Distinct neural correlates of visual long-term memory for spatial location and object identity: A positron emission tomography study in humans

(visual cortex/hippocampus)

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ABSTRACT The purpose of the present study was to investigate by using positron emission tomography (PET) whether the cortical pathways that are involved in visual perception of spatial location and object identity are also differentially implicated in retrieval of these types of information from episodic long-term memory. Subjects studied a set of displays consisting of three unique representational line drawings arranged in different spatial configurations. Later, while undergoing PET scanning, subjects' memory for spatial location and identity of the objects in the displays was tested and compared to a perceptual baseline task involving the same displays. In comparison to the baseline task, each of the memory tasks activated both the dorsal and the ventral pathways in the right hemisphere but not to an equal extent. There was also activation of the right prefrontal cortex. When PET scans of the memory tasks were compared to each other, areas of activation were very circumscribed and restricted to the right hemisphere: For retrieval of object identity, the area was in the inferior temporal cortex in the region of the fusiform gyrus (area 37), whereas for retrieval of spatial location, it was in the inferior parietal lobule in the region of the supramarginal gyrus (area 40). Thus, our study shows that distinct neural pathways are activated during retrieval of information about spatial location and object identity from long-term memory.

A primary question in research on the neuroanatomical basis of memory is whether long-term memory (LTM) for object identity and spatial location is mediated by different neural systems (1–5). With regard to perception, studies in humans and other species have indicated that the dorsal visual pathway that includes regions of parietal cortex is involved in perception of spatial location, whereas the ventral visual pathway that includes structures in inferotemporal cortex is involved in processing information about object identity[§] (6, 8–12). Models of recognition memory have posited that the very pathways involved in perceptual processing of stimuli also participate in their storage and recovery (13–15). Recovery of information about spatial location and object identity from LTM should, therefore, activate the dorsal and ventral pathways differentially. Partial support for this hypothesis comes from positron emission tomography (PET) studies in humans in which it has been reported that retrieval from LTM for words and faces activates areas in the posterior and inferior convexity of the temporal lobes, structures that are also involved in perception of these materials (16, 17). There are no PET studies, however, on LTM for spatial location nor any studies designed to determine whether memory for the location and identity of the

very same stimuli is mediated by different structures. The purpose of the present study was to investigate by using PET whether the cortical pathways that have been shown to be involved in perception of spatial location and object identity (11, 12) are also differentially implicated in retrieval of these types of information from episodic LTM.

Brain activity was measured while subjects' memory for spatial location and object identity was tested. Subjects were presented with pairs of displays and had to indicate which was novel and which was identical to one they had studied earlier. The novel one differed with respect to either spatial location (spatial retrieval task) or identity of an object depicted in the drawings (object retrieval task). To determine whether distinct neural pathways were involved in retrieval of these two types of information from episodic LTM, we subtracted the brain activity associated with one type of retrieval from the activity associated with the other. If the dual pathway hypothesis also holds for LTM, then subtracting spatial-memory activity from object-memory activity should reveal greater activation in the ventral pathway, whereas when the subtraction is reversed, activation should be greater in the dorsal pathway. As a check that the brain activity we were measuring was related to retrieval from LTM memory rather than merely to perceptual, attentional, and working memory processes involved in comparing two displays, we included a perceptual task in which subjects merely had to indicate whether two displays were the same or different from each other without any reference to LTM. To control for possible confounding effects of different stimulus variables across tests, we used identical target stimuli in each of the conditions.

METHODS

Experimental Procedure. While lying in the PET scanner, 15 min prior to the first scan, subjects studied 28 visual displays of the type illustrated in Fig. 1a. Each display consisted of representational line drawings (18) of three unique objects arranged in unique spatial configurations and presented on a computer screen at a distance of 60 cm. Each drawing could appear in any but the corner positions of an imaginary 6 × 8 grid into which the 38-cm screen was divided. The set of

Abbreviations: LTM, long-term memory; PET, positron emission tomography; rCBF, regional cerebral blood flow.

[§]Although there is no disputing the existence of the dorsal and ventral pathways, opinions differ regarding their function. For example, whereas Ungerleider and Mishkin (6) emphasize the type of information, spatial and object, processed in the two streams, Goodale and Milner (7) focus on the action and cognitive systems to which the pathways belong. For Goodale and Milner (7), the dorsal stream is part of an action system that codes information necessary for manipulation and movement. The ventral stream, on the other hand, is concerned with identification and awareness.

