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Face encoding and recognition in the human brain

(positron emission tomography/cerebral blood flow)

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ABSTRACT **A dissociation between human neural systems that participate in the encoding and later recognition of new memories for faces was demonstrated by measuring memory task-related changes in regional cerebral blood flow with positron emission tomography. There was almost no overlap between the brain structures associated with these memory functions. A region in the right hippocampus and adjacent cortex was activated during memory encoding but not during recognition. The most striking finding in neocortex was the lateralization of prefrontal participation. Encoding activated left prefrontal cortex, whereas recognition activated right prefrontal cortex. These results indicate that the hippocampus and adjacent cortex participate in memory function primarily at the time of new memory encoding. Moreover, face recognition is not mediated simply by recapitulation of operations performed at the time of encoding but, rather, involves anatomically dissociable operations.**

In humans and nonhuman primates, damage to the hippocampus and adjacent cortex produces a profound anterograde amnesic syndrome that impairs the ability to form and store new explicit memories (1–5). Although recall for previously stored information can remain largely intact (1, 4, 6), the retrieval of recently formed memories may be impaired (3). Thus, for a limited time after initial storage, access to memories does depend on the integrity of the medial temporal structures, suggesting that these structures may actively participate not only in memory storage but also in the retrieval of recently stored memories.

Despite this clear evidence of memory impairment after medial temporal lesions, functional brain imaging studies of human memory have been mostly unsuccessful in demonstrating the participation of the hippocampus and adjacent cortex in either the encoding or the retrieval of new long-term memories (7–12). These same studies, however, consistently demonstrate that the frontal lobes participate in episodic memory encoding and retrieval, although studies of the effects of frontal lobe lesions suggest these areas do not play a critical role in episodic memory processing (13–18). Most previous functional brain imaging studies of memory have used verbal materials and have demonstrated a functional dissociation between left and right prefrontal areas. Whereas left prefrontal areas are activated during episodic verbal memory encoding, right prefrontal areas are activated during retrieval. Although some studies suggest that right prefrontal areas might also be involved in the retrieval of nonverbal long-term memories, no studies of nonverbal memory encoding have been reported.

To clarify the roles played by these brain structures in episodic memory, we investigated memory for a different type of information—namely faces—using an experimental design that allows separate identification of neural systems that participate in memory encoding and recognition. The results demonstrated an almost complete dissociation between these memory functions.

Some of the data from this study are presented elsewhere (19) in a less complete form as a basis for comparison in a study of the effects of normal aging.

METHODS

Subjects. Ten healthy young adults (eight men and two women) participated in this study. All gave written, informed consent.

Tasks. Eight positron emission tomography (PET) regional cerebral blood flow (rCBF) scans were obtained while subjects performed face encoding, face recognition, face perception control, and sensorimotor control tasks. Stimuli for all tasks consisted of three white squares, each containing either a face or a nonsense pattern (Fig. 1) and were presented for 4 sec with a 1-sec interstimulus interval. On the face encoding task, a set of 32 faces was presented sequentially three times in different orders, for a total duration of 8 min. Subjects were instructed to try to commit each face to memory and were told that their memory for the faces would be tested on a later scan. On the face recognition task, subjects were asked to indicate which choice stimulus was one of the faces they had attempted to memorize. On the face perception control task, subjects were asked to indicate which of the lower squares (choice stimuli) contained the same face as the upper square (sample stimulus). On the sensorimotor control task, all three squares contained the nonsense pattern and no perceptual or memory judgments were required. The faces for all tasks were unfamiliar and were not repeated on subsequent tasks, except for the presentation of memorized faces on the recognition task. On all tasks, subjects responded by pressing a button with the right or left thumb. On the face perception and recognition tasks, subjects pressed the button on the side of the matching choice stimulus. On the face encoding task, subjects pressed the button on the side that the face appeared. On the sensorimotor control task, subjects pressed the buttons in alternating order. Prior to the day of scanning, subjects were pretrained on a complete set of these tasks with different faces.

The sensorimotor control task was always presented on the first and last scans. The other tasks were always presented in the same order: face encoding, face perception, and face recognition. Two such triplets of face processing scans, using different sets of faces, were obtained for each subject. Scans were obtained at 12-min intervals. Consequently, 16 min separated the presentation of the last encoding item and the first recognition item. This delay included over 5 min of face

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Abbreviations: PET, positron emission tomography; rCBF, regional cerebral blood flow.

