

Hemispheric encoding/retrieval asymmetry in episodic memory: Positron emission tomography findings

(frontal lobes/semantic memory/laterality)

ENDEL TULVING*†, SHITIJ KAPUR‡, FERGUS I. M. CRAIK*†, MORRIS MOSCOVITCH*†, AND SYLVAIN HOULE‡

*Rotman Research Institute of Baycrest Centre, 3560 Bathurst Street, North York, ON Canada M6A 2E1; †Department of Psychology, University of Toronto, Toronto, ON Canada M5S 1A1; and ‡Positron Emission Tomography Centre, Clarke Institute of Psychiatry, University of Toronto, 250 College Street, Toronto, ON Canada M5T 1R8

Contributed by Endel Tulving, December 6, 1993

ABSTRACT Data are reviewed from positron emission tomography studies of encoding and retrieval processes in episodic memory. These data suggest a hemispheric encoding/retrieval asymmetry model of prefrontal involvement in encoding and retrieval of episodic memory. According to this model, the left and right prefrontal lobes are part of an extensive neuronal network that subserves episodic remembering, but the two prefrontal hemispheres play different roles. Left prefrontal cortical regions are differentially more involved in retrieval of information from semantic memory and in simultaneously encoding novel aspects of the retrieved information into episodic memory. Right prefrontal cortical regions, on the other hand, are differentially more involved in episodic memory retrieval.

This article is concerned with the neuroanatomical correlates of encoding and retrieval processes of episodic memory as revealed by positron emission tomography (PET). Episodic memory is a form of human memory that enables people to remember personally experienced events, including experimentally produced events in laboratory studies of memory (1–3). Cognitive encoding operations that take place when the individual originally experiences an event initiate the storage of information representing the event in episodic memory. On a subsequent occasion, retrieval processes may operate on the stored information and bring about the conscious experience of remembering the event (2, 4).

Since the 1960s, when encoding and retrieval were experimentally distinguished (5), a great deal of reliable behavioral evidence has been accumulated about variables related to encoding and retrieval processes (2, 6–9). Little is known, however, about neuroanatomical correlates of encoding and retrieval processes. Neuropsychological studies of brain-damaged patients have yielded a lot of data on “localization” of brain structures involved in memory, but they cannot distinguish between encoding and retrieval. For example, an anterograde amnesic patient’s inability to remember a recent event may be caused by the impairment of encoding or difficulty in retrieving, but there is no known method for distinguishing between these two possibilities.

Recently, however, PET has provided a means by which the neuroanatomical correlates of various cognitive processes can be investigated (10–13). In a recent PET study we focused on episodic memory encoding processes (14). We measured regional cerebral blood flow with ^{15}O -labeled water while subjects, healthy male university students, engaged in either a “shallow” or a “deeper” encoding activity (6, 15). The results revealed an association between blood flow data and encoding processes. Relative to shallower encoding, deeper processing at encoding was accompanied by a prom-

inent left prefrontal activation and resulted in higher recognition of the studied material. The prefrontal activation was asymmetric: encoding conditions showed no significant difference in blood flow in right prefrontal regions.

In another recent PET study with ^{15}O -labeled water (16) we focused on episodic memory retrieval. Healthy subjects’ brains were scanned while they listened either to novel sentences or to comparable sentences that they had learned the previous day. All other conditions were held constant between the two types of scan. Subjects recognized the “old” sentences without difficulty, and their experience of recognition was accompanied by increases in blood flow in several cerebral loci, including dorsolateral prefrontal cortical regions in the right hemisphere. The prefrontal activation was again asymmetric. There was some increase in the latero-posterior portion of the left prefrontal cortex, but the regions of activation on the left and on the right were not homotopical.

The asymmetric pattern of prefrontal activation in these studies prompted us to examine the literature for comparable findings. The review suggested a functional neuroanatomical model of encoding and retrieval of episodic memory information. We call the model the hemispheric encoding/retrieval asymmetry (HERA) model of prefrontal activation, and we describe it, and evidence relevant to it, in this article.

The idea that the frontal lobes, especially the prefrontal cortical regions, are involved in episodic memory is not new. Indirect evidence for such involvement has been suggested by clinical and neuropsychological studies of brain-damaged patients (17–22), by correlations between measures of source amnesia and indices of frontal lobe pathology (23, 24), and by preliminary studies of regional cerebral blood flow (25, 26). What has not been previously reported, or even suspected, is the prefrontal hemispheric asymmetry in episodic memory encoding and retrieval processes.

