Functional Neuroanatomy of Recall and Recognition: A PET Study of Episodic Memory

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Abstract

■ The purpose of this study was to directly compare the brain regions involved in episodic-memory recall and recognition. Changes in regional cerebral blood flow were measured by positron emission tomography while young healthy test persons were either recognizing or recalling previously studied word pairs. Reading of previously nonstudied pairs served as a reference task for subtractive comparisons. Compared to reading, both recall and recognition were associated with higher blood flow (activation) at identical sites in the right prefrontal cortex (areas 47, 45, and 10) and the anterior cingulate. Compared to recognition, recall was associated with higher activation in the anterior cingulate, globus pallidus, thalamus, and cerebellum, suggesting that these components of the cerebello-frontal pathway play a role in recall processes that they do not in recognition. Compared to recall, recognition was associated with higher activation in the right inferior parietal cortex (areas 39, 40, and 19), suggesting a larger perceptual component in recognition than in recall. Contrary to the expectations based on lesion data, the activations of the frontal regions were indistinguishable in recall and recognition. This finding is consistent with the notion that frontal activations in explicit memory tasks are related to the general episodic retrieval mode or retrieval attempt, rather than to specific mechanisms of ecphory (recovery of stored information). ■

INTRODUCTION

Episodic memory refers to memory for specific events that a person has experienced at a particular time and place, including miniature events in a laboratory setting, such as the appearances of particular words, word pairs, or other items in a to-be-learned list (Tulving, 1983). In the standard laboratory paradigm, test persons are first exposed to these events, and subsequently tested for the information stored. Traditionally, two large classes of tests have been used: recall or recognition. In a typical recognition test (yes/no test), studied and nonstudied items are presented in a mixed sequence, and the test person's task is to decide which items are "old" (encountered in the study list) and which are "new" (not encountered in the study list). In a recall test, the test person's task is to produce the names of the studied items, either to general instructions alone (free recall) or to specific cues (cued recall).

Because episodic-memory recognition and recall tests require the test person to retrieve information about specific, prior, remembered events (exposure of items in the study list), they are referred to as "explicit" memory tests. They differ from "implicit" memory tests, such as those used to assess semantic-memory (general knowledge) retrieval, in which recognition and recall of test items is based on criteria other than previous personal witnessing of (encounter with) particular happenings. Thus, for example, test persons in a semantic-memory recognition test may be shown a name (e.g., Cooper or Churchill) and asked whether or not they recognize it as belonging to a famous person. In a semantic-memory cued recall test, they may be given the first name of a person (e.g., Winston, or James Fenimore) and asked to produce the corresponding surname on the basis of their general knowledge of the world (Neely, 1989).

A rich cognitive literature exists on the facts and theory of explicit recall and recognition, the psychological processes involved, and the relationship between

them (for a review, see Tulving, 1983). Virtually nothing, however, is known about the neuronal substrates of the two modes of episodic retrieval. First, the traditional lesion-based "deficit" approach is more appropriate for identifying neuroanatomical structures and pathways that are necessary for executing memory tasks than it is for the identification of brain regions associated with specific component processes of memory. Second, the more recently adopted imaging approach, based on functional neuroimaging techniques, such as positron emission tomography (PET) and functional magnetic resonance imaging (FMRI), which do allow such an analysis, have not yet been applied to a direct comparison of recognition and recall processes under conditions in which all other variables are controlled by experimental design. The purpose of the study reported here was to make such a direct comparison, and thus to identify some of the brain regions that are shared by and that differ between recall and recognition.

Lesion data concerning the functional neuroanatomy of recall and recognition is inconclusive. The main evidence has been provided by amnesic patients, who typically show damage in the structures of the medial temporal lobe and diencephalic midline. Amnesic patients' memory performance is severely impaired in tests that require conscious awareness of the study episode (explicit memory tests), such as recall and recognition tests, but not on tests that do not require such awareness (implicit memory tests), such as priming tests (for a review, see Moscovitch, Vriezen, & Goshen-Gottstein, 1992). The idea that recognition performance benefits not only from conscious recollection but also from a feeling of familiarity (Johnston, Dark, & Jacoby, 1985; Mandler, 1980)—an implicit component—suggested that it should be less impaired in amnesics than recall performance, which is a more purely explicit test. Consistent with this idea, some studies found larger amnestic deficits on recall than on recognition (Hirst et al., 1986; Hirst et al., 1988). However, other studies found amnesic patients to be equally impaired in recall and recognition tests (Haist, Shimamura, & Squire, 1992; Shimamura & Squire, 1988; Squire & Shimamura, 1986).