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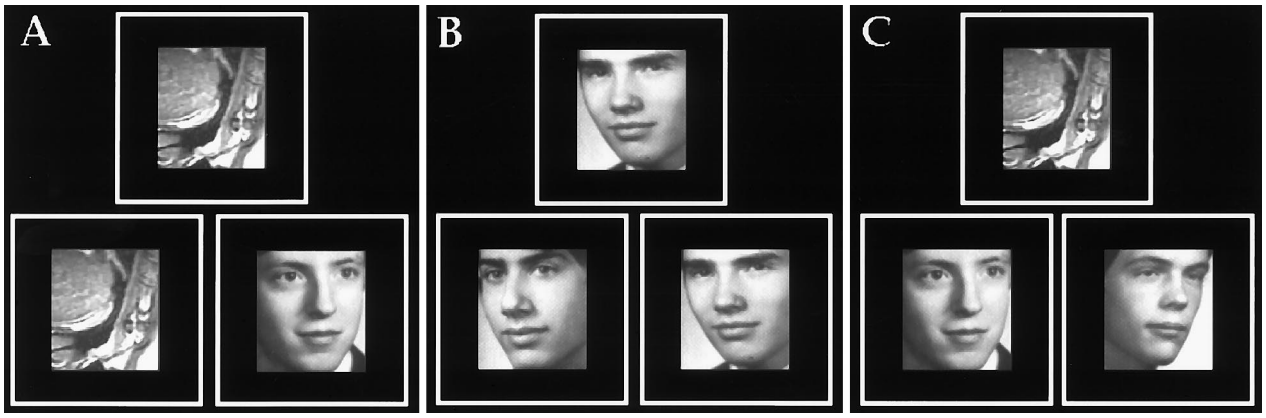

FIG. 1. Examples of stimuli for the face encoding (*A*), face perception (*B*), and face recognition (*C*) tasks.

perception items, with unfamiliar faces, preventing covert rehearsal of the face memories.

PET Scanning. PET scans were obtained with a Scanditronix model 2048-15B scanner (Scanditronix, Milwaukee) using methods described elsewhere (20). Each task began 1 min before the intravenous injection of 37.5 mCi (1 Ci = 37 GBq) of $H_2{}^{15}O$. rCBF values, in units of ml per 100 g per min, were calculated for each pixel (21).

Statistical Analysis. Data were analyzed using statistical parametric mapping (22–24) to identify voxels demonstrating rCBF differences between tasks, as described elsewhere (20, 25). The statistical significance of activations and deactivations was assessed based on their spatial extent (26).

Two sets of comparisons were made to identify the brain regions that participated in the memory processes associated with face encoding and recognition. The first set compared rCBF during the encoding and recognition tasks to rCBF during the perception control task. These comparisons identified regions that demonstrated changes in activity specifically associated with memory operations over and above activity associated with perceptual operations shared by all tasks. The second set compared rCBF during the encoding and recognition tasks to rCBF during the sensorimotor control task. These comparisons were made primarily to detect whether any of rCBF increases relative to the perception task are attributable to deactivation during perception as opposed to activation during a memory task.

RESULTS

Comparisons between the memory tasks and the perception control task demonstrated almost no overlap between brain regions activated by encoding new memories for faces and by subsequent recognition of those faces (Fig. 2 and Table 1). The face encoding task was associated with increased rCBF in a right medial temporal region that included the hippocampus and adjacent cortex and with additional cortical activations in an extensive region of left prefrontal cortex, with foci in mid and inferior frontal gyri, in anterior cingulate cortex, and in the left inferior temporal gyrus. By contrast, the face recognition task was associated with increased rCBF in an extensive region of the right prefrontal cortex, with foci in mid and inferior frontal gyri, in anterior cingulate cortex, in bilateral inferior parietal cortex, in bilateral ventral occipital cortex, and in the cerebellum. Recognition was also associated with a significant rCBF decrease in a left anterior temporal area that could be either insular or lateral cortex near the superior temporal sulcus. Both encoding and recognition were associated with decreased rCBF in calcarine cortex.

