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Functional activation of the human ventrolateral frontal cortex during mnemonic retrieval of verbal information

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ABSTRACT **Regional cerebral blood flow was measured with positron emission tomography during the performance of a verbal free recall task, a verbal paired associate task, and tasks that required the production of verbal responses either by speaking or writing. Examination of the differences in regional cerebral blood flow between these conditions demonstrated that the left ventrolateral frontal cortical area 45 is involved in the recall of verbal information from long-term memory, in addition to its contribution to speech. The act of writing activated a network of areas involving posterior parietal cortex and sensorimotor areas but not ventrolateral frontal cortex.**

Damage to the human lateral frontal cortex does not result in a general memory impairment, but it can impair specific aspects of mnemonic performance (1). For instance, patients with frontal cortical damage perform poorly on a self-ordered working memory task that requires monitoring of self-generated choices from a list of stimuli (2). Work with nonhuman primates has shown that the mid-dorsolateral frontal cortex (areas 9 and 46) is critical for this type of monitoring (3, 4). Patients with frontal cortical damage can also exhibit impairments in other domains of mnemonic performance, such as on free recall tasks in which they are required to retrieve a specific list of words presented during an earlier study period (5–7).

A recent theoretical model of frontal cortical function has proposed that the mid-portion of the ventrolateral frontal cortex (areas 45 and 47) is critical for the active (i.e., strategic) encoding and retrieval of specific information held in posterior cortical association regions (8). The mid-dorsolateral frontal cortex (areas 9 and 46), on the other hand, is involved in the monitoring of mnemonic performance on the basis of the subject's current plans (8).

In recent studies with positron emission tomography (PET), it has been possible to extend to the human brain the demonstration from the animal work (3, 4) that the mid-dorsolateral frontal cortex is critical for the monitoring, within working memory, of self-ordered and externally ordered responses (9, 10). The present PET investigation attempted to test the prediction that the mid-ventrolateral frontal cortex is involved in active (i.e., voluntary) retrieval of specific information from long-term memory (8).

In the human brain, ventrolateral frontal cortical areas 45 and 47 occupy the inferior frontal gyrus. In the left hemisphere, these areas and the caudalmost part of the inferior frontal gyrus (area 44) are known to be involved in various aspects of language production (11–14). The present study examined the possible role of the *left* ventrolateral frontal cortex in the retrieval of verbal information from long-term memory. Although it is impossible to specify the connections of the human ventrolateral frontal cortex, it has been shown that, in the monkey, area 45 is most strongly connected with the middle part of the superior temporal cortex and adjoining superior temporal sulcal cortex (15). In the human brain, this region of the temporal cortex, especially in the left hemisphere, is specialized for the comprehension of language (14, 16–18). It is thus reasonable to predict that the left ventrolateral frontal cortex within or near area 45 should be the one most actively involved in explicit retrieval of verbal information from long-term memory.

The main experimental task used in the present investigation required free recall of a list of words studied before scanning, since it has been shown that free recall engages active strategic retrieval processes (19, 20). Two other conditions that also required the verbal production of stimuli, a repetition and a paired associate task, provided the background needed to establish the specificity of the contribution of any activated ventrolateral frontal area to strategic mnemonic retrieval. The repetition task required simple verbal production of words, while the paired associate task involved, in addition, the nonstrategic retrieval of highly learned verbal responses to particular stimuli.

Although a severe expressive aphasia is almost always accompanied by an impairment in writing, there is evidence that writing can be dissociated from the more restricted disorder in speech produced by lesions limited to the left ventrolateral frontal cortex (21, 22). For this reason, a writing-to-dictation condition was also included in the present investigation to see whether any part of the inferior frontal gyrus, and in particular area 45, would be activated.

METHODS

Subjects. Eleven right-handed male subjects participated in this experiment. Their ages ranged from 18 to 32 years (mean age, 24 years). The subjects gave informed, written consent for participation in this study, which was approved by the Ethics Committee of the Montreal Neurological Hospital.

