Seeing the Forest Through the Trees:
The Cross-Function Approach to Imaging Cognition

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During the last decade, the field of functional neuroimaging of cognition has grown exponentially. From a handful of studies in the early 1990s, this research domain expanded to more than 800 studies by the early 2000s. Today, positron emission tomography (PET) and functional MRI (fMRI) studies cover almost every aspect of human cognition, from motion perception to moral reasoning. If each study is seen as a tree, the field has grown from minimal vegetation to a luxuriant tropical forest in less than ten years. Yet, functional neuroimaging researchers sometimes focus exclusively on their own cognitive domain and do not see the forest through the trees. The goal of the present chapter is to call attention to the forest, that is, to what many functional neuroimaging studies of cognition have in common.

When we say that most researchers are focused on the trees, we refer to the fact that the vast majority of functional neuroimaging studies investigate a single cognitive function, such as attention, working memory, or episodic memory. Yet, with the accumulation of functional neuroimaging data, it has become obvious that the brain is not organized like a cognitive psychology textbook with dedicated systems for perception, attention, working memory, episodic memory, and so forth. Instead, the neural correlates of cognitive functions overlap considerably, with each brain region being involved in a variety of cognitive functions. What cognitive processes do these common regions mediate? By comparing patterns of brain activity across different cognitive functions, answers to this question can be generated.

-------- Figure 1 about here --------

The matrix in Figure 1 illustrates the difference between the traditional within-function approach and the cross-function approach we are advocating in this chapter.

Let us assume that in functional neuroimaging studies Cognitive Function A typically is associated with activations in Brain Regions 1 and 3, Cognitive Function B with activations in Brain Regions 2 and 3, and Cognitive Function C with activations in Brain Regions 1 and 2. In the standard *within-function approach*, functional neuroimaging researchers are primarily concerned with one cognitive function and interpret activations in relation to this particular function. Thus, in a situation like the one depicted in Figure 1, researchers of Function A would attribute the activation of Region 1 to a certain aspect of Function A, whereas researchers of Function C would attribute the activation of the same region to a certain aspect of Function C. For instance, left ventrolateral prefrontal cortex activations have been attributed to language processes by language researchers, to working memory processes by working memory researchers, to semantic memory processes by semantic memory researchers, and so forth (Cabeza & Nyberg, 2000). In contrast with the within-function approach, the *cross-function approach* focuses on the columns of the matrix rather than on the rows, and asks questions about the functional role of a brain region (e.g., Region 1) that is recruited by different cognitive functions (e.g., Functions A and C).

Thus, the basic question the cross-function approach asks is why the same brain region is recruited by different cognitive functions. There are at least three possible answers to this question. First, according to a *sharing view,* the common region is involved in cognitive operations that are recruited by different cognitive functions. In the case of Figure 1, the sharing view would argue that Region 1 mediates processes that are engaged both by Function A and C. A *reductionistic interpretation* of the sharing view

would say that shared operations "belong" to one of the two functions, and are "borrowed" by the other function. For example, prefrontal cortex (PFC) regions activated both by episodic memory and working memory could mediate working memory processes that are also tapped by episodic memory (e.g., Wagner, Desmond, Glover, & Gabrieli, 1998). In contrast, an *abstractive interpretation* of the sharing view would argue that the shared processes should be described in more abstract terms than either of the two functions. For instance, dorsolateral PFC regions common to episodic and working memory could reflect general monitoring operations that were tapped by both functions (e.g., Cabeza, Dolcos, Graham, & Nyberg, in press)

Second, according to a *subdivision view,* when different functions activate the same region, the region actually consists of several subregions that are differentially involved in each of the functions. In the case of Figure 1, the subdivision view would argue that Function A and Function C activate different subregions of Region 1 (e.g., Subregion 1a and Subregion 1c). From this point of view, the goal of the cross-function approach would not be to identify a common process shared by different functions, but to dissociate the functions of each subregion by increasing the spatial resolution of functional neuroimaging techniques and/or the specificity of experimental manipulations. Much of the functional neuroimaging work on visual recognition favors the subdivision view, and researchers in this area have identified subregions on the ventral surface of the temporal lobes that are specialized in recognizing faces, places, animals, and tools (for reviews, see Kanwisher, Downing, Epstein, & Kourtzi, 2001; Martin, 2001). It should be noted, however, that the subdivision view does not necessarily imply modularity, because one may argue that a region can be divided into subregions without assuming that these subregions have the properties typically attributed to neurocognitive modules, such as domain specificity, cognitive impenetrability, shallow output, etc. (Fodor, 1983).