Relative to the sensorimotor control task, the face encoding and recognition tasks demonstrated activations in an extensive, bilateral region of ventral occipitotemporal cortex in addition to most of the areas demonstrating activations relative to the perception control task (Table 2). The overlap between areas demonstrating activation relative to the perception and sensorimotor control tasks was incomplete in three locations. Relative to the sensorimotor control, the left frontal area associated with encoding did not include the midfrontal region, the right hippocampal region associated with encoding included the posterior but not the anterior sector, and the left parietal area associated with recognition was not of sufficient spatial extent to attain statistical significance (volume = 0.9 cm^3). Significant decreases relative to the sensorimotor control task were observed for both face encoding and recognition in an extensive bilateral region of perisylvian and postcentral cortex in addition to all of the areas demonstrating decreases relative to the perception control task. The face perception task, as compared to the sensorimotor control task, was not associated with any trend toward activation in frontal cortex but was associated with an rCBF decrease in the left midfrontal gyrus (local maximum: −28, 32, 36; $Z = -4.13$).

Performance on the recognition task was significantly less accurate compared to the perception control task [80% (SD = 7%) vs. 99% (SD = 2%)] with slower response times [2005 ms (SD = 602) vs. 1544 ms (SD = 550)].

DISCUSSION

These results demonstrate that right medial temporal lobe structures participate in memory for faces at the time the visual experience is committed to memory but not in the subsequent recognition of recently stored memories. A region including the right hippocampus and adjacent cortex was activated while subjects attempted to commit unfamiliar faces to memory but was not activated when subjects attempted to recognize the faces they had memorized. Moreover, cortical regions that participate in face memory encoding and recognition are largely dissociable. Whereas left prefrontal and left inferior temporal areas were associated with face memory encoding, right prefrontal and bilateral parietal and ventral occipital areas were associated with face recognition. The lateralization of prefrontal activations is consistent with Tulving's hemispheric encoding and retrieval asymmetry (HERA) hypothesis and demonstrates that it holds for visual nonverbal as well as for verbal memory processing.

Lesions to medial temporal lobe structures in humans and monkeys result in a dense anterograde amnesia (1–5), indicating that they play a critical role in the encoding of new memories. Lesion studies have also shown that for an extended period of time after the initial encoding of a memory, access to that memory is dependent on the integrity of these same medial temporal structures (3). This dependency, however, was not evident as reactivation of the hippocampus or adjacent cortex at the time of memory recognition, suggesting that these