Scanning Methods and Data Analysis. PET scans were obtained with a Scanditronix PC-2048 tomograph, which produces 15 image slices at an intrinsic resolution of $5.0 \times 5.0 \times 6.0$ mm (23). The regional distribution of cerebral blood flow (rCBF) was measured by means of the water bolus $H_2{}^{15}O$ methodology (24) during 60-sec scanning conditions. Each subject also underwent a high-resolution magnetic imaging resonance (MRI) scan (64 slices, 2 mm thick) obtained with a Philips Gyroscan (1.5T). The MRI volumes were coregistered with the PET data (25) and each matched pair of MRI and PET datasets was linearly resampled into a standardized stereotaxic coordinate system (26, 27). The PET images were reconstructed with a 20-mm Hanning filter to overcome residual anatomical variability. PET data were normalized for global rCBF, averaged across subjects for each activation state, and the mean rCBF difference image volume was obtained (23). This volume was converted to a *t*-statistic volume by dividing each voxel by the mean standard deviation in nor-

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

malized rCBF for all intracerebral voxels (28). Individual MRI images were subjected to the same averaging procedure, such that composite MRI and PET volumes were merged to localize t-statistic peaks (26).

The statistical significance of focal changes was tested by a method based on three-dimensional Gaussian random field theory (28). For an exploratory search involving all peaks within the grey matter volume of 600 cm^3, the threshold for reporting a peak as significant was set at $t = 3.50$, corresponding to an uncorrected probability of $P < 0.0002$ (28). A directed search within the lateral frontal cortex for predicted activation foci in particular cytoarchitectonic areas was also carried out and for this analysis the threshold for significance was set at $t = 3.00$, corresponding to an uncorrected probability of $P < 0.0013$.

Testing Procedure. The subjects were scanned with PET for 60 sec under each one of seven different conditions of testing. Four of these conditions constitute the present experiment and were always administered during the first four scans. The remaining three conditions were part of another experiment. One of these last conditions involved scanning during a resting period with eyes open and was intended to serve as a baseline for some subtractions in the present and the other experiment. The stimuli used in the present experiment were abstract low-imagery words, rated below 3.2 on a 7-point scale measuring their image-evoking properties (29). All words used had medium to high Thorndike–Lorge frequency ratings to ensure that rare words, which the subjects might not have known, would be excluded. Before each scanning condition, the experimenter explained the requirements of the task to be performed and the subjects practiced the task once. The subjects kept their eyes open during scanning, but visual stimulation was reduced by dimming the lights within the scanning room and by surrounding the subject with a black curtain.

Recall condition. This was the main experimental condition. In the 10-min period preceding scanning, the subject heard a list of 20 words that were read aloud six times by the experimenter. These words were presented in a different random order each time, and, after each presentation, the subject attempted to recall them in any order he wished. During scanning, the subjects were required to recall these words in any order they wished. It was made clear to the subjects that the essence of this condition was the process of constantly recalling words throughout the 60-sec scanning period. They were therefore instructed that if, at any point during the scanning period, they could no longer recall any more words, they were to start recalling the words from the beginning, again in any order they wished.

Repetition condition. During scanning in this control condition, the experimenter read words aloud, one at a time, and the subject was simply required to repeat each word. The next word was presented as soon as the subject had finished repeating the previous one. The purpose of this condition was to provide a control for the comprehension and speaking of words inherent in the recall condition.