FIG. 1. Examples of displays used in the different experimental tasks. (a) Study task. (b) Perceptual baseline task. (c) Object retrieval task. (d) Spatial retrieval task.

displays was presented five times in random order and the subjects were instructed to memorize the objects and their spatial location.

After the study phase and while in the PET scanner, subjects undertook the three different tasks of interest, each presented twice in counterbalanced order while PET scans were taken. In each task, pairs of displays were presented successively. Each pair consisted of two triplets presented for 1 sec each with a 0.75-sec interdisplay interval. The interpair interval was 2.25 sec. The subjects reported their responses by pressing the keys of a computer mouse with the right hand. In the perceptual baseline task, two successive displays were both from the studied pool of 28 and subjects had to indicate whether the two displays were identical or different (Fig. 1*b*). The memory tasks were two-item forced-choice recognition tests. In the object retrieval task (Fig. 1*c*), one display in each pair had been studied previously and the other was identical to it except that one of the objects was replaced by a new one that had not been seen earlier. In the spatial retrieval task (Fig. 1*d*), one display of each pair had been studied previously and the other was identical to it except that the spatial location of one of the objects was altered. In both memory tasks, subjects had to indicate which display was the altered one. These memory tasks are comparable to delayed nonmatching-to-sample tasks that are used to test recognition memory in nonhuman species.

Subjects. Twelve male and one female young right-handed volunteers participated in the present study. Subjects were screened to ensure the absence of any medical, neurological, or psychiatric disorder. Data for all subjects are presented here.

PET Scanning. Subjects were scanned in a GEMS-PC-2048-15B scanner with a custom-fitted thermoplastic face mask that permitted unobstructed viewing of the computer screen on which the stimuli were presented. Each scan was acquired after a bolus injection of 40 mCi of [^{15}O]water (1 Ci = 37 GBq) injected into a left forearm vein through an indwelling catheter (19). The cognitive task was started 45 sec prior to the 60-sec data acquisition for each scan. The scans were 11 min apart. The PET images were attenuation-corrected by using a transmission scan acquired prior to the first PET scan. The scans were reconstructed by using a Hanning filter with a cut-off frequency of 0.5 Hz. In an effort to avoid the invasiveness associated with an arterial puncture, normalized integrated regional counts were used as an index of regional cerebral blood flow (rCBF), as has been done in other studies (20, 21), because integrated regional counts are linearly correlated with rCBF (22).

PET scans were analyzed by using statistical parametric mapping developed and made available to us by K. J. Friston and colleagues at the Hammersmith Hospital (London). The statistical parametric mapping method of PET image analysis involves stereotactic reorientation of images, a transformation of images to fit a standard space, and correction for global differences in counts across scans (23, 24). The obtained normalized index for rCBF is then compared between different tasks at every voxel. Significance of any observed changes is determined by dividing the observed difference with the error variance at that voxel. 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). Empirically, such a method of analysis has been shown to guard against the excessive occurrence of false-positive errors (25).

RESULTS

At the behavioral level, response accuracy was >87% in each of the conditions, indicating that the brain activity being measured was associated with consistently successful perceptual processing and memory retrieval. Performance, however,

FIG. 2. Cerebral regions that show an increased rCBF (at $P < 0.001$) in the four comparisons. (a) Spatial retrieval minus perceptual baseline. (b) Object retrieval minus perceptual baseline. (c) Spatial retrieval minus object retrieval. (d) Object retrieval minus spatial retrieval. To aid visualization, the right-sided activations are rendered onto idealized drawings of the right lateral cortical surface, which were taken from the Talairach and Tournoux atlas (24) (see Table 1 for a complete listing of observed activations).

was significantly higher in the perceptual baseline task (97.7% correct) than in the object retrieval [92.8% correct, $t(12) = 4.49$, $P < 0.001$] and the spatial retrieval task [87.4% correct, $t(12) = 4.28$, $P < 0.001$]. Compared to the perceptual baseline task, both retrieval tasks produced greater activity in both the ventral and dorsal pathways in the right hemisphere (Fig. 2 *a* and *b* and Table 1) and in the midline cerebellum and the cuneus region bilaterally. Ventrally, this activity extends as a discrete band into the right-sided occipitotemporal and fusiform gyrus (area 37), whereas dorsally it extends into right-sided superior occipital gyrus (area 19) and the angular-supramarginal gyrus in the inferior parietal lobe (Brodmann's areas 39 and 40). These increases were predominantly lateralized to the right hemisphere. Retrieval in each of the memory tasks was associated with a significant localized activation in the right prefrontal cortex, in the posterior regions of the right inferior frontal and right middle frontal gyrus.