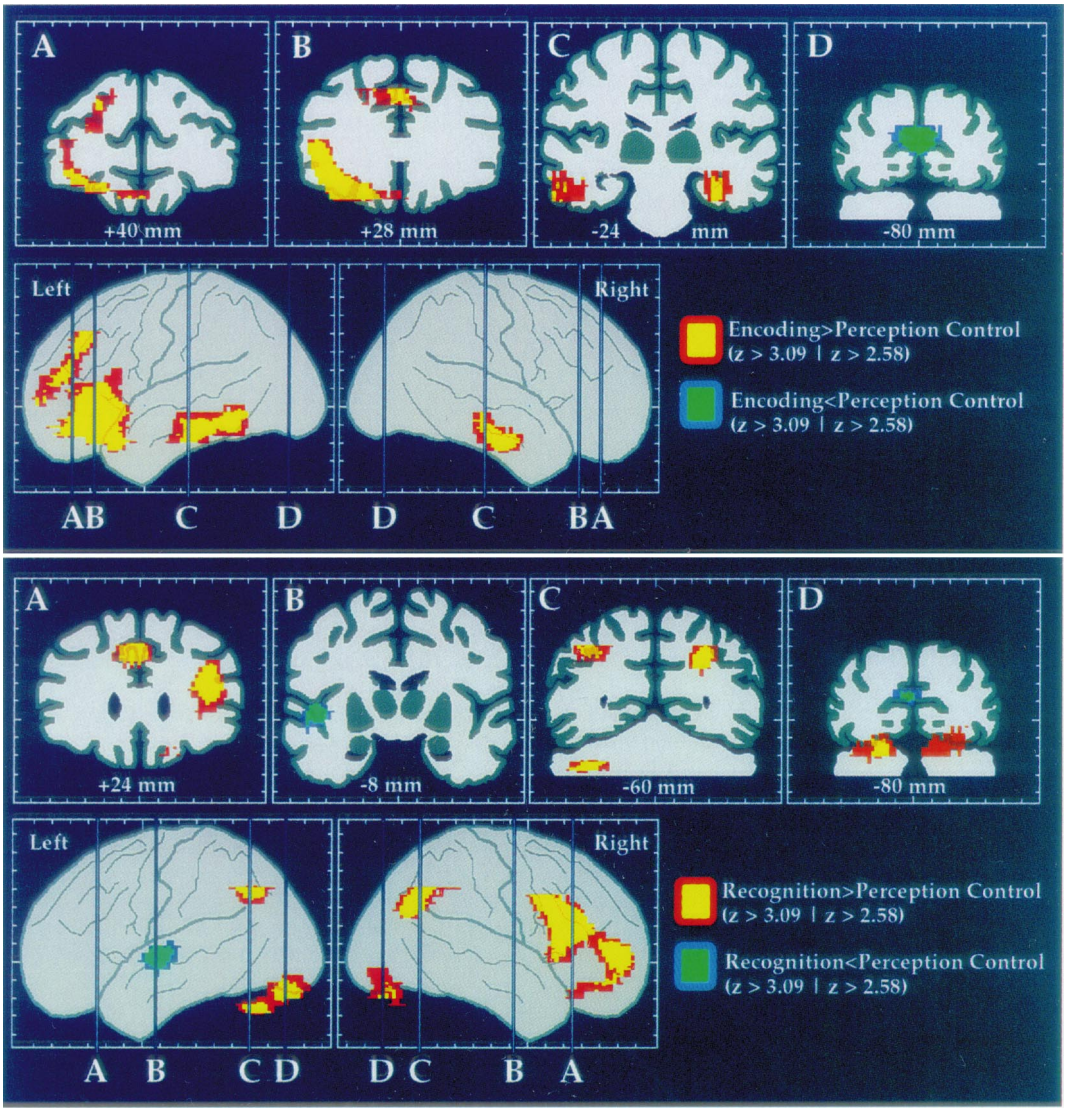

FIG. 2. Areas that showed significant increases and decreases in rCBF associated with face memory encoding (*Upper*) and face recognition (*Lower*) as compared to a face matching perceptual control task. Only clusters of contiguous voxels of sufficient spatial extent to be statistically significant ($P < 0.05$) are shown (26). Lateral views show maximum intensity projections of voxels more than 2 cm from the midline. Coronal sections indicate the depth within cortex of activations and deactivations. The levels from which coronal sections were made are indicated on the lateral views. Tick marks on the frames around each view are placed at 1-cm intervals relative to the location of the anterior commissure. Note that the right temporal area of activation during encoding (coronal section C) is located medially, whereas the left temporal area is located laterally.

structures do not participate in the representation of recently stored memories or in operations involved in their retrieval. Rather, our findings suggest that recently stored memories could be represented only in neocortex, as older memories presumably are, but in a less stable form. After initial storage, the role of the hippocampus and adjacent cortex may be to convert this unstable representation to a more stable one over an extended period of time. This process may be unrelated to operations that are performed at the time of memory retrieval. According to this view, an amnesia-producing insult would stop this protracted consolidation process, leading to increased forgetting of recently stored memories.

In contrast to this study of face memory, functional brain imaging studies of verbal memory have not demonstrated the participation of the hippocampus and adjacent cortex during encoding (8, 10, 11) and have been mostly unsuccessful in demonstrating their participation during retrieval. One study of cued word recall found a right medial temporal activation (7), but follow-up studies showed that the effect was related to the physical form of the cue, not to the verbal memory (12). In another set of verbal memory studies (28–30), hippocampal activation was associated with a task that did not distinguish between encoding and retrieval. The hippocampal activation associated with face memory encoding may be due to a fundamental difference between word and face memorization. Words on a memorization list are familiar, whereas faces in a memorization set are novel and unfamiliar. Perhaps the hippocampal activity associated with face encoding reflects the detection of novelty and the encoding of an unfamiliar face's unique configuration.

The most striking neocortical dissociation involved the lateralization of prefrontal participation in face memory, with left prefrontal areas participating in encoding and right prefrontal areas participating in recognition, which is the same direction of prefrontal asymmetry that has been found in prior PET-rCBF studies to be associated with encoding and retrieval of verbal material (8–11). Moreover, the prefrontal regions activated by face memory processing coincide with the regions that are activated by verbal memory processing, suggesting that their general role in memory is independent of information type. The left prefrontal area associated with face encoding was primarily in the inferior and orbitofrontal cortex and

Table 1. Local maxima in regions demonstrating significant rCBF increases and decreases during encoding and recognition tasks as compared to the perceptual matching task