Paired associate condition. Before scanning, the subjects mastered a paired associate task, which consisted of five stimulus–response pairs of abstract words. After having read out the five pairs of words, the experimenter proceeded to read out the stimulus word of each pair and the subject was required to produce the correct response. If the subject made an error or could not produce the response, the experimenter provided the correct answer, before proceeding to say the next stimulus

Table 1. Repetition compared with the resting state

Stereotaxic coordinate				
x	*y*	*z*	*t*	Brain area
				Repetition minus resting state
				Left hemisphere
−39	22	8	3.71	Mid-ventrolateral frontal area 45
−58	−26	9	7.68	Superior temporal areas 22/42
−48	5	13	3.33	Broca's area (areas 44/6)
−17	−66	−17	4.98	Cerebellum
−42	−45	−22	3.66	Cerebellum
−13	−6	2	4.04	Ventral striatum
				Right hemisphere
39	25	9	4.43	Mid-ventrolateral frontal area 45
62	−16	0	7.41	Posterior temporal areas 22/21
1	8	60	4.60	Supplementary motor cortex
29	−59	−26	3.88	Cerebellum
				Resting state minus repetition
				Left hemisphere
−27	46	−15	4.01	Orbitofrontal cortex (area 11)
−51	−40	45	3.63	Inferior parietal area 40
−13	−64	54	3.51	Caudal superior parietal area 7
				Right hemisphere
31	46	21	3.63	Mid-dorsolateral frontal area 46
28	24	42	4.12	Mid-dorsolateral frontal area 9
39	−68	36	4.34	Posterior parietal cortex (area 7)

Peaks of statistically significant changes in normalized cerebral blood flow are presented (see text). The stereotaxic coordinates are expressed in mm. x, Medial-to-lateral distance relative to the midline (positive = right); y, anterior–posterior distance relative to the anterior commissure (positive = anterior); z, superior–inferior distance relative to the anterior commissure–posterior commissure line (positive = superior). t = t-statistic value.

Table 2. Recall compared with repetition

Stereotaxic coordinate				
x	*y*	*z*	*t*	Brain area
				Recall minus repetition
				Left hemisphere
−23	25	3	3.96	Mid-ventrolateral frontal area 45
−40	49	26	3.30	Mid-dorsolateral frontal areas 9/46
−50	−9	38	3.75	Premotor cortex (area 6)
−5	−73	49	4.33	Medial parietal cortex (area 7)
−27	−69	42	5.07	Prestriate cortex (area 19)
−1	−18	11	3.92	Dorsomedial nucleus of thalamus
				Right hemisphere
43	32	38	4.91	Mid-dorsolateral frontal areas 9/46
36	51	33	3.55	Mid-dorsolateral frontal area 9
32	8	62	4.78	Premotor cortex (area 6)
13	−11	22	3.92	Anterior cingulate area 24
4	17	44	3.67	Anterior cingulate area 32
9	−76	39	4.86	Medial parietal cortex (area 7)
19	−92	0	3.67	Prestriate cortex (area 18)
38	−68	35	4.82	Prestriate cortex (area 19)
				Repetition minus recall
				Left hemisphere
−47	−71	3	5.02	Temporo-occipital area 37
−52	−44	6	4.77	Middle temporal area 21
−51	−9	2	4.40	Auditory cortex (area 42)
−59	−23	9	4.32	Superior temporal area 22
−54	−35	30	3.95	Supramarginal cortex (area 40)
−44	−62	18	3.78	Parieto-occipital area 39
−3	61	2	3.66	Medial frontal area 10
				Right hemisphere
54	−11	2	5.27	Superior temporal area 22
51	3	−12	4.77	Middle temporal areas 21/22
60	−42	−3	4.19	Middle temporal area 21
52	−57	15	4.19	Middle temporal area 21
3	37	51	3.91	Medial frontal area 8

word. When all five pairs were tested, the experimenter presented the five stimulus words in a new random sequence, and again the subject was required to produce the correct response word for each stimulus. This procedure was repeated until the subject achieved 100% correct performance in five consecutive presentations of the stimulus words. During scanning, the experimenter read out the first word of each pair and the subject responded by saying the word associated with it. If an error were made, the experimenter did not correct it, but simply proceeded to present the next stimulus word. When all five stimuli were presented, a new random sequence was administered, and this procedure was continued until the end of the scanning period. The experimenter presented a stimulus word as soon as the subject had finished giving his response, so as to maintain continuous cognitive performance during scanning.