Third, according to a *network view,* the finding that the same region is activated by several functions does not imply that the common region performs the same cognitive operations in all the functions. On the contrary, this view assumes that the cognitive operations performed by a brain region depend on the interactions between the region and the rest of the brain, and since these interactions change across functions, so do the operations performed by the region (McIntosh, 1999; Nyberg & McIntosh, 2000). In the case of Figure 1, the network view would argue that Region 1 performs different operations in Functions A and C, because during Function A it interacts with Region 3, whereas during Function C it interacts with Region 2. An extreme version of the network view would say that—with

the exception of primary sensory and motor cortices—brain regions are not specialized in particular cognitive process, and their operations are completely determined by network interactions. A moderate version of the network view would state that there is a broad specialization, but the specific operations performed by a region are determined by network interactions. For example, Region 1 may have a broad specialization in fast on-line computations, but these computations may be applied to speech processing during a language task or to rotating an object during an imagery task. It should be noted that the idea that brain regions have broad specializations is close to the abstractive interpretation of the sharing view.

Regardless of what view one endorses—the three views are not incompatible and may be combined in different ways—it seems clear that in order to understand why the same brain regions are activated by a variety of cognitive functions one must go beyond the standard within-function approach and adopt a cross-function approach. The cross-function approach has two basic methods, and both are described in the present chapter. One method is to conduct a metaanalysis combining the results of studies that originally investigated a single cognitive function (Cabeza & Nyberg, 2000; Christoff & Gabrieli, 2000; Duncan & Owen, 2000; Fletcher & Henson, 2001). Another method is to conduct functional neuroimaging studies that compare different cognitive functions directly within-subjects (Braver et al., 2001; Cabeza et al., in press; Cabeza, Dolcos et al., submitted; LaBar, Gitelman, Parrish, & Mesulam, 1999; Nyberg, Forkstam, Petersson, Cabeza, & Ingvar, 2002; Nyberg et al., submitted; Ranganath & D'Esposito, 2001). The present chapter describes both methods: first, we report a cross-study metaanalysis, and then we review the results of the first crop of studies that compare different functions within-subject.

Comparing different cognitive functions across studies

This section reports a metaanalysis of functional neuroimaging data. First, we describe the methods of the metaanalysis, including the characteristics of the dataset, the rationale for the classification employed, and the calculation of activation frequency. Then, we describe and discuss the results of the metaanalysis for prefrontal, midline, parietal, temporal, and medial temporal regions.

Methods

From the dataset of a previous large-scale metaanalysis (Cabeza & Nyberg, 2000), we selected 136 studies in five cognitive domains: (1) attention, (2) perception, (3) working memory, (4) semantic memory retrieval and episodic memory encoding, and (5) episodic memory retrieval. The rationale for considering semantic

memory retrieval and episodic memory encoding within the same category is that these two processes tend to co-occur and are very difficult to differentiate: semantic retrieval involves incidental episodic encoding and intentional episodic encoding involves incidental semantic retrieval (for a discussion, see Nyberg, Cabeza, & Tulving, 1996; Tulving, Kapur, Craik, Moscovitch, & Houle, 1994). Consistent with this idea, semantic retrieval and episodic encoding tend to show very similar activation patterns, except in medial temporal lobe (MTL) regions (see below).