Region	Brodmann area*	Talairach coordinates†			*Z* score
		x	*y*	*z*	
Encoding					
Left frontal (33 cm^3, $P < 0.0001$)‡					
Inferior and orbitofrontal	11/47	−33	27	−12	4.55
Midfrontal	46	−26	42	16	3.80
Midfrontal	8/9	−20	36	32	3.59
Anterior cingulate	32	2	26	36	3.66
Right medial temporal (5.9 cm^3, $P < 0.002$)					
Hippocampus		28	−10	−20	3.86
Hippocampus		34	−24	−12	3.80
Left inferior temporal (9.7 cm^3, $P < 0.0001$)					
Inferior temporal	20	−56	−34	−12	3.65
Inferior temporal	37	−50	−52	−8	3.68
Medial occipital (9.7 cm^3, $P < 0.0001$)					
Calcarine	17	−4	−86	12	−4.82
Recognition					
Right frontal (19.4 cm^3, $P < 0.0001$)					
Mid and inferior frontal	9/45	36	22	20	4.35
Mid and inferior frontal	8/44	44	8	32	3.77
Midfrontal	10	34	54	4	3.98
Anterior cingulate (4.7 cm^3, $P < 0.01$)					
Anterior cingulate	8/32	−2	24	40	4.83
Right parietal (4.4 cm^3, $P < 0.02$)					
Inferior parietal	7/39	26	−64	28	3.79
Left parietal (3.2 cm^3, $P < 0.05$)					
Inferior parietal	7/39	−38	−62	36	3.64
Right ventral posterior (4.6 cm^3, $P < 0.01$)					
Ventral occipital	18	24	−84	−8	3.07
Lateral cerebellum		14	−78	−20	3.32
Left ventral posterior (6.9 cm^3, $P < 0.001$)					
Ventral occipital	18	−36	−84	−12	2.82
Lateral cerebellum		−41	−63	−28	3.82
Lateral cerebellum		−20	−80	−20	3.61
Midline cerebellum		−4	−66	−28	3.10
Medial occipital (3.9 cm^3, $P < 0.05$)					
Calcarine	17	−4	−86	12	−4.53
Anterior temporal (3.6 cm^3, $P < 0.05$)					
Insula/superior temporal sulcus	22	−46	−8	4	−4.08

*Designation of Brodmann areas is approximate and based on a brain atlas.
†Brain atlas coordinates are in millimeters along left–right (*x*), anterior–posterior (*y*), and superior–inferior (*z*) axes (27).
‡Numbers in parentheses are the volumes for each region and the probability that a region of contiguous voxels exceeding a threshold *Z* score of 2.58 could occur anywhere in the brain by chance.

included the foci associated with verbal memory encoding in two previous PET-rCBF studies (9, 11). A left midfrontal area demonstrated a significant increase relative to the perception control but not to the sensorimotor control, suggesting it may have been activated by both the face encoding and the sensorimotor control task. Activation during the sensorimotor control task may reflect the working memory required by this task because of alternating responses. The right prefrontal region associated with face recognition included an anterior midfrontal area and a large, more posterior area that included both midfrontal and inferior frontal areas. The anterior midfrontal area and the dorsal part of the posterior area coincide well with foci associated with verbal memory retrieval in three previous PET-rCBF studies (10–12), but the inferior part of the posterior area coincides with a focus in only one of these studies (11).

Although PET-rCBF memory studies consistently implicate prefrontal cortex, neuropsychological studies of patients with frontal lesions suggest that this cortex is not critical for either memory encoding or retrieval. In general, patients with frontal lesions perform well on tests of delayed memory for prose, paired associates, word lists, spatial locations, and objects (13–18). On the other hand, patients with frontal lesions do demonstrate impairment on tests of memory for temporal and sequential information (17, 18, 31, 32). Prefrontal activations associated with memory encoding and retrieval, therefore, may be due to encoding and retrieving the circumstances of the event during which learning occurred, operations that may be invoked relatively automatically (33), even when contextual information is not critical for memory test performance. Encoding and retrieval of the spatiotemporal context of an event is the hallmark of episodic memory. In another PET-rCBF study of face recognition that involved semantic, as opposed to episodic, memory retrieval, no dorsolateral frontal activations were observed in either hemisphere (34), indicating that the frontal activations associated with face recognition in the current study may be specifically related to the more episodic nature of the face memories.