A similar disagreement exists concerning the role of the frontal lobes in recall and recognition tests. The conventional idea was that the frontal lobes are involved in memory for source but play little or no role in memory for content, as measured by standard recall and recognition tests (Squire, 1987; Stuss & Benson, 1986). However, some studies found that frontal lesions did not reliably impair performance in recognition tests but they produced significant reductions in recall tests (Janowsky et al., 1989; Jetter et al., 1986). The finding that frontal dysfunction impairs recall, but not recognition, is consistent with the assumed role of frontal regions on goal-directed strategic processes (Moscovitch, 1992) and with the idea that recognition, but not recall, can be performed on the basis of an automatic (nonfrontal)

feeling of familiarity (Johnston et al., 1985; Mandler, 1980). Nevertheless, a recent empirical review of the relevant literature since 1984 (Wheeler, Stuss, & Tulving, 1995) showed that frontal lesions also tend to disrupt recognition performance; in 18 out of 21 (86%) relevant comparisons, frontal patients' recognition performance was numerically worse than that of control subjects. Thus, although frontal lesions tend to produce larger effects on recall than on recognition tests, recognition performance is not completely intact in frontal patients. In sum, evidence from amnesic and frontal patients has not yet provided conclusive evidence concerning the similarities and differences in the neural substrates of recall and recognition.

As for neuroimaging data, PET studies on recall and recognition have consistently found increases in regional cerebral blood flow (RCBF) in the following six brain regions (see Table 1): (1) the prefrontal cortex, particularly on the right hemisphere; (2) the hippocampal and parahippocampal regions of the medial temporal lobe; (3) the anterior cingulate cortex; (4) the posterior midline area that includes posterior cingulate, retrosplenial, precuneus, and cuneus regions; (5) the inferior parietal cortex, especially on the right hemisphere; and (6) the cerebellum, particularly on the left.[1] The specific role of each of the six main regions in episodic retrieval is still unclear, but some ideas have been suggested. The right prefrontal cortex has been related to retrieval attempt (Kapur et al., 1995; Nyberg et al., 1995); the medial temporal lobes to conscious recollection (Schacter et al., 1996); the anterior cingulate to response selection (Fletcher et al., 1995); the posterior midline region to imagery (Fletcher et al., 1995; Grasby et al., 1993; Kapur et al., 1995; Shallice et al., 1994); the inferior parietal to awareness of space (Tulving et al., 1994); and the cerebellum to self-initiated retrieval (Bäckman et al., 1997).

The fact that activations in the six regions in Table 1 have been observed during both recall and recognition does not imply that they are equally involved in these two tests. Differences in the extent or magnitude of these activations cannot be determined across experiments. Also, cross-experiment comparisons are complicated by differences in experimental conditions. In order to determine clearly the similarities and differences between the functional neuroanatomy of recall and recognition memory, it is necessary to compare directly the pattern of activation generated by these tests in a situation in which subjects, materials, procedures, PET techniques, and methods of data analysis are kept constant. Moreover, if one wishes to attribute the results of such a comparison to qualitative differences between the neural bases of recall and recognition memory, rather than to quantitative differences in cognitive effort, it is desirable that the levels of difficulty of the two tests be equated.

In the present PET study, we compared the functional neuroanatomy of recall and recognition by measuring

Table 1. Six Brain Regions Consistently Found in PET Studies of Episodic Memory Retrieval

Study	Materials	Prefrontal cortex	Medial temporal lobe*	Anterior cingulate cortex	Posterior midline cortex†	Inferior parietal cortex	Cerebellum
Recognition							
Haxby et al., 1996	faces	R	R, L	M	pC	R, L	L, R
Andeasen et al., 1996	faces	R		M		R	L
Moscovitch et al., 1995	objects	R			rS, pC, C, P	R	L, R
Owen et al., 1996	objects	R	R		pC	R	
Tulving et al., 1996	pictures	R, L		M	rS	R	
Roland et al., 1995	patterns	R					
Schacter et al., 1995	drawings	R, L	R, L				
Tulving et al., 1994b	sentences	R, L		L		R, L	
Nyberg et al., 1995	words	R	R	L	rS		L, R
Nyberg et al., 1996	words	R, L		L, M		L	
Andreasen et al., 1995	words	R, L		M	P	R, L	L
Kapur et al., 1995	words	R, L		L	pC, C, P	R, L	
Cued-recall							
Buckner et al., 1995	words	R	R				
Fletcher et al., 1995	words	R		M	P		
Schacter et al., 1996	words	R, L	R, L	L, R	C, P	R, L	L
Bäckman et al., 1997	words	R, L		M			L

Notes: In those studies with more than one subtraction isolating retrieval process (e.g., Nyberg et al., 1995: recognition after deep encoding, recognition after shallow encoding, etc.), the results of all these subtractions are considered together. In those cases in which the same data was reported in more than one study, the most complete report is referenced. The studies by Kapur et al. (1995) and Grasby et al. (1993) are not reported in the table, because their episodic memory conditions involved not only retrieval but also encoding operations.
* Regions including the hippocampal formation and the parahippocampal gyrus.
† Area including the posterior cingulate (pC), retrosplenial (rS), precuneus (pC) and cuneus (C) regions. L = left; R = right; M = midline. In the case of the anterior cingulate activations, a peak was classified midline if its x coordinate (Talairach & Tournoux, 1988) was between −5 and +5.