Novel Semantic Memory Retrieval Is Episodic Memory Encoding

Although few PET studies have focused explicitly on encoding processes, it is possible to interpret a number of studies done for other purposes as encoding studies. The key idea is that an act of retrieval, whether supported by episodic memory or semantic memory, frequently constitutes an input into episodic memory (3). This means that cognitive tasks that require the subject to retrieve semantic memory information over the temporal interval of a PET scan, also bring about the storage of information into episodic memory and, in that sense, can be thought of as episodic memory encoding tasks.

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. §1734 solely to indicate this fact.

Abbreviations: HERA, hemispheric encoding/retrieval asymmetry; PET, positron emission tomography.

Consider the verb generation task that has been used in a number of PET studies by the Washington University group of investigators (27, 28). In this task, subjects see or hear a noun and have to produce a meaningfully related verb (e.g., hear "ladder," say "climb"). The procedure is repeated with different nouns at a rapid pace many times. In the corresponding control task (noun repetition), subjects see or hear nouns and have to repeat back the same word (e.g., hear "paper," say "paper"). Prominent left-frontal activation has invariably been associated with the verb generation task (27, 28).

The verb generation task and the noun repetition task perform two functions concurrently: retrieval of information from semantic memory and encoding of information into episodic memory. For the subject to be able to respond with an appropriate verb to a presented stimulus noun, he or she must retrieve relevant information from semantic memory. But information about the event of doing so also is encoded into episodic memory: the subject, with a certain probability, can subsequently remember the event of hearing "car" and saying "drive." Whether or not subjects have been instructed to memorize the material under these conditions is immaterial. It is the nature of encoding processes, or encoding operations, rather than the subjects' intention to learn, that determines the retrievability of stored information (15).

It can be surmised (29) that the verb generation task is a more effective encoding task than the noun repetition task. Subjects would be expected to remember a larger proportion of nouns following the verb generation task than the noun repetition task.

To verify this conjecture we did an experiment in which we manipulated the depth of encoding and tested subjects' recognition of the nouns. We used the Washington University nouns as the materials to be remembered. In the first session, 82 undergraduates were exposed to four lists of 20 printed nouns each. In two of the lists their instructions were to write appropriate verbs as responses to the nouns (deeper encoding task). In the other two lists the instructions were to copy (repeat) the nouns (shallower encoding task). Speed of completion was emphasized, and no mention was made of any later test. The conditions were counterbalanced over subjects and lists. In the second session, 5 days later, the subjects were given an unexpected yes/no recognition test consisting of the 80 original nouns plus 80 new nouns, randomly mixed. They had to decide whether or not they had seen a given noun in any of the lists presented 5 days before. The hit rate for repeated nouns was 0.26, whereas the hit rate for verb-generation nouns was 0.50. The false-alarm rate, common to the two conditions, was 0.11. These data correspond to d' values of 0.58 and 1.23, respectively. The difference is statistically highly significant.

Thus, our cognitive study showed that the verb generation task is associated with higher recognition performance of the noun stimuli than is the noun repetition task. The Washington University studies have shown that the same verb generation task is associated with higher activation of left prefrontal cortex than is the noun repetition task. The combined pattern of data from the two sets of studies is the same as that found in our PET study of encoding (14): deeper encoding, resulting from more elaborate semantic memory retrieval, is associated with enhanced left frontal but not right frontal neuronal activity and enhanced subsequent episodic memory retrieval.

Encoding and Left Prefrontal Activation

The reasoning just outlined allows us to identify certain tasks used in PET studies as encoding tasks. The findings from these tasks relating to the involvement of the prefrontal cortical regions are summarized in the upper part of Table 1. For the purposes of the present article we ignore other

Table 1. Summary of PET findings with healthy human subjects concerning prefrontal activation associated with episodic memory encoding and retrieval processes

Study	Left	Right
Encoding		
Kapur <i>et al.</i> (14)	+	-
Petersen <i>et al.</i> (27)	+	-
Petersen <i>et al.</i> (30)	+	-
Frith <i>et al.</i> (31)	+	-
Frith <i>et al.</i> (32)	+	-
Wise <i>et al.</i> (33)	+	-
Raichle <i>et al.</i> (28)		
Trial 1	+	-
Trial 5	-	-
Buckner <i>et al.</i> (34)	+	-
Retrieval		
M.M. <i>et al.</i> (unpublished)		
Spatial Information	-	+
Object Information	-	+
Tulving <i>et al.</i> (16)	+	+
Squire <i>et al.</i> (35)	-	+
Buckner <i>et al.</i> (34)		
Different case	-	+
Auditory	-	+
Haxby <i>et al.</i> (36)	-	+
Jones-Gottman <i>et al.</i> (37)	-	+