-------- Table 1 about here --------

As Table 1 shows, for each cognitive domain, we classified activations according to whether the study involved verbal, object, or spatial stimuli. There were slight differences in the type of stimuli used in each domain, however. For verbal stimuli, the Working Memory domain included both words and numerical stimuli. In the Attention domain, studies in the verbal category used the Stroop task, and hence, are characterized not only by their verbal nature but by the conflict monitoring operations tapped by this task as well. In the Perception domain, the verbal category corresponded to word reading studies in which overt verbal responses were absent or subtracted out by the control task. Differences in the spatial category existed as well. The memory conditions also included imagery operations and the semantic retrieval category included letter rotation studies.

As in our previous metaanalysis (Cabeza & Nyberg, 2000), we used Brodmann Areas (BAs) as the unit of analysis (see Figure 2). Some BAs (e.g., 3/1/2, 4, 5, 33, 43, 38) were excluded because they showed very few activations, and some areas were collapsed together (BAs 41 and 42; BAs 30 and 31) to simplify analyses. Medial temporal lobe (MTL) regions were treated as a unit because the overall area is small and the localization of activations in different regions is not always clear. Due to space limitations, we do not report or discuss the results for occipital regions, basal ganglia, thalamic, and cerebellar regions.

-------- Figure 2 about here --------

In our previous metaanalysis (Cabeza & Nyberg, 2000), we identified typical activation patterns for each cognitive function using a qualitative evaluation of the frequency of activations across studies. Although we emphasized representative activations, we also noted exceptions to the general pattern and discussed specific findings and studies. By contrast, in the present metaanalysis, we used a quantitative measure of activation frequency and focused on aggregate results without discussion of individual studies. The quantitative measure employed is the number of activations reported in each BA or brain region in the studies reviewed. The number of activations is defined by the number of different coordinates reported, with some studies reporting more than one coordinate in each BA.

The rationale for using this measure is that the numbers of coordinates reported tended to be positively correlated with the size of the activations, and hence, this measure provides an indirect index of both frequency and relative size of the activations. The numbers of activations in each brain region were separately analyzed for each cognitive function and stimulus type (see Figures 2-7). Since the total number of activations varied across cognitive domains and stimulus type, we express the number of activations as a percentage of the number of activations in each cell in Table 1. Although using percentages provides a straightforward method to compare across category/stimuli cells, these percentages should be considered with caution in the case of cells with few activations (e.g., spatial perception), because they may reflect the peculiarities of the few studies in the cell rather than a general pattern.

Results

Prefrontal regions

The distribution of activations in the prefrontal cortex (PFC) for the five cognitive functions is shown in Figures 3 and 4. The lateralization of activation for semantic retrieval/episodic encoding and for episodic retrieval was consistent with the *hemispheric encoding/retrieval asymmetry (HERA) model* (Lars Nyberg et al., 1996; Nyberg, Cabeza, & Tulving, 1998; Tulving et al., 1994), which postulated that left PFC is differentially more involved in retrieving information from semantic memory and in simultaneously encoding novel aspects of this information into episodic memory, whereas right PFC is differentially more involved in retrieving information from episodic memory. At the same time, the lateralization of PFC activity was also affected by stimulus type: right lateralized activations during semantic retrieval/episodic encoding usually occurred for nonverbal materials and left lateralized activations during episodic retrieval usually occurred for verbal materials. Thus, the lateralization of PFC activity depends both on processes (Lars Nyberg et al., 1996; Nyberg et al., 1998) and stimuli (e.g., Kelley et al., 1998; McDermot, Buckner, Petersen, Kelley, & Sanders, 1999; Wagner et al., 1998)

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Turning to the activation pattern for different PFC subregions, Figure 3 shows the frequency of activation for anterior (BA 10), and dorsolateral (BAs 9 and 46) PFC regions. Anterior PFC (BA 10) activations were frequent for episodic memory retrieval, particularly in the right hemisphere. Frontopolar activity during episodic retrieval has been attributed to the generation and maintenance of the mental set of episodic retrieval, or *episodic retrieval mode* (Cabeza et al., 1997; Düzel et al., 1999; Lepage, Ghaffar, Nyberg, & Tulving, 2000; Nyberg et al., 1995). This idea is supported by evidence that activity in BA 10