Table 2. Instructions and Examples of Stimuli and Responses in the Reading, Recognition, and Recall Scans

Task	Visual input	Verbal output	Condensed instructions
Reading	*parents-piano*	*piano*	Read the first word silently and the second word aloud, without trying to remember the words
Recognition	*parents-piano*	*piano* or *pass*	If you think the second word is the original one, read it aloud; otherwise, say *pass*
Recall	*parents-word?*	*piano* or *pass*	If you can remember the original second word, say it aloud; otherwise, say *pass*

the brain activity of test persons while they were reading, recognizing, or recalling paired-associates. The stimuli, responses, and instructions of reading, recognition, and recall scans are summarized in Table 2. Visual input and verbal output were almost identical across the three tasks, and the difference in cognitive effort between recall and recognition tests was reduced by manipulating the number, speed, and occasion of the study trials.

Four comparisons of RCBF were performed: (1) recognition-minus-reading, (2) recall-minus-reading, (3) recall-minus-recognition, and (4) recognition-minus-recall. The first two comparisons were expected to identify brain areas more active during recall or recognition memory than during reading, whereas the last two comparisons were expected to reveal areas more active during recall than during recognition, or vice versa.

RESULTS

Behavioral Data

The mean proportion of recalled items was 0.78 (SD = .19), and the mean corrected recognition (hits minus false alarms) was 0.86 (SD = .09). The difference between these two measures was not statistically significant, t (df = 11) = 2.0, p > .05, suggesting that the attempt to equate the difficulty difference between recall and recognition tests was reasonably successful. It should be noted, however, that performance is only an indirect index of test difficulty or cognitive effort.

PET Data

The location of the peaks of significant RCBF increase in the four comparisons investigated are reported in Table 3. The shape and size of the activated areas can be observed in the t-maps in Figure 1. Significant RCBF increases in the recognition-minus-reading subtraction were found in three areas: the right prefrontal cortex, the anterior cingulate cortex, and the inferior parietal cortex. The right prefrontal activation was located in Brodmann areas 47, 45, and 10. The parietal activation occurred in the region of the angular gyrus (area 39), in almost identical locations in both hemispheres. The right prefrontal and anterior cingulate regions were also significantly activated when the reading condition was subtracted from the recall condition. The location of the right prefrontal RCBF increase was very similar to the one in the recognition-minus-reading subtraction (area 47). The anterior cingulate activation was more extended in recall, and clearly left-lateralized. Additionally, the recall-minus-read subtraction yielded activations in four other areas: the lenticular nucleus (globus pallidus and putamen), the thalamus, the brainstem, and the cerebellum. Several regions were higher in the reading than in the recognition and recall condition, but they will not be discussed in this paper.[2]

The recall-minus-recognition subtraction yielded an activation in the anterior cingulate, and in three areas that were found in the recall-minus-read subtraction but not in the recognition-minus-read subtraction: the lenticular nucleus (globus pallidus and putamen), the thalamus, and the left cerebellum. The only region that was more active during recognition than during recall was the right inferior parietal. There were no significant differences in the right prefrontal cortex in the recall-minus-recognition or in the recognition-minus-recall subtractions.

DISCUSSION

To summarize, both recall and recognition activated the right prefrontal and the anterior cingulate cortices, when compared to reading. Recall activated the anterior cingulate more than did recognition, and involved in addition the globus pallidus/putamen, the thalamus, and the cerebellum. The only area that was more active during recognition than during recall was the right inferior parietal cortex. We will focus the discussion on four areas that have been repeatedly found in PET recall and recognition studies (see Table 1) and seem to be related to similarities and differences between these tests: the

Table 3. Brain Regions Showing Significant RCBF increases in the Four Comparisons of Interest

| Brain regions | BA | Coordinates | | | Z value |
		x	y	z	
Recognition-minus-reading					
Right prefrontal	47	22	22	0	6.04
	45	24	24	8	5.98
	10	24	34	0	5.51
Anterior cingulate	32	−4	18	44	4.51
Inferior parietal	39	−34	−66	28	4.69
	39	36	−60	32	4.26
Recall-minus-reading					
Right prefrontal	47	28	22	0	6.14
Anterior cingulate	32	−8	22	28	6.75
Globus pallidus/putamen		10	2	4	4.82
		20	12	−4	4.79
Thalamus		−10	−28	16	4.30
		−2	−28	12	4.22
Brainstem		4	−32	−8	5.27
		0	−34	−16	5.09
Cerebellum		−10	−52	−28	4.89
		−2	−64	−24	4.44
		2	−70	−28	4.21
		−12	−92	−28	4.18
Recall-minus-recognition					
Anterior cingulate	32	−10	20	32	4.34
	32	−4	34	12	3.56
	32	−6	26	8	3.86
Globus pallidus/putamen*		10	2	4	3.85
Thalamus*		10	−12	16	3.76
Cerebellum		8	−48	−16	4.56
		0	−56	−20	4.34
		−10	−58	−20	4.26
Recognition-minus-recall					
Right inferior parietal	39	44	−70	12	3.75
	19	28	−70	20	3.73
	40	40	−56	32	3.70

Notes: The coordinates are from the atlas of Talairach & Tournoux (1988), where x, y, and z correspond to the right-left, anterior-posterior, and superior-inferior dimensions, respectively. In the recognition-minus-reading and recall-minus-reading subtractions only those activations with Z > 4 are reported.
* Spatial extent: p < 0.1. BA = Brodmann area.