Statistically significant evidence of prefrontal involvement is indicated by +, absence of similar evidence by -.

blood-flow findings from these studies. The upper part of Table 1 lists eight pairs of observations from PET studies in which regional cerebral blood flow was measured while subjects were engaged in cognitive tasks assumed to lead to high levels of episodic memory retrieval. [Episodic memory retrieval is also referred to as "explicit" memory (38).] With a single exception, which we will discuss presently, all studies found high levels of blood flow in left prefrontal cortical regions, without comparable activity in right prefrontal regions.

Kapur *et al.* (14) compared living/nonliving judgments with "a" checking. Petersen *et al.* (27), Buckner *et al.* (34), and Wise *et al.* (33) compared verb generation with noun repetition. Petersen *et al.* (30) compared noun reading with the baseline task of looking at cross hairs on the screen. Although noun reading, like noun repetition, is a shallow encoding task in comparison with more elaborate semantic judgments, it does allow a certain degree of episodic encoding and therefore can be included in the sample. Frith *et al.* (31, 32) compared verbal fluency tasks with word repetition. Verbal fluency tasks can be thought of as generation tasks—subjects generate instances of conceptual categories (such as jobs), or words beginning with a specified letter (such as a). Verbal fluency tasks require deeper processing than does the word repetition task. Finally, Buckner *et al.* (34) compared the (nonprimed) stem completion task with the baseline cross-hair fixation task. Like the other tasks in the upper part of Table 1, the nonprimed stem completion task, which involves semantic memory retrieval, was accompanied by left prefrontal activation, in the absence of comparable activation on the right. Buckner *et al.* (34) found a similar left prefrontal activation in a task in which subjects merely inspected the word stems, presumably because subjects covertly generated words from semantic memory.

Raichle *et al.* (28) studied semantic association as revealed by the verb generation task used by Petersen *et al.* (27). Subtraction of the noun repetition control condition from verb generation yielded a region of activation in the left prefrontal cortex, without any active regions shown in the right frontal lobes. A new, and important, finding was that

this pattern held only for “naive” subjects—i.e., for subjects who were performing the verb generation task for the first time. After the subjects had received an additional eight practice trials in generating verbs to the same set of nouns, the left prefrontal activation disappeared. This disappearance was attributable to the increased familiarity (reduced novelty) of the materials rather than increased familiarity with the procedural aspects of the task: when the “practiced” subjects had to generate verbs to a new set of nouns, the left prefrontal activation reappeared.

The disappearance of the left prefrontal activation after practice implies that not every act of semantic memory retrieval is encoded into episodic memory, and that only novel events are. The events in psychological experiments, such as seeing a to-be-remembered word or seeing a particular noun and generating a related verb in response to it, tend to be novel and are therefore duly encoded. When the same nouns have appeared repeatedly, in the same situation and context, and have elicited the same verb repeatedly, the noun-verb events cease to be novel and cease to be encoded into episodic memory. According to this reasoning the left frontal activation indicates encoding of novel information into episodic memory; it need not reflect the semantic memory operations as such.

In summary, we suggest that left frontal activation signals the involvement of the left-frontal cortical regions in the encoding of novel information into episodic memory, at least for verbal or verbalizable materials. Because all the relevant studies supporting this generalization used verbal materials, however, we do not know to what extent the rule would also hold for encoding of nonverbal information.

Retrieval and Right Prefrontal Activation

Consider now the PET findings associated with retrieval of information from episodic memory. Relevant data come from experiments in which subjects are exposed to specific information in a particular setting and then, under PET, are asked to recollect that information. The results of our retrieval study (16), together with other PET data from our laboratory (M.M., S.K., S. Kohler, and S.H., unpublished work) alerted us to the possibility of a frontal activation laterally opposite from that associated with encoding. On examination of the literature it turned out that our findings fit well with those reported by others. A summary of the current situation is depicted in the lower part of Table 1.

In our retrieval study (16), 12 normal subjects underwent PET scanning while they were listening to either new or old meaningful sentences. Subjects had never encountered the new sentences before, whereas they had heard the old sentences in a non-scanned study session 24 hr earlier. Under the PET scan, subjects’ recognition of old sentences was uniformly high. The PET data, in the form of a subtraction of the new sentence image from the old sentence image, showed, in addition to several posterior sites of activation, a prominent strip of increased activation in the right dorsolateral prefrontal cortex that extended from area 10 through areas 46 and 9 to area 6. There was also increased activation in the left frontal area, but most of it was situated along the cingulate sulcus, near the medial prefrontal cortex.