remains constant across different levels of episodic retrieval performance (Nyberg et al., 1995) and different types of episodic retrieval tasks (Cabeza et al., 1997) and is sustained throughout the retrieval task (Düzel et al., 1999). Although not shown in Figure 3, activations in BA 10 are also frequent during problem solving (Cabeza & Nyberg, 2000), suggesting that this region has a more general role of monitoring internally generated information (Christoff & Gabrieli, 2000). Dorsolateral PFC (BAs 9 and 46) activations were frequent for working memory, semantic retrieval/episodic encoding, and episodic retrieval (see Figure 3). A sharing account of this overlap would be that semantic retrieval/episodic encoding and episodic retrieval depend on working memory(reductionistic interpretation) or that the three functions depend on monitoring operations (abstractive interpretation). However, sharing accounts cannot easily explain why the lateralization of dorsolateral PFC changes across functions, tending to be bilateral for working memory, left lateralized for semantic retrieval/episodic encoding, and right lateralized for episodic retrieval (see Figure 3). The subdivision view could argue that this different lateralization pattern reflects the existence of different subregions within dorsolateral PFC, whereas the network view could argue that the function of dorsolateral PFC, as well as its lateralization, is determined by its interactions with other brain regions (e.g., parietal cortex in for working memory, left temporal cortex for semantic retrieval/episodic encoding, etc.).

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Figure 4 shows the frequency of activations in ventrolateral (BAs 47 and 45), ventral/posterior (BA 44), and posterior (BA 6) PFC regions. BA 47 activations were lateralized similarly to dorsolateral PFC, but unlike dorsolateral PFC activations, they were also frequent not only for memory domains but also for the attention domain. This pattern suggests that BA 47 is involved in processes that are shared by working, semantic, and episodic memory as well as by attention tasks. In contrast, BA 45 seems to be more specific to semantic retrieval/episodic encoding, particularly in the left hemisphere and for verbal stimuli, consistent with the idea that this region is involved in semantic processing (Gabrieli, Poldrack, & Desmond, 1998; Poldrack et al., 1999). Like BAs 47 and 45, BA 44 also shows left lateralized activation during semantic retrieval/episodic encoding, but unlike BAs 47 and 45, left BA 44 is often activated during verbal working memory tasks. This pattern is in keeping with the notion that left BA 44, which overlaps with Broca's area, is involved in phonological maintenance and rehearsal (for a review, see Smith & Jonides, 1999). Thus, the present results are consistent with the notion that the anterior part of the left inferior frontal gyrus (BA 47 and 45) is involved in semantic processing, whereas the posterior part (BA44) is involved in

phonological working memory (Kapur et al., 1996; Poldrack et al., 1999). Yet, left BA 44 activations have also been found in working memory studies that employed faces and meaningless shapes (Cabeza & Nyberg, 2000), suggesting that the function of this region is not strictly verbal. The role of right BA 44—the homologue of Broca's area in the right hemisphere—is also unclear. Finally, the distribution of activations in posterior PFC (BA 6) looks quite different than the ones previously described. Activation overlaps in BA 6 are difficult to interpret because this is a very large Brodmann area that probably comprises two or more different functional subregions. The inferior part of BA 6 is close to Broca's area, and some of the left BA 6 activations during verbal working memory and semantic retrieval may reflect phonological rehearsal. In contrast, more dorsal parts of BA 6 may be more related to attentional and working memory processes.