Figure 1. Maps of *t*-statistic of regions showing significant RCBF increases in the recognition-minus-read, recall-minus-read, recall-minus-recognition, and recognition-minus-recall subtractions. The areas in black represent the voxels showing a significant RCBF difference at a significance level of $Z > 4$ in the case of the recognition-minus-read and recall-minus-read comparisons and at a level of $Z > 3$ in the case of the recall-minus-recognition and recognition-minus-recall comparisons.

Recognition Minus Read

Recall Minus Read

Recall Minus Recognition

Recognition Minus Recall
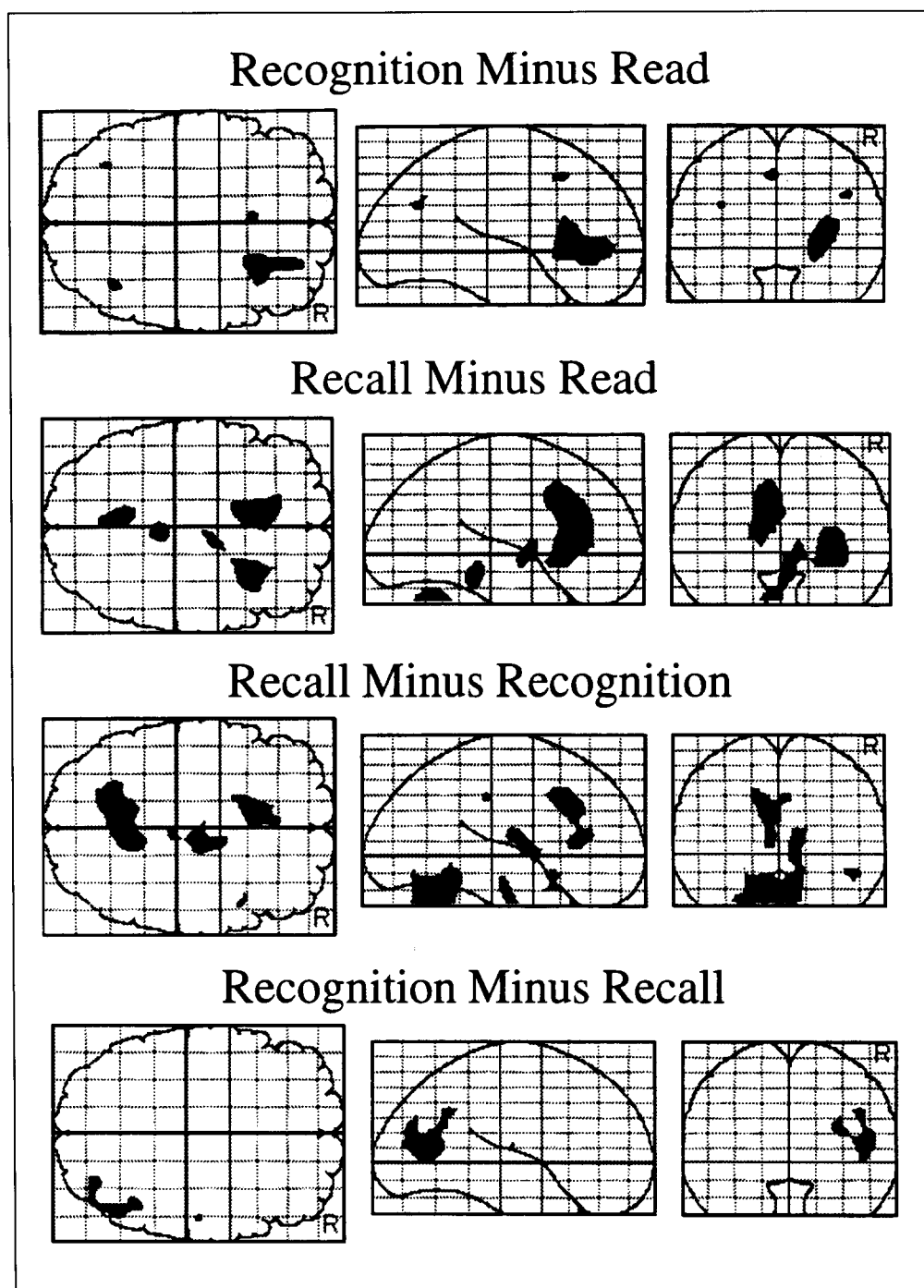
right prefrontal, the anterior cingulate, the right inferior parietal, and the cerebellum. The first two regions were more active during recall and recognition than during reading, the third was more active during recognition than during recall, and the fourth was more active during recall than during recognition. Although these regions will be considered in separate sections, it should be kept in mind that they most likely constitute components of distributed networks of brain regions (Andreasen et al., 1995; McIntosh & Gonzalez-Lima, 1994; McIntosh et al., 1994; Nyberg, McIntosh et al., 1996).