Writing-to-dictation condition. During scanning, the experimenter read out a word and, as soon as the subject had written it, a new word was read out. The subject wrote the words on a sheet of paper with his right hand. Since the subject was lying in the PET scanner in a supine position and the sheet of paper was placed on a hard surface on the bedside, the subject could not see what he was writing. The subjects had been given extensive practice in writing in this position before scanning. The words used during this practice period were different from those used during scanning.

The four conditions described above were administered to the subjects in a counterbalanced manner, but the repetition condition always preceded the recall condition.

RESULTS

Behavioral Data. In the repetition condition, the subjects repeated a mean of 18.45 (range, 14–21) words during scanning with 100% accuracy. In the paired associate task, the mean number of words produced by the subjects in response to the presentation of the stimulus words was 20.45 (range, 16–24) and the mean correct performance was 97.18%. In the recall task, the subjects were required to retrieve as many of the 20 target words as they could, but if they reached a point at which they could recall no more words, they were asked to start retrieving the words from the beginning. The mean number of words produced during the scanning period in this task was 19 (range, 14–26). Thus, the total verbal output of the subjects during the recall task was comparable to that in the repetition and paired associate tasks. The recall process, however, was demanding with only a mean of 66.82% of the words on the list being successfully retrieved during the scanning period. None of the subjects produced words that were not on the list. In the writing-to-dictation condition, the mean number of words written during the scanning period was 12.09 (range, 9–14) with a mean of 95% accuracy in spelling.

PET Data. The first set of comparisons carried out was intended to establish whether the repetition, the paired associate, and the recall tasks, all of which require various aspects of verbal response production, were effective in activating ventrolateral frontal cortical area 45. To address this question, we subtracted activation in the resting condition from that in the repetition, the paired associate, and the recall tasks. In all of these subtractions, mid-ventrolateral frontal cortical area 45 was bilaterally activated, as well as various other regions that are known to be involved in language production and comprehension. As an example of this, we present, in Table 1, the peaks of significant differences in rCBF observed when the repetition condition was compared with the resting state. This subtraction showed that the act of repeating words presented auditorily activates posterior temporal neocortex, which is involved in the comprehension (i.e., semantic processing) of words (11, 16–18), as well as a large portion of the inferior frontal gyrus involved in spoken language production (10–14).

Two comparisons were carried out to test the hypothesis that there is significant activation within the left ventrolateral frontal cortex specifically related to the strategic retrieval of verbal episodic information. First, activity in the repetition condition was subtracted from that in the recall task. This subtraction controls for the processes involved in verbally producing words that were present in the recall task over and above the processes of strategic retrieval. Second, activity in the paired associate condition was subtracted from that in the recall task to compare strategic retrieval (inherent in free recall) with highly learned nonstrategic stimulus–response retrieval of words. Significant activation within the left ventrolateral frontal cortical area 45 was observed in both of these subtractions (Tables 2 and 3), providing a strong confirmation of the hypothesis that the mid-ventrolateral frontal cortex is involved in the strategic retrieval of verbal information.

Activity in the repetition condition was also subtracted from the paired associate condition (Table 4). The activation in area 45 previously observed in the paired associate minus resting state subtraction was no longer significant, suggesting that highly practiced production of words to the presentation of particular stimuli engages ventrolateral frontal cortex to the same extent as repetition.

Finally, the writing-to-dictation condition was compared with each one of the three verbal production tasks to demonstrate the cerebral areas involved specifically in the act of writing. The writing-to-dictation condition activated very similar areas when compared with each one of the three verbal production conditions. We therefore present here only one of these subtractions, the writing-to-dictation minus recall (Table

Table 3. Recall compared with the paired-associate task

Stereotaxic coordinate				
x	*y*	*z*	*t*	Brain area
				Recall minus paired associate condition
				Left hemisphere
−23	22	2	3.50	Mid-ventrolateral frontal area 45
				Paired-associate minus recall condition
				Left hemisphere
−58	−13	0	3.87	Posterior temporal areas 22/21
				Right hemisphere
54	−2	−11	3.76	Anterior temporal area 21
54	−13	3	4.69	Posterior temporal area 22