The memory-related operations performed by other neocortical areas are undetermined. The left inferior temporal area activated during encoding may be an extrastriate visual area recruited for elaborative perceptual processing. The parietal and anterior temporal areas that demonstrated increased and decreased rCBF, respectively, with recognition

Table 2. Local maxima in regions demonstrating significant rCBF increases and decreases during encoding and recognition tasks as compared to the sensorimotor control task

Region	Brodmann area	Talairach coordinates			*Z* score
		x	*y*	*z*	
Encoding					
Frontal (18.5 cm^3, $P < 0.0001$)					
Left orbitofrontal	11	−24	32	−16	3.78
Left inferior frontal	45	−42	24	8	3.73
Midline orbitofrontal	11	4	38	−20	3.90
Right anterior cingulate	24	16	32	8	3.50
Bilateral ventral occipitotemporal (62 cm^3, $P < 0.0001$)					
Right fusiform	19	34	−64	−12	6.03
Left posterior fusiform	18	−20	−76	−12	5.43
Left midfusiform/inferior temporal	37/20	−44	−42	−12	4.49
Left perisylvian and postcentral (19 cm^3, $P < 0.0001$)					
Primary auditory	41	−50	−14	8	−4.96
Inferior parietal	40	−50	−34	32	−4.93
Right perisylvian and postcentral (29 cm^3, $P < 0.0001$)					
Insula		38	−10	0	−4.16
Inferior parietal	40	50	−30	28	−4.64
Medial occipital (4.6 cm^3, $P < 0.005$)					
Calcarine	17/18	−6	−88	16	−3.91
Recognition					
Right frontal (4.8 cm^3, $P < 0.005$)					
Orbital and inferior frontal	11/47	20	40	−16	3.88
Right frontal (8.5 cm^3, $P < 0.0001$)					
Mid and inferior frontal	9/45	40	24	20	4.05
Midfrontal	46	30	44	8	3.94
Bilateral occipitotemporoparietal (62 cm^3, $P < 0.0001$)					
Right posterior fusiform	18	30	−74	−12	6.68
Right midfusiform	37	36	−52	−20	6.00
Left posterior fusiform	18	−20	−78	−12	5.87
Left posterior fusiform	19	−36	−76	−16	5.40
Lingual	18	−2	−72	0	4.58
Right inferior parietal	7/39	30	−64	36	4.13
Left perisylvian and postcentral (43 cm^3, $P < 0.0001$)					
Superior temporal	22	−46	−8	4	−7.30
Inferior parietal	40	−50	−36	32	−6.17
Right perisylvian and postcentral (58 cm^3, $P < 0.0001$)					
Superior temporal/insula	22	38	−10	0	−5.54
Postcentral/inferior parietal	2/40	52	−28	32	−5.24
Medial occipital and mid/posterior cingulate (21.8 cm^3, $P < 0.0001$)					
Calcarine	17/18	−2	−84	16	−3.26
Posterior cingulate	23/31	−4	−50	32	−5.83
Midcingulate	31	−4	−18	40	−4.74
Left mid and superior frontal (8.3 cm^3, $P < 0.0001$)					
Midfrontal	8/9	−30	34	36	−4.66
Midfrontal	8/9	−31	35	30	−4.64
Orbitofrontal (5.1 cm^3, $P < 0.005$)					
Orbitofrontal	24/32	−2	20	4	−3.72
Orbitofrontal/anterior cingulate	32	0	36	−4	−3.49

Designation of Brodmann areas, brain atlas coordinates, and statistical significances are as in Table 1.

have also been identified in PET-rCBF studies of auditory–verbal memory (9, 28), suggesting that they, like the prefrontal areas, may perform memory functions that are independent of information type.

The dissociation of areas activated during encoding and recognition indicates that operations that lead to explicit recognition of faces are not simply a recapitulation of operations performed during the initial visual experience. Areas in ventral occipitotemporal cortex that are associated with face perception (20) were activated by all face processing tasks, including perception, suggesting that these areas perform the same perceptual operations when viewing faces independent of mnemonic operations associated with the additional areas activated by encoding and recognition. It is still possible, however, that the activity in extrastriate perceptual areas does differ during encoding and recognition in ways that are not evident as changes in blood flow rates, perhaps as changes in the pattern of single cell responses or in the correlation with activity in other regions (35, 36).

In sum, distinct neural systems exist for face memory encoding and recognition. Many of the components of these systems appear to perform memory functions that are independent of the type of information to be encoded or retrieved. From the lesion literature, the structures known to be most critical to memory encoding and access to recently stored memories are the hippocampus and adjacent cortices. In the intact brain these structures were activated during memory encoding but not recognition, suggesting they do not participate in the

representation or retrieval of recently stored memories. Rather, these structures seem to act at the time of a visual experience to establish the representation of a new memory for that experience elsewhere, presumably in neocortex.

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