Right Prefrontal Cortex

In contrast with lesion studies showing larger effects of frontal damage on recall than on recognition (Janowsky et al., 1989; Jetter et al., 1986), the present experiment showed that the right prefrontal cortex was involved by the two tests to about the same degree. The notion of similar frontal involvement in recall and recognition is suggested by previous PET data (see Table 1), but the present study is the first one in which neural correlates of the two tests are directly compared. One possible

explanation of the inconsistency between lesion and PET data is that frontal regions are similarly involved in recall and recognition but are more essential for the former than for the latter; for example, because recognition, but not recall, can be based on nonfrontal automatic processes (Moscovitch, 1992). Alternatively, larger effects of frontal damage on recall than on recognition might not reflect a qualitative difference between the neural substrates of two forms of episodic memory, but only the fact that recall tests are usually more difficult than recognition tests. The fact that no frontal differences were found when recall and recognition were approximately matched in difficulty is consistent with the second hypothesis. However, a direct test of this hypothesis would require a within-subject study that compares recall and recognition activations both when difficulty is matched and when recall is more difficult than recognition. This is a problem for future research.

The finding that the right prefrontal cortex was similarly involved in recall and recognition suggests that it contributes to an aspect of retrieval that is common to both tests. One aspect of retrieval that has been attributed to the right prefrontal and that is common to recall and recognition is what has been called "retrieval attempt" (Kapur et al., 1995) or "retrieval mode" (Nyberg et al., 1995; Tulving, 1983; see also Moscovitch, 1989). Retrieval mode refers to the processing of incoming information as retrieval cues or as items to be remembered, rather than as a component of or guide to ongoing cognition or behavior. It represents a necessary condition of episodic retrieval, and it is independent of retrieval success. Nyberg et al. (1995) found that a right prefrontal region—a few millimeters away ($xyz = 28, 24, 8$) from the one found in the present study—was activated when test persons tried to recognize words, regardless of whether recognition performance was high or low, and regardless of whether test words had been studied or not. This result suggests that the role of the right prefrontal in retrieval is not related to the actual recovery of stored information (ecphory), but to the attempt or effort for such recovery. Since retrieval mode is common to recall and recognition, the concept of retrieval mode can explain the lack of frontal differences between the neural correlates of the two tests.

Anterior Cingulate Cortex

The anterior cingulate cortex is assumed to play an important role in various aspects of human behavior, including affect, verbal expression, response selection, and initiation of action (for a review, see Devinsky, Morrell, & Vogt, 1995). The role of the anterior cingulate in initiation of action is jointly supported by neuropsychological and neuroimaging evidence. Bilateral lesions in the anterior cingulate can produce akinetic mutism, a condition characterized by the almost complete absence of spontaneous motor or verbal responses (Barris &

Schuman, 1963; Faris, 1969; Nemeth, Hegedus, & Molnar, 1988). PET studies have found anterior cingulate activations in tasks involving more initiation than the control task, including generation tasks (Petersen et al., 1989; Petersen et al., 1988), willed-action tasks (Frith et al., 1991), Stroop tasks (Pardo et al., 1990), self-ordered tasks (Petrides, Alivisatos, Evans, & Meyer, 1993; Petrides, Alivisatos, Meyer, & Evans, 1993), metaphor interpretation tasks (Bottini et al., 1994), and imagery tasks (Kosslyn et al., 1993). The initiation hypothesis can account for the present findings that the anterior cingulate was more active during recall and recognition than during reading, and more active during recall than during recognition. First, initiation of action is more prominent during memory retrieval than during simple reading. Second, one of the main differences between recall and recognition is that recall involves more "self-initiated processing" than the latter (Craik, 1983).

Right Inferior Parietal Cortex

Even though inferior parietal activations have been repeatedly found in PET recall and recognition studies (see Table 1), the role of this region in episodic memory retrieval has seldom been discussed. In the present study, inferior parietal regions, particularly on the right hemisphere, were more involved in recognition than in recall. These parietal activations may be related to the larger perceptual component of recognition. In recognition tests, targets are re-presented, and hence, their physical attributes can contribute to the retrieval process. For example, recognizing the word "automobile" can be based on deciding whether the corresponding concept was dealt with during the study phase, but it can be also based on deciding whether the visual stimulus "automobile" was seen in the study list. In contrast, in recall tests, because targets are not re-presented, the perceptual component of retrieval is smaller. In some recall tests, such as the stem cued-recall (e.g., GAR____), in which perceptual information about the targets is provided, perceptual processing is likely to play a more important role. It is interesting to note that significant parietal activations during recall (see Table 1) were found using such tests (Buckner et al., 1995; Schacter et al., 1996).

