and Brodmann areas is approximate and based on the same atlas.

related to object identification, was eliminated by subtraction.

Figure 2 shows the brain regions which were significantly more activated during object matching than spatial matching, and hence are specifically associated with visual matching of object identity. All activations were located in ventral posterior regions (Table 1). Foci of activation were found bilaterally, though stronger and more extensive in the left hemisphere. Left-sided activation was found in inferior temporal cortex in the region of fusiform gyrus (BA 19, 37) and extended posteriorly into lingual gyrus (BA 18, 17). Right-sided activation was found in ventral occipital cortex in the region of fusiform gyrus (BA 18). The only additional foci of activation were observed in left- and right-sided lateral cerebellum.

Discussion

Our results provide direct evidence in support of Ungerleider and Mishkin's dual pathway model of vision in humans. A dorsal region in the right-sided inferior parietal lobule was more activated during spatial matching than object matching whereas bilateral ventral occipitotemporal regions were more activated, especially on the left side, during object matching than spatial matching. Moreover, this double dissociation was observed even though stimulus arrangements of the same kind were used in both tasks, the only difference between tasks being the cognitive operations that were performed.

The dorsal region that was more activated during spatial matching than object matching corresponds to the site of lesion that produces selective deficits in perceptual matching of spatial location in neurological patients.[11,12] Unilateral right inferior parietal activation has also been observed in PET studies involving matching of spatial location as part of a visual working memory[13] and a visual long-term memory task.[14] In contrast, a PET study involving matching of spatial location as part of a mental rotation task[3] revealed bilateral activation in parietal cortex which extended into more posterior and superior regions than the inferior parietal lobule. In accord with a previous suggestion,[13] we believe that the right parietal region activated in the present study specifically subserves the computation and matching of coordinates specifying the spatial location of objects. Other spatial processing components, such as the rotation of these coordinates or their transformation for visuomotor control[15] might involve the participation of a more extensive, possibly bilateral network of parietal regions which extends into superior parietal cortex (BA 7).[3]

The ventral occipitotemporal regions which were more activated during object matching than during spatial matching correspond to the site of lesions which produce severe impairments in identifying objects in humans. These deficits occur in particular if the lesion affects the left hemisphere.[4,16] Occipitotemporal activations in similar partially overlapping regions were also found in a previous PET study of visual object identification which required the matching of visually presented objects with object names[17] and a PET study of semantic judgements regarding visually presented objects.[18] In addition, two PET studies involving visual processing of faces showed similar occipitotemporal activations.[3,18] However, the PET studies using faces showed stronger activation in ventral regions of the right hemisphere, whereas the PET studies using common objects, including the present one, showed stronger activation in ventral regions of the left hemisphere. This pattern of lateralization is in line with the human lesion literature.[4] It should be noted that the PET studies involving semantic processing of objects demonstrated additional activation in more anterior temporal lobe regions which were not implicated in the present study.[18] Taken together, these data suggest that the ensemble of posterior occipitotemporal regions activated in the present study specifically subserves the identification and matching of common objects based on presemantic perceptual characteristics or what has been termed 'structural descriptions'[19] of objects.

The ventral posterior activations also extended into regions outside of cortex, namely the right- and left-sided lateral cerebellum. The cerebellum has been strongly implicated in previous PET studies of motor phenomena.[20] However, it is unlikely that the cerebellar activation found in the present study reflects motor contributions to performance in the object matching task because the motor demands, such as manual response execution, were identical in both matching tasks. Instead, it is more likely that this activation reflects cognitive contributions of the cerebellum to visual object matching. In this respect, our study adds to the growing evidence showing cerebellar involvement in non-motor functions,[21,22] although the specific component processes of visual object matching that are mediated by the cerebellum have yet to be determined.

Conclusion

The present results provide direct support for Ungerleider and Mishkin's dual pathway model of vision in humans. They extend previous findings in that they show that this model also holds for visual object identification and object localization when common objects rather than faces are processed. Compared with previous PET results, the results of the present study demonstrate that the pattern of lateralization may vary in the ventral pathway depending on whether common objects or faces are processed, and in the dorsal pathway depending on what type of spatial processing is required.

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General Summary
A brain imaging study was conducted in humans to compare by using positron emission tomography (PET) which brain regions are activated during visual object identification and during visual object localization. Subjects engaged in a spatial task in which they matched the location of common objects, and an object task in which they matched the identity of common objects. Our brain imaging data showed that a right-sided region in the parietal cortex was more active during spatial than object matching whereas bilateral, prevailing left-sided regions in the occipitotemporal cortex were more active during object than spatial matching. These results provide support for models of the brain which propose that the visual system of humans can be divided into two pathways, one that is specialized for identifying 'what' an object is, and another one that is specialized for locating 'where' an object is. Our findings also suggest that both visual pathways may be differently organized in the two hemispheres.