Table 4. Paired associate task compared with repetition

Stereotaxic coordinate				
x	*y*	*z*	*t*	Brain area
				Paired associate minus repetition
				Left hemisphere
−31	−66	44	4.59	Posterior parietal area 7
−4	−44	−11	3.78	Cerebellum
				Right hemisphere
48	30	35	3.63	Mid-dorsolateral frontal areas 9/46
20	48	−8	4.04	Orbitofrontal area 11
36	6	54	3.78	Premotor cortex (area 6)
36	−71	39	4.48	Posterior parietal area 7
3	−76	44	4.22	Medial parietal area 7
13	−62	33	4.48	Posterior cingulate area 31
				Repetition minus paired associate
				Left hemisphere
−39	41	−13	4.86	Mid-ventrolateral frontal area 47
−34	6	0	4.11	Claustro-insular cortex
−47	5	13	3.67	Opercular premotor cortex
−46	−71	0	3.74	Prestriate cortex (area 19)

Table 5. Writing compared with the recall condition

Stereotaxic coordinate				
x	y	z	t	Brain area
				Writing minus recall
				Left hemisphere
−34	−28	56	11.27	Sensorimotor cortex (areas 4/3)
−7	−13	47	7.28	Supplementary motor cortex
−39	−6	5	4.77	Insula
−51	−35	36	7.80	Supramarginal parietal area 40
−50	−66	5	5.44	Posterior temporal area 37
				Right hemisphere
17	−9	58	3.96	Premotor cortex (area 6)
16	−50	−21	6.77	Cerebellum
36	−42	47	6.40	Intraparietal area 7
15	−62	58	4.48	Superior parietal area 7
52	−31	38	3.67	Supramarginal parietal area 40
62	−31	31	3.67	Supramarginal parietal area 40
59	−47	−6	3.52	Posterior temporal area 37
58	−57	−2	3.52	Posterior temporal area 37
				Recall minus writing
				Left hemisphere
−32	20	12	3.94	Mid-ventrolateral frontal area 45
−25	25	5	3.86	Mid-ventrolateral frontal area 45
−16	30	−12	4.08	Orbitofrontal area 11
−68	−35	0	3.64	Posterior temporal area 21
−19	−92	2	6.30	Striate cortex (area 17)
−15	−90	3	6.00	Striate cortex (area 17)
				Right hemisphere
46	29	40	4.16	Mid-dorsolateral frontal areas 9/46
29	42	−5	4.23	Orbitofrontal area 47
60	−9	18	4.60	Central opercular area 43
54	−6	44	4.60	Motor cortex (area 4)
67	−14	−3	4.82	Posterior temporal area 21
15	−90	0	7.04	Striate cortex (area 17)
9	−85	15	7.48	Prestriate cortex (area 18)
11	−88	29	6.30	Prestriate cortex (area 18)

5). Significant peaks were observed in the left sensorimotor cortex, insula, posterior temporal cortical area 37, as well as in the superior and inferior parietal cortex of the right hemisphere. Note, however, that there was no significant activation in the left ventrolateral frontal cortical area 45 in the writing-to-dictation condition (e.g., Table 5). This was also true when the resting state was subtracted from the writing-to-dictation condition.

DISCUSSION

The aim of the present investigation was to establish whether the middle part of the human ventrolateral frontal cortex, in the left hemisphere, is involved in the strategic retrieval of verbal information from long-term memory (8). To engage the subject in active retrieval of specific verbal information from long-term memory, the main experimental condition involved the free recall of a list of words studied before scanning. The free recall task involves, in addition to strategic retrieval of verbal episodic information, the understanding and retrieval of words from semantic memory as well as the production of verbal responses. In the recall minus repetition subtraction (Table 2), processes involved in strategic mnemonic recall of specific verbal information are dissociated from those involved in accessing general semantic information inherent in the act of understanding and repeating words. As predicted, significant activation in the left mid-ventrolateral frontal cortical area 45 was observed in this subtraction. The activation was located in the cortex lining the inner part of the upper bank and the fundus of the horizontal sulcus. We have recently examined the cytoarchitecture of this region and found that it is occupied by cortical area 45 (30). We refer to this region as sulcal area 45. It is noteworthy that simple verbal repetition (Table 1) activated the lateral part of area 45 rather than its sulcal part.