Midline regions

Figure 5 shows the frequency of activations in midline regions, including the anterior cingulate cortex (BAs 32 and 24) and the precuneus (BA 31). Central cingulate activations are not depicted because they were scarce, but they show a pattern similar to those in the anterior cingulate. Anterior cingulate activations were frequent during attention (e.g., Stroop tasks), working memory, and episodic retrieval. The role of the anterior cingulate in cognition has been attributed to initiation of action (Posner & Petersen, 1990) and to conflict monitoring (for a review, see Botvinick, Braver, Barch, Carter, & Cohen, 2001), among other processes (for a review, see Devinsky, Morrell, & Vogt, 1995). The initiation of action hypothesis accounts well for activations during demanding cognitive tasks, such as working memory and episodic retrieval, whereas the conflict monitoring hypothesis provides a better account for anterior cingulate activations during Stroop tasks (see verbal-attention in Figure 5). Obviously, these two views are not incompatible: the anterior cingulate cortex could both initiate appropriate responses and suppress inappropriate ones (Paus, Petrides, Evans, & Meyer, 1993). Given the heterogeneous structure and complex connectivity of the anterior cingulate (Devinsky et al., 1995), it is quite possible that different processes are tapped depending on the particular sub-region engaged (subdivision view, e.g., Bush et al., 2002) and its interactions with the rest of the brain (network view).

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Precuneus activations in BA 31 showed a very different functional pattern than those in the anterior cingulate cortex. They were not frequent during Stroop or object working memory tasks, and were more specifically associated with the processing of spatial information in working memory, semantic retrieval/episodic encoding,

and episodic retrieval tasks. The association between the precuneus region and memory for spatial stimuli fits well with the idea that this region is involved in imagery (Fletcher et al., 1995; Shallice et al., 1994), although evidence against this hypothesis has been reported (Buckner, Raichle, Miezin, & Petersen, 1996; Krause et al., 1999). The present results also link the precuneus to the processing of spatial information, which is a link that has been discussed relatively little in the functional neuroimaging literature.

Parietal Regions

Figure 6 shows the frequency of activations in parietal regions (BAs 7, 40, and 39). BA 7 activations were frequent during attention, perception, and working memory, and also common during semantic retrieval/episodic encoding tasks involving spatial stimuli. This pattern fits well with the idea that this region is part of a dorsal pathway involved in spatial perception (Ungerleider & Mishkin, 1982). However, BA 7 is also activated by verbal attention, working memory, and episodic retrieval studies, and it is unclear how the spatial processing hypothesis can account for these activations. Also, the spatial processing hypothesis cannot easily account for activations in BA 40, which are frequent for attention, perception, and working memory regardless of stimuli. Working memory activations in left BA 40 have been attributed to the storage of verbal information in working memory (Awh, Jonides, Smith, Schumacher, & et al., 1996; for a review, see D'Esposito, 2001; Jonides, Smith, Marshuetz, Koeppe, & Reuter-Lorenz, 1998; Paulesu, Frith, & Frackowiak, 1993). The involvement of this region in spatial semantic retrieval could be related to a verbal component in some of these studies [e.g., letter rotation; \Alivisatos, 1997 #23; encoding the location of nameable objects; \Owen, 1996 #1751]. Finally, BA 39 activations seem to reflect both a spatial and verbal processing component. Left BA 39 activations in verbal perception studies may reflect the link between the left angular gyrus and graphemic/phonological processing (for a review, see Binder & Price, 2001).

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Temporal Regions

Figure 7 shows the frequency of activations in lateral temporal regions: BAs 22, 21, 20 and 37. Activations in left BA 22 were much more frequent for verbal than for object and spatial stimuli, suggesting they are primarily associated with language processing. Left BA 22 overlaps with Wernicke's Area, which has been strongly linked to language comprehension in research with aphasic patients (Benson, 1988). In contrast, left BA 21 activations were frequent not only for verbal but also for object stimuli. From a sharing-abstractive point of view, this pattern

suggests that BA 21 is involved in a process common to processing verbal and object stimuli, such as meaning-based analyses. Finally, consistent with its location along the ventral pathway for object processing (Ungerleider & Mishkin, 1982), activations in BAs 20 and 37 were more frequent when objects were used as stimuli. Thus, the distribution of activations over the lateral surface of the left temporal lobes, from the superior to the inferior temporal gyri, can be described as a gradient from verbal to object processing with more abstract (stimulus-independent) semantic processing in the middle.