Cerebellum

The function of the cerebellum was traditionally described as motor. In the history of learning and memory, Thompson and his colleagues brought attention to the role of the cerebellum in classical conditioning and in the storage of memory engrams (McCormick & Thompson, 1984; Thompson & Donegan, 1986). More recently, neuropsychological, neuroimaging, and anatomical evidence has converged on the idea that the cerebellum also makes important contributions to cognition (for reviews, see Leiner, Leiner, & Dow, 1991;

Leiner, Leiner, & Dow, 1995; Schmahmann, 1991). Cerebellar damage has been found to produce deficits in a variety of cognitive measures, including intelligence (Botez et al., 1989), processing speed (Botez, 1992), cognitive skill learning (Fiez & Petersen, 1993), visuospatial processing (Botez, 1992), time judgment (Ivry & Keele, 1989), cognitive planning (Botez, 1992; Grafman et al., 1992), verbal fluency (Akshoomoff et al., 1992), and recall (Akshoomoff et al., 1992; Appollonio et al., 1993; Bracke-Tolkmitt et al., 1989; Canavan et al., 1994). PET studies have found cerebellar activations not only in motor learning (Blaxton et al., 1996; Decety et al., 1994; Decety et al., 1990; Jenkins et al., 1994; Kim et al., 1993; Molchan et al., 1994), but also in perception (Köhler et al., 1995), language (Price et al., 1994), working memory (Paulesu, Frith, & Frackowiak, 1993; Petrides et al., 1993), semantic memory (Petersen et al., 1989; Petersen et al., 1988), and episodic memory (see Table 1) tasks. Finally, a cognitive cerebello-thalamo-cortical pathway has been recently traced from the dentate nucleus to the contralateral prefrontal cortex, with a loop in the contralateral globus pallidus (Middleton & Strick, 1994). The activations in the recall-minus-reading subtraction seem to follow this circuit; there were activations in the left cerebellum, including the left dentate nucleus (e.g., $xyz = -10, -52, -28$), the right thalamus, the right globus pallidus, and the right prefrontal cortex.

It has been suggested that the cerebellum plays a role in self-initiated retrieval (Bäckman et al., submitted). This hypothesis is consistent with the finding that the cerebellum was more active during recall than during recognition, because, as previously stated, recall has been assumed to involve more "self-initiated processing" (Craik, 1983). In particular, the cerebellum could be involved in the generation of "candidate responses" during retrieval. For example, Petersen et al. (Petersen et al., 1989; Petersen et al., 1988) found that the cerebellum was more active during word generation (e.g., cake → eat) than during word repetition (e.g., cake → cake). These activations were right-lateralized, whereas the present ones were left-lateralized. This difference might be related to whether generation is focused on semantic memory or on episodic memory. The hemispheric encoding/retrieval asymmetry (HERA) model (Nyberg, Cabeza, & Tulving, 1996; Tulving, Kapur, Craik et al., 1994) postulates that semantic retrieval involves the left prefrontal cortex more than the right, whereas episodic memory retrieval involves the right prefrontal cortex more than the left. Since cerebello-frontal connections are crossed, this model may be extended to include that cerebellar activity: more right-lateralized during semantic retrieval and more left-lateralized during episodic memory retrieval. The tendency for left-lateralization of cerebellar activations during episodic memory retrieval (Andreasen et al., 1996; Andreasen et al., 1995) in the present and previous PET studies (see Fig. 2) is consistent with this prediction.

CONCLUSIONS

Our findings confirmed and extended the results reported previously in related PET studies. Both recall and