In another study in our laboratory (M.M., S.K., S. Kohler, and S.H., unpublished work), a novel spatial and object memory test was administered to 12 subjects who underwent PET scans while performing the tasks. Before scanning, subjects studied drawings of common objects. During two subsequent scans, subjects were tested either for recognition of the identity of studied objects or for recognition of their spatial location in the display. Cognitive performance was high in both object and spatial location tests. When the baseline perceptual PET image was subtracted from the two

recognition conditions, differential activation of the right prefrontal cortex was observed. Although in both “memory” conditions several posterior regions also revealed increased blood flow, there was no significant activation in the left frontal regions.

The Squire *et al.* (35) and the Buckner *et al.* (34) studies were explicitly designed to examine regional cerebral blood flow in episodic (explicit) retrieval. In these studies the experimental task was stem-cued recall of words from lists studied earlier, whereas the control task was (nonprimed) stem completion, as described earlier in this article. The comparison of the PET images from these tasks showed that episodic retrieval (explicit memory) was associated with right prefrontal activation in the absence of comparable activation on the left. Some left prefrontal activation was seen, but it was much less prominent than that observed on the right.

Haxby *et al.* (36) reported a PET study showing that episodic recognition of previously studied faces was accompanied by right prefrontal activation in the absence of comparable left frontal activation.

Finally, Jones-Gotman *et al.* (37) reported right frontal activation, but no left frontal activation, in a PET study in which subjects made episodic memory recognition judgments about olfactory stimuli. However, because an earlier study (39) also revealed right frontal activation in a nominally nonmemory task of odor identification, the interpretation of the results of the memory task must be regarded as equivocal.

In summary, then, we suggest that right frontal activation indicates the involvement of the right frontal cortical regions in the retrieval of information from episodic memory. Relevant studies supporting this generalization used different kinds of materials (words, faces, drawings of objects, odors) and included recall and recognition tests, as well as shorter and longer retention intervals.

The HERA Model

The data we have described suggest a hemispheric asymmetry in frontal lobe activation between encoding and retrieval of episodic information. Encoding tasks engage the left prefrontal regions, in the absence of comparable right frontal activation, whereas retrieval tasks engage the right prefrontal areas, frequently in the absence of comparable left frontal activation. The specific regions activated in the two frontal hemispheres show diversity, possibly because of the variability in materials and methods used in different experiments. The hemispheric encoding/retrieval asymmetry, however, holds rather generally. It is this asymmetry that provides support for the HERA model. We describe it as follows.

(i) The HERA model asserts that the left and the right prefrontal cortical regions are differentially involved in episodic and semantic memory processes.

(ii) Left prefrontal cortical regions are involved in retrieval of information from semantic memory to an extent that right prefrontal areas are not, at least insofar as verbal information is concerned.

(iii) Left prefrontal cortical regions are involved in encoding information about novel happenings into episodic memory to an extent that right prefrontal areas are not, at least insofar as verbal information is concerned.

(iv) Right prefrontal cortical regions are involved in retrieval of episodic information to an extent that left prefrontal areas are not.

(v) Right prefrontal cortical regions are involved in retrieval of episodic information to an extent that does not hold for retrieval of semantic information.

The HERA model has features in common with the interpretations of the results of PET studies done by the Washington University group. Petersen and Fiez (11), in their

extensive review of PET studies, suggested that the prefrontal activation may reflect the use of semantic information in tasks requiring controlled (nonautomatic and not overlearned) responding. Raichle *et al.* (28) hypothesized that there exist two pathways for verbal response selection, one for overlearned auditory tasks, the other for novel auditory tasks. This latter pathway overlaps with cortical regions involved in episodic memory encoding as envisaged in HERA. The right prefrontal activation associated with episodic memory retrieval in HERA agrees with suggestions made by Buckner *et al.* (34) that their recall task was subserved by the same pathway that subserved the stem completion task, but with the additional and specific involvement of the right prefrontal cortex in explicit (episodic) memory retrieval.

Complexities and Caveats

We think of the prefrontal lobes as components of an extensive neuronal network that subserves episodic remembering. Other components of this network probably include medial temporal lobe and diencephalic structures (19, 20, 22), as well as posterior cortical areas (16).