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Medial temporal lobes

Finally, Figure 8 shows the frequency of activations in the medial temporal lobes (MTL). These activations were frequent during episodic memory encoding and retrieval, consistent with the evidence that lesions in this area impair episodic memory functions (for a review see Squire, 1992). The role of MTL in episodic memory has been attributed to binding (Henke, Buck, Weber, & Wieser, 1997; Lepage et al., 2000) and novelty detection (Tulving, Markowitsch, Craik, Habib, & Houle, 1996) during encoding, and to trace recovery (Cabeza et al., 2001; Nyberg, McIntosh, Houle, Nilson, & Tulving, 1996) and recollection (Eldridge, Knowlton, Furmanski, Bookheimer, & Engle, 2000; Schacter, Alpert, Savage, Rauch, & Albert, 1996) during retrieval (for a review, see Cohen et al., 1999). MTL has been also linked to spatial processing (Maguire, Frith, Burgess, Donnett, & J, 1998; O'Keefe & Nadel, 1978) but this idea cannot easily explain the relative lack of MTL activations during spatial attention, spatial perception, and spatial working memory. In contrast, MTL activations during attention and perception tasks were frequent when object stimuli were employed (see Figure 8). This pattern fits well with the notion that MTL is an anterior part of the ventral pathway for object processing. It is unclear if the episodic memory and object processing roles of MTL can be subsumed under a more general function (sharing view), whether they involve different subregions of MTL (subdivision view), or whether they reflect different interactions between MTL and the rest of the brain (network view).

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Summary

Table 2 summarizes the results previously displayed in Figures 3 to 8. For each brain region (e.g., BA 10), the presence of a symbol indicates that the frequency of activations for a stimuli/function combination (e.g., verbal episodic retrieval) was above the average for the region, and the size of the symbol indicates whether the frequency was slightly above average, high, or very high. Activations are displayed as lateralized (black = right, white = left,

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rosette = bilateral) when the frequency in one hemisphere was at least twice the frequency in the other hemisphere.

As illustrated by Table 2, anterior PFC activations in BA 10 were particularly frequent during episodic memory retrieval tasks. These activations have been attributed to episodic retrieval mode (Cabeza et al., 1997; Düzel et al., 1999; Lepage et al., 2000; Nyberg et al., 1995), but the involvement of anterior PFC in problem solving (Cabeza & Nyberg, 2000) suggests this region has a general role in monitoring internally generated information (Christoff & Gabrieli, 2000). Dorsolateral PFC activations in BA 9 and 46 were very frequent during working memory, semantic retrieval/episodic encoding, and episodic retrieval tasks, possibly reflecting working memory (Wagner, 1999) or monitoring (Cabeza et al., in press) operations. Ventrolateral PFC activations in BA 47 were also common during attention tasks. In the left hemisphere, BA 45 activations were particularly frequent during verbal semantic retrieval/episodic encoding tasks and BA 44 activations, during verbal working memory tasks. This pattern is consistent with the idea that the anterior part of the left inferior frontal gyrus is involved in semantic processing and the posterior part (i.e., Broca's area), in phonological rehearsal (Kapur et al., 1996; Poldrack et al., 1999). Finally, posterior PFC activations in BA 6 were most frequent during attention and working memory tasks.

Midline activations include those in anterior cingulate (BAs 32 and 24) and precuneus (BA 31) regions. Anterior cingulate activations were common for all functions, but—consistent with the conflict monitoring hypothesis (for a review, see Botvinick et al., 2001)—they were particularly frequent for Stroop tasks (verbal attention category). In contrast, precuneus activations were especially frequent for spatial memory tasks. Although the precuneus has been associated with imagery (Fletcher et al., 1995; Shallice et al., 1994), a specific link with spatial processing has been discussed very little in the literature.

Table 2 also shows the frequency of activation in parietal, temporal, and MTL regions. Parietal activations in BA 7 were common for all functions, and—consistent with the ventral/dorsal pathway distinction (Ungerleider & Mishkin, 1982)—they were often found during spatial tasks. In contrast, parietal activations in BA 40 were particularly frequent during attention and working memory tasks regardless of the stimuli. BA 39 were often found in the left hemisphere during verbal perception (reading) and verbal semantic retrieval/episodic encoding tasks, possibly reflecting the role of the left angular gyrus in language processing (for a review, see Binder & Price, 2001). Temporal activations in the left hemisphere can be described as a gradient from verbal processing in the superior temporal gyrus (BA 21) to object processing in the inferior temporal gyrus (BAs 20 and 37), with more abstract semantic processing in the middle (BA 22).