Figure 2. Peaks of significant cerebellar activation in studies of episodic memory retrieval (see Table 1). The peaks are plotted in a horizontal slice of the cerebellum, collapsed across the z dimension (inferior-superior). The outline of the cerebellum is only approximate.
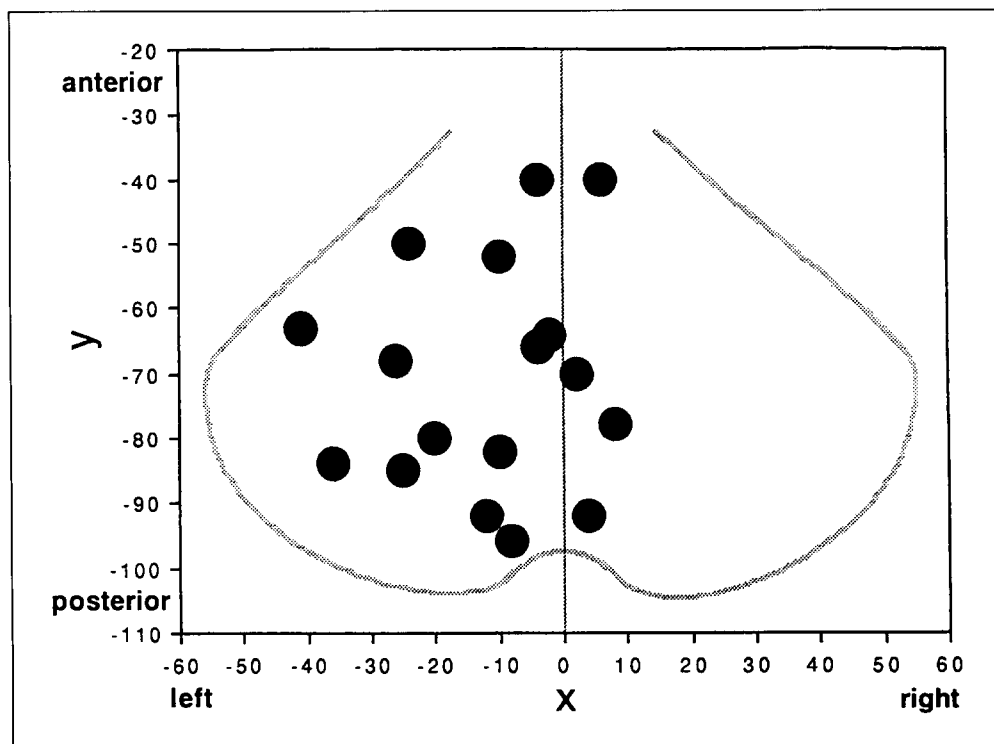
recognition, when compared with reading, were associated with differential activation of right prefrontal, but not left prefrontal, cortex at or near Brodmann areas 47, 45, and 10, thus confirming once again the pattern described by the HERA model (Buckner, 1996; Nyberg, Cabeza, & Tulving, 1996; Tulving, Kapur, Craik et al., 1994), and in agreement with the interpretation of the right-frontal retrieval activation in terms of retrieval attempt or retrieval mode (Kapur et al., 1995; Nyberg et al., 1995; Tulving, 1983). Further confirmation of previous results was seen in the association of both recall and recognition with the activation of the anterior cingulate and the cerebellum, regions that have been implicated in episodic recall and recognition in a number of previous studies (see Table 1). Tentatively, the anterior cingulate may be thought to be involved in the initiation of action, whereas the cerebellum may either complement the operations of the contralateral frontal lobes (retrieval mode, retrieval attempt) or subserve the implicit generation of candidate responses during retrieval, or both.

The relatively more novel information provided by our findings concerned the identification of brain regions that are differentially involved in the two modes of episodic retrieval. Areas more active during recall than recognition included the anterior cingulate, the right globus pallidus, the thalamus and the cerebellum. Thus, the anterior cingulate, although active in both recall and recognition, is more so in recall. A parallel pattern held in the present study for the cerebellum that showed differential activity in recall not only in comparison with reading but also with recognition. The interpretation of the thalamic activation in recall is problematic, because of the pattern of findings: when recall was compared with reading, thalamic activation was statistically significant on the left; when compared with recognition, it was significant on the right. The resolution of this apparent puzzle will have to await future research.

Finally, the right inferior parietal cortex was more active during recognition than during recall, possibly reflecting the larger perceptual component of the former. The fact that there seem to be brain regions that are more active during the "easier" task of recognizing than during the "more difficult" task of recall lends credibility to the popular dual-process theory of recognition (Atkinson & Juola, 1974; Mandler, 1980), and it also helps to understand rare but striking cases in which brain damage impairs the patient's ability to recognize previously known stimuli while having little effect on recall (Delbecq-Derouesne, Beauvois, & Shallice, 1990).

One of the notable findings of the present study was that the differences between the neural correlates of recall and recognition memory did not occur in frontal areas, as one might have expected on the basis of lesion data yielded by frontal patients. Instead, the differences appeared in parietal, cingulate, and cerebellar regions. This means that the present results, like those in numer-

ous other PET studies of memory, could have not been predicted from available lesion data. They thus represent a good example of the complementary roles played by the deficit and imaging approaches to cognitive neuroscience of memory, and underscore the continuing need to integrate evidence from both sources.

METHODS

Test Persons

The test persons were 12 university students (six male, six female) with an age range of 19-31 years. All test persons were right-handed, and had no history of neurological or psychiatric illness. The study was approved by the Human Subject Use Committee of the University of Toronto and the Baycrest Centre.