Both encoding and retrieval processes are complex and can be further analyzed into more specific components. We do not know what aspects of encoding and retrieval are reflected in left and right prefrontal activations. Cognitive neuroscientists have speculated about the role that prefrontal lobes play in conscious awareness and in attentional, supervisory, executive, strategic, and other such "higher-order" functions (19, 20, 22, 40). It is possible that the asymmetry of prefrontal involvement described by the HERA model is attributable to only one of these functions or to some combination of them. Future research will clarify this issue.

The prefrontal cortex is complex. A rich literature suggests that prefrontal structures are made up of several different anatomical and functional regions and that they are involved in a great variety of cognitive and behavioral performances (24, 40–42). A more precise identification of specific prefrontal regions involved in episodic memory processes remains to be worked out.

The data that we summarized earlier in the article painted a picture of a relatively clean functional separation between the left and right precortical regions' involvement in episodic memory, although there were also some apparent exceptions to the asymmetry of HERA. A protracted cognitive task, extending over the period of a PET scan, frequently may comprise both episodic encoding and episodic retrieval processes. In such a situation we would expect to see both left and right frontal activation (16, 43–45). It is possible to speculate that these kinds of bilateral findings reflect concurrent encoding and retrieval operations.

The HERA model aptly illustrates the advantages of combining psychological and physiological methods in the study of the relations between brain and mind. Many new problems raised by HERA will be solved by using the same kind of cognitive neuroscience approach.

We thank Gregory M. Brown, Randy Buckner, Reza Habib, Douglas Hussey, Stefan Kohler, Donald T. Stuss, Alan A. Wilson, and David Wilson for help and assistance. E.T.'s research is supported by an endowment by Anne and Max Tanenbaum in support of research in cognitive neuroscience and by the Natural Sciences and Engineering Research Council of Canada. F.I.M.C.'s research is supported by a grant from the National Sciences and Engineering Research Council of Canada.