Another test of the hypothesis that the left ventrolateral frontal cortex is involved in strategic mnemonic retrieval of verbal information was provided by the recall minus paired associate subtraction (Table 3). In the paired associate task, retrieval of specific words is nonstrategic as it is based on the production of highly practiced associates. In this subtraction, there was only one brain area with a blood flow response significantly greater in the recall condition, and this area was the left mid-ventrolateral frontal cortex (Table 3). Note that the paired associate minus repetition subtraction (Table 4) yielded no significant rCBF response in ventrolateral frontal cortex, demonstrating that stimulus-driven nonstrategic retrieval does not involve ventrolateral frontal cortex to a greater extent than the lexical search inherent in the act of producing a verbal response.

In our earlier work with PET (10), the mid-dorsolateral region of the frontal cortex, but not the ventrolateral, was shown to be activated in relation to the monitoring, within working memory, of self-generated and externally generated verbal responses. It was therefore to be expected that, in the free recall and the paired associate conditions in which the subjects were constantly monitoring, within working memory, their output from long-term memory, there would also be significant activity in the mid-dorsolateral region of the frontal cortex. This was confirmed in the recall minus repetition (Table 2) and the paired associate minus repetition (Table 4) subtractions, which revealed activity in the mid-dorsolateral frontal cortex.

Significant activity in the dorsolateral frontal cortex had been previously observed in a number of other PET studies that examined retrieval from verbal episodic memory (31–33). In these studies, with the exception of one recent investigation (34), no activation of the ventrolateral frontal cortex was observed. The present results suggest that the earlier failure to observe activation in ventrolateral frontal cortex from the retrieval of verbal episodic memory might have been due to the fact that the control tasks used also activated, to the same extent, ventrolateral frontal cortex.

The present results, taken together with earlier work (3, 4, 8–10, 31–33), indicate that the dorsolateral and the ventrolateral frontal cortex are involved in the performance of tasks requiring retrieval from verbal episodic long-term memory, but their contributions differ (8). The mid-dorsolateral frontal region participates in free recall by virtue of its role in the on-line monitoring, within working memory, of the output from long-term memory, whereas the mid-ventrolateral frontal cortex is more directly involved in active retrieval mechanisms (see ref. 8).

The writing-to-dictation condition, when compared with any of the other verbal tasks, permitted the demonstration of the network of areas that are involved in the act of writing when controlling for the processes involved in the comprehension of linguistic information. There was activation of the left sensorimotor cortex and supplementary motor cortex as well as extensive bilateral activation of the posterior parietal region. This pattern of activity is consistent with knowledge of the cortical system underlying writing based on lesion studies (35). The only part of the temporal cortex exhibiting greater activity in the writing condition was the posterior temporal area 37. This activation is of particular interest because damage near this region leads to what has been termed "lexical agraphia"—i.e., an impairment in writing which spares selectively writing that can be based on phonological processing (36).

In conclusion, the results of the present investigation are consistent with the hypothesis that the ventrolateral frontal cortex is involved in the active retrieval of specific information from long-term memory (8). Active retrieval in this context refers to an active search initiated and directed on the basis of the subject's intentions and plans. It can be distinguished from the more passive forms of retrieval that occur in posterior cortical "association" areas when incoming or recalled stimuli automatically trigger stored representations (e.g., on the basis of preexisting associations or matching to stored representations). The latter forms of retrieval do not involve ventrolateral frontal cortex. In this respect, it is important to note that lateral frontal cortical lesions do not produce primary impairments in memory (1), although performance on tasks that require active retrieval processes can be impaired (5–7).

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