Decreases in activation in comparison to perceptual baseline were observed for both the spatial and object retrieval task in mesial frontal cortex bilaterally and in the left superior and right inferior middle temporal gyrus. Decreases in activation were noted in the retrosplenial and cingulate cortex bilaterally

and in the left inferior middle temporal gyrus only for the spatial memory task.

A direct comparison of the retrieval tasks shows greater activity during the spatial retrieval task in a circumscribed region of the dorsal pathway, the right inferior parietal lobule in the region of the supramarginal gyrus (Fig. 2*c* and Table 1). This region corresponds to the site of lesion that produces selective spatial memory deficits in neurological patients (8–10). In contrast, object retrieval distinctively activated the ventral pathway in the right posterior inferotemporal cortex in the region of the fusiform gyrus (Fig. 2*d* and Table 1).

DISCUSSION

Our results provide clear evidence in support of the dual pathway model for episodic LTM: although both pathways were activated in each memory task, retrieval of object identity was associated with greater activity in the right posterior inferotemporal cortex, whereas retrieval of spatial location was associated with greater activity in the right inferior parietal lobule (6, 11). That both pathways were activated in each retrieval task suggests that recognition in either memory task

Table 1. Brain areas manifesting significant activation changes in rCBF

		Talairach and Tournoux coordinates, mm				
Parameter	Region	x	y	z	Z score	
Spatial memory minus perceptual baseline Increases	Bilateral cuneus (areas 18 and 19)	26	−74	20	3.9	
		−22	−74	20	3.7	
	Right inferior temporal/fusiform gyrus (areas 20 and 37)	42	−52	−16	4.3	
		42	−62	−8	4.2	
	Left inferior temporal (areas 19 and 37)	−40	−74	−12	3.9	
	Right supramarginal/inf. parietal lobule (areas 39 and 40)	22	−64	32	5.0	
		26	−58	40	5.5	
		28	−50	48	4.0	
	Right inferior midfrontal (areas 44, 45, and 46)	34	32	16	3.8	
		36	22	24	4.9	
	Bil. ant. sup. cerebellum	−10	−52	−4	3.8	
	Mid. retrosplenial, cingulate (areas 23, 29, and 30)	2	−48	20	4.1	
		2	−48	32	4.4	
		Rt. inf. mid. temporal gyrus (areas 20 and 21)	48	−2	−12	4.0
Decreases	Lt. inf. mid. temporal gyrus (areas 20 and 21)	−50	−12	−16	3.8	
	Lt. superior temporal gyrus (area 22)	−50	−52	20	4.4	
	Bil. mesial frontal (areas 9, 10, and 32)	0	52	−4	4.1	
		−10	54	8	3.5	
		8	46	24	4.0	
	Object memory minus perceptual baseline Increases	Rt. cuneus (area 19)	26	−70	20	3.5
		Rt. supramarginal/inf. parietal lobule (areas 39 and 40)	24	−60	32	4.2
			26	−56	40	4.0
		Rt. inferior temporal/fusiform gyrus (areas 20 and 37)	40	−52	−16	5.1
			42	−54	−12	4.5
			40	−60	−4	3.4
		Rt. inf. mid. frontal (areas 44 and 46)	40	24	24	3.7
		Bil. ant. sup. cerebellum	6	−40	−12	4.1
			−4	−40	−4	3.7
		Rt. inf. mid. temporal gyrus (areas 20 and 21)	38	0	−12	3.4
Lt. sup. temporal gyrus (area 22)		−50	−48	16	3.8	
Bil. mesial frontal (areas 9, 10, and 32)		0	48	−8	4.0	
		2	56	4	4.7	
		6	44	24	4.0	
Spatial memory minus object memory	Right supramarginal/inferior parietal lobule (area 40)	44	−36	36	3.5	
Object memory minus spatial memory	Right inferior temporal/fusiform gyrus (area 37)	30	−52	−12	3.6	

Activated regions are listed by name and Brodmann area number(s) with representative peak coordinates as described by the Talairach and Tournoux atlas (24). The magnitude of those activations is expressed as a Z score. Names and Brodmann areas were chosen to capture best the sets of activated voxels with Z scores >3.1.

involves retrieval of both types of information to some extent. In addition, there is some suggestive evidence from our findings that in comparison to perceptual baseline, differences between spatial and nonspatial memory processes are found in retrosplenial cortex and cingulate cortex, two structures anatomically linked to the hippocampus. If confirmed and extended, the latter finding would support the theory that spatial and nonspatial memory are mediated by different components of the hippocampal complex. Because identical stimuli were used in all conditions, the different patterns of activation observed in the two memory conditions cannot be attributed to stimulus variables.