1. Tulving, E. (1993) *Curr. Perspec. Psychol. Sci.* **2**, 67–70.
2. Tulving, E. (1983) *Elements of Episodic Memory* (Clarendon, Oxford).
3. Tulving, E. (1972) in *Organization of Memory*, eds. Tulving, E. & Donaldson, W. (Academic Press, New York), pp. 381–403.
4. Tulving, E. (1991) in *Memory: Organization and Locus of Change*, eds. Squire, L., Lynch, G., Weinberger, N. M. & McGaugh, J. L. (Oxford Univ. Press, New York), pp. 3–32.
5. Tulving, E. & Pearlstone, Z. (1966) *J. Verb. Learn. Verb. Behav.* **5**, 381–391.
6. Craik, F. I. M. & Lockhart, R. S. (1972) *J. Verb. Learn. Verb. Behav.* **11**, 671–684.
7. Lockhart, R. S. & Craik, F. I. M. (1990) *Can. J. Psychol.* **44**, 87–112.
8. Tulving, E. & Thomson, D. M. (1973) *Psychol. Rev.* **80**, 352–372.
9. Craik, F. I. M. (1983) *Philos. Trans. R. Soc. London Ser. B.* **302**, 341–359.
10. Posner, M. I., Petersen, S. E., Fox, P. R. & Raichle, M. E. (1988) *Science* **240**, 1627–1631.
11. Petersen, S. E. & Fiez, J. A. (1993) *Annu. Rev. Neurosci.* **16**, 509–530.
12. Raichle, M. E. (1989) in *Wenner-Gren International Symposium Series, 53: Visualization of Brain Functions*, eds. Ottoson, D. & Rosthne, W. (Stockton, New York), pp. 127–135.
13. Herscovitch, P., Markham, J. & Raichle, M. E. (1983) *J. Nucl. Med.* **24**, 782–789.
14. Kapur, S., Craik, F. I. M., Tulving, E., Wilson, A. A., Houle, S. & Brown, G. M. (1994) *Proc. Natl. Acad. Sci. USA* **91**, 2008–2011.
15. Craik, F. I. M. & Tulving, E. (1975) *J. Exp. Psychol. Gen.* **104**, 268–294.
16. Tulving, E., Kapur, S., Markowitsch, H. J., Craik, F. I. M., Habib, R. & Houle, S. (1994) *Proc. Natl. Acad. Sci. USA* **91**, 2012–2015.
17. Milner, B., Petrides, M. & Smith, M. L. (1985) *Hum. Neurobiol.* **4**, 137–142.
18. Schacter, D. L. (1987) *Psychobiology* **15**, 21–36.
19. Moscovitch, M. (1992) *J. Cognit. Neurosci.* **4**, 257–267.
20. Warrington, E. K. & Weiskrantz, L. (1982) *Neuropsychologia* **20**, 233–249.
21. Shimamura, A. P., Janowski, J. S. & Squire, L. R. (1990) *Neuropsychologia* **28**, 803–813.
22. Squire, L. R. (1987) *Memory and Brain* (Oxford Univ. Press, New York).
23. Schacter, D. L., Harbluk, J. & McLachlan, D. (1984) *J. Verb. Learn. Verb. Behav.* **23**, 593–611.
24. Craik, F. I. M., Morris, L. W., Morris, R. G. & Loewen, E. R. (1990) *Psychol. Aging* **5**, 148–151.
25. Deutsch, G., Papanicolaou, A. C., Eisenberg, H. M., Loring, D. W. & Levin, H. S. (1986) *Neuropsychologia* **24**, 283–287.
26. Tulving, E., Risberg, J. & Ingvar, D. H. (1988) *Bull. Psychon. Soc.* **26**, 522 (abstr.).
27. Petersen, S. E., Fox, P. T., Posner, M. I., Mintun, M. & Raichle, M. E. (1988) *Nature (London)* **331**, 585–589.
28. Raichle, M. E., Fiez, J. A., Videen, T. O., MacLeod, A. K., Pardo, J. V., Fox, P. T. & Petersen, S. E. (1994) *Cereb. Cortex*, in press.
29. Slamecka, N. J. & Graf, P. (1978) *J. Exp. Psychol. Hum. Learn. Mem.* **4**, 592–604.
30. Petersen, S. E., Fox, P. T., Snyder, A. Z. & Raichle, M. E. (1990) *Science* **249**, 1041–1044.
31. Frith, C. D., Friston, K. J., Liddle, P. F. & Frackowiak, R. S. J. (1991) *Proc. R. Soc. London Ser. B* **244**, 241–246.
32. Frith, C. D., Friston, K. J., Liddle, P. F. & Frackowiak, R. S. J. (1991) *Neuropsychologia* **29**, 1137–1148.
33. Wise, R., Chollet, F., Hadar, U., Friston, K., Hoffner, E. & Frackowiak, R. S. J. (1991) *Brain* **114**, 1803–1817.
34. Buckner, R. L., Petersen, S. E., Ojemann, J. G., Miezin, F. M., Squire, L. R. & Raichle, M. E. (1993) *Soc. Neurosci. Abstr.* **19**, 1001 (abstr.).
35. Squire, L. R., Ojemann, J. G., Miezin, F. M., Petersen, S. E., Videen, T. O. & Raichle, M. E. (1992) *Proc. Natl. Acad. Sci. USA* **89**, 1837–1841.
36. Haxby, J. V., Horwitz, B., Maisog, J. M., Ungerleider, L. G., Mishkin, M., Schapiro, M. B., Rapoport, S. I. & Grady, C. L. (1993) *J. Cereb. Blood Flow Metab.* **13** (Suppl. 1), S499 (abstr.).

37. Jones-Gotman, M., Zatorre, R. J., Evans, A. C. & Meyer, E. (1993) *Soc. Neurosci. Abstr.* **19**, 1002 (abstr.).
38. Graf, P. & Schacter, D. L. (1985) *J. Exp. Psychol. Learn. Mem. Cognit.* **11**, 501–518.
39. Zatorre, R. J., Jones-Gotman, M., Evans, A. C. & Meyer, E. (1992) *Nature (London)* **360**, 339–340.
40. Stuss, D. T. & Benson, D. F. (1986) *The Frontal Lobes* (Raven, New York).
41. Goldman-Rakic, P. S. (1988) *Annu. Rev. Neurosci.* **11**, 137–156.
42. Rademacher, J., Galaburda, A. M., Kennedy, D. N., Filipek, P. A. & Caviness, V. S., Jr. (1992) *J. Cognit. Neurosci.* **4**, 352–374.
43. Grasby, P. M., Frith, C. D., Friston, K. J., Bench, C., Frackowiak, R. S. J. & Dolan, R. J. (1993) *Brain* **116**, 1–20.
44. Petrides, M., Alivisatos, B., Evans, A. C. & Meyer, E. (1993) *Proc. Natl. Acad. Sci. USA* **90**, 873–877.
45. Petrides, M., Alivisatos, B., Meyer, E. & Evans, A. C. (1993) *Proc. Natl. Acad. Sci. USA* **90**, 878–882.