Finally, MTL activations were common during long-term memory and episodic and semantic tasks, consistent with the involvement of MTL in declarative memory (Squire, 1992). They were also associated with object perception and attention, suggesting that MTL is the anterior part of the ventral pathway for object processing (Ungerleider & Mishkin, 1982)

Comparing different cognitive functions within-subjects

Although cross-function comparisons in large-scale metaanalyses of imaging data like the one previously described (see also, Cabeza & Nyberg, 2000; Christoff & Gabrieli, 2000; Duncan & Owen, 2000) can help identify regions that show activation overlap across functions, their results are usually confounded with differences in stimuli, tasks, and imaging methods. Although these differences could be considered an advantage from a sharing point of view (because activation overlaps reflect similarities in processes rather than similarities in methods), they are a disadvantage from a subdivision point of view (location differences may reflect methodological differences rather than functional differences). More generally, the problem of cross-study comparisons is that they only allow qualitative statements about the involvement of a certain region in various functions but not quantitative statistical measures of the strength of these activations across functions. Thus, activations that appear to differ across functions may actually be similar (e.g., a threshold effect), and activations that appear similar across functions may actually be different (e.g., activation intensity). Thus, in order to accurately determine similarities and differences in activation across different functions it is critical to compare these functions directly, within-subjects, and under similar experimental conditions.

Only a few functional neuroimaging studies have tried such direct within-subject comparisons. One reason for this scarcity is historical: since most cognitive researchers specialize in a single cognitive function, it was only natural that they maintained this specialization when they started conducting functional neuroimaging studies. In addition, functional neuroimaging researchers inherited a long list of research questions about each particular function from cognitive psychology, and this list of questions kept them focused for many years on their favorite function. Another reason for the dearth of cross-function studies is that these studies are particularly difficult to design. First, the paradigms used to investigate different cognitive functions tend to be dissimilar (e.g., the cuing paradigm used to study attention vs. the old/new recognition paradigm used to study episodic retrieval), and it is challenging to design tasks for two different functions that have a similar structure in terms of stimuli, responses, and timing. Thus, trying to compare different functions may appear

sometimes as trying to "compare apples and oranges." It should be noted, however, that if one does not compare apples and oranges, one may miss the fact that they are both round and sweet fruits. Second, some functions are inherently more difficult than others. For example, in the case of working memory and episodic memory, if the memory load is kept constant (e.g., one word), then retrieval from working memory is always easier than retrieval from long-term memory. In these situations, one is faced with the dilemma of matching experimental conditions at the expense of having differences in task difficulty or matching task difficulty at the expense of introducing differences in experimental conditions. Despite all these problems, successful direct cross-function studies can be designed, and they offer unique insights into the role of different brain regions across various functions.

The next two sections review comparisons of different functions within-subjects (see Table 3). The first section reviews studies that used blocked fMRI and PET designs, and the second section, studies that employed event-related fMRI designs. An advantage of blocked designs for cross-function comparisons is that they measure both item- and state-related activity. Item-related activity refers to transient changes associated with cognitive operations specific to particular items within the task (e.g., old vs. new stimuli in a memory test), whereas state-related activity refers to sustained changes associated with mental states that are characteristic of the task (Donaldson, Petersen, Ollinger, & Buckner, 2001; Düzel et al., 1999). Since different functions can resemble each other or differ both in terms of item-related or state-related activity, it is convenient that blocked designs measure both of them at the same time. Event-related fMRI designs have several advantages for cross-function research. Importantly, these designs provide separate measures of different task components, such as the encoding, maintenance, and retrieval components of working memory tasks. Also, they allow separate analyses of trials associated with successful vs. unsuccessful