Materials

The critical stimuli were 192 word pairs (e.g., tattoo-motorcycle, parents-piano). The pairs were randomly divided into 8 lists of 24 pairs, which were assigned to the 8 scans in one order for half of the test persons, and in the opposite order for the other half. In the recall scans, the second word of each pair was replaced with the word "word," and in the recognition scans, some second words were replaced by lures (see Table 2). The word pairs were presented in lowercase white letters on a black background, on a computer screen suspended 60-75 cm in front of the test persons. During the scans, each pair was presented for 4 sec, and followed by a 1-sec interval (i.e., the presentation of one list lasted 2 min). The presentation of each list started 35-45 sec before the beginning of the 60-sec PET scan, and finished 15-25 sec after the end of the scan.

Procedure

Prior to the day of the scanning, test persons visited the laboratory and completed a health questionnaire and several neuropsychological tests (e.g., CVLT, FAS) necessary for eventual comparisons with other subject populations. During this visit, they also practiced the tasks to be performed during the experiment. On the scanning day, each subject undertook a total of eight PET scans, two scans in each of the following four conditions: reading, encoding, recognition, and recall. The order of the first four scans was either reading-recognition-encoding-recall; or reading-recall-encoding-recognition. Scans four through eight were a mirror-image of the first four (ABCD-DCBA), thus providing for an overall linear counterbalancing of any order effects. The results of the encoding scans are being reported elsewhere (Kapur et al., 1996), and hence, this condition will not be considered in this article. The scans were performed every 11 min. During the intervals before recall and recognition

scans, test persons studied the pairs to be tested during the scan. In these study trials, test persons were instructed to learn the pairs for a subsequent memory test by noting meaningful relations between the two words in each pair. The difference in difficulty between recall and recognition tests was attenuated by three manipulations selected with pilot studies: (1) the study list was presented once for recognition and twice for recall; (2) presentation rate was one pair every 4 sec for recognition, and one pair every 5 sec for recall; and (3) the interval between the end of the study phase and the test was 5 min for recognition and 2 min for recall. Although these manipulations introduced differences between the study conditions of recall and recognition, they can be assumed to affect quantitative rather than qualitative aspects of the memory trace. The stimuli, responses, and instructions of the reading, recognition, and recall scans are summarized in Table 2. The amount of visual input (two words) and verbal output (one word) of each trial was basically identical in the three tasks. In the recognition scan, the second word of three pairs at the beginning of the list (before the start of the scan) and of three pairs near the end of the list (after the end of the scan) was replaced by a lure (moderately related to the first word). Thus, in both recall and recognition, all items during the scan window could potentially originate successful retrieval.

PET Methods

PET scans were obtained with a GEMS-Scanditronix PC2048-15B head scanner using a bolus injection of 40 mCi (1.48 GBq) of ^{15}O-H$_2$O. The PET data were analyzed with the Statistical Parametric Mapping (SPM) technique (using software from the Wellcome Department of Cognitive Neurology, London, UK) implemented in Matlab (Mathworks Inc., Sherborn, MA). 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 (Talairach & Tournoux, 1988) by matching to a reference image that already conforms to the standard space. These images were then smoothed using an isotropic Gaussian kernel of FWHM of 15 mm. The effects of the conditions (cognitive tasks) on the regional cerebral blood flow at each voxel were then estimated using a general linear model, wherein the changes in global counts are considered as a covariate (Friston et al., 1991; Friston et al., 1995). The effects of each comparison are estimated using linear contrasts. These contrasts yield a t-statistic for a given comparison at each voxel, which is usually expressed as a standardized Z-score. An activation was considered significant if its peak had a $Z > 3.0$ (equivalent to $p < .05$ after correction for multiple comparisons), and its spatial extent (i.e., the number of voxels

above the significance level) had a probability smaller of .05 (no correction necessary).

Notes

1. Activation in other areas, such as the lateral temporal cortex (Kapur et al., 1995; Moscovitch et al., 1995; Nyberg et al., 1995), the occipital cortex (Haxby et al., 1996; Roland & Gulyás, 1995; Schacter et al., 1996), the basal ganglia (Nyberg et al., 1995; Roland & Gulyás, 1995), the thalamus (Fletcher et al., 1995; Haxby et al., 1996), and the mesencephalon (Bäckman et al., submitted; Schacter et al., 1995) has also been observed, but in fewer studies and sometimes in association with stimulus characteristics (e.g., occipital activations for face stimuli; Haxby et al., 1996; Roland & Gulyás, 1995; Schacter et al., 1996).

2. Areas more active during reading than during recognition included right Sylvian (area 22: 50, 4, 4) and bilateral premotor (left area 6: 42, −6, 40; right area 8: −30, 26, 44) regions. Areas more active during reading than during recall included bilateral Sylvian (left area 42/43: −56, −22, 16; right area 22: 50, 4, 4), right temporoparietal (area 21/37: 48, −54, 8; area 37/39: 42, −70, 8; area 40: 56, −26, 28), and left prefrontal regions (area 9: −30, 30 32). Some of these activations can be related to the novelty of the stimuli in the reading condition (see Tulving & Kroll, 1995; Tulving et al., 1996; Tulving et al., 1994).

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