In their exact location, the areas implicated in retrieval, from LTM are closely related to, yet different from those involved in perception (11, 12), attention (26, 27), and working memory (28, 29) for spatial location and object identity. Whereas the dorsal and ventral areas are typically activated bilaterally in perceptual tasks (11), activation is predominantly unilateral in the memory tasks in our study and in other PET (16) and lesion (4, 5) studies. This pattern of results is consistent with a model of hemispheric specialization that posits that lateralization occurs primarily at later stages of processing (30). In addition, memory retrieval, in comparison to perception, involves greater activation of the right prefrontal cortex. This frontal asymmetry has been observed in all published PET studies regardless of whether the material was verbal or nonverbal, suggesting that the right prefrontal cortex is differentially involved in retrieving information from LTM (31, 32). Our results indicate that the same region of prefrontal cortex is activated in both memory tasks albeit somewhat more strongly by the spatial location one.

It is also unlikely that our results only reflect differences between object identity and spatial location in working memory and attention. The working memory component of the perceptual baseline task is comparable to that in the two LTM tasks. Subtracting the activation associated with the perceptual baseline task from that of the memory tasks should not have produced any differences. More to the point, the regions that were differentially activated by the two memory tasks are in the posterior neocortex and not in the prefrontal cortex, as one would expect them to be if the primary differences between them were in working memory (28, 29).

Similarly, the areas involved in allocating attention to spatial location and to object identity do not correspond to those we observed in our memory tests. Allocating attention to spatial location and to objects involves, among other regions, superior parietal cortex (area 7) and posterior inferior temporal cortex on the left (26, 27), respectively, whereas it was inferior parietal cortex (area 39) and the inferior temporal lobe (area 37) on the right that were differentially activated during the memory tests. Our finding of relative decreases in activation in the left temporal cortex is consistent with the idea that this area may be activated more during perception than memory. Moreover, areas that are typically activated during attention, such as the pulvinar and the anterior cingulate (33, 34), were not activated in the memory conditions and even showed relative deactivation in the region of the anterior cingulate.

Thus, the different patterns of cerebral activation that we found in the parietal and temporal lobes likely reflect differences in episodic memory for spatial location and object identity rather than differences in perception, working memory, and attention. Our finding of right prefrontal activation on both memory tasks suggests that recognition was not based only on familiarity, a relatively automatic process that is mediated by structures other than prefrontal cortex, but included active search and monitoring of information in LTM (15, 35).

The observed activation of the cerebellum adds to the growing body of evidence that the cerebellum is involved in a variety of cognitive tasks, particularly those associated with

learning and memory (36, 37). Exactly what role the cerebellum plays in retrieval from LTM has yet to be determined.

Decreased activation in the retrosplenial and posterior cingulate cortex was found during retrieval of spatial location but not object identity. Lesions of the retrosplenial cortex are associated with severe memory deficits in humans (38, 39) and other species (40), presumably because this region receives output from structures that make up the hippocampal system and that are known to be crucial for memory. The different pattern of decreased activation in the spatial location and object memory tasks hints that structures in the hippocampal system are differentially involved. Consistent with our observation of greater activation during perception than retrieval, recent evidence indicates that the hippocampus and related structures are activated more strongly when individuals process novel, as compared to familiar, photographs of complex visual scenes (41). These results suggest that the hippocampus and related structures are involved more at encoding than at retrieval. Additional PET studies should be able to build on these findings to help resolve the long-standing debate concerning the function of the hippocampus and surrounding structures in spatial and nonspatial memory (1–5).

Our findings are consistent with the view that retrieval from LTM is a multicomponent process that involves a network of structures. Our results support those models of memory that propose that engrams of particular events are represented in domain-specific posterior neocortical structures closely related to those initially involved in perception and identification of those events (13–15). Thus, the inferior parietal cortex and inferotemporal cortex in the right hemisphere are differentially involved in recovering information about spatial location and object identity from LTM. Whether this division extends to structures making up the hippocampal formation is still not known. In contrast, the frontal lobes were found to be implicated on tests of both types of memory, a finding that supports the idea that the frontal lobes are central system structures (15, 42) that mediate organizational and strategic operations across domains and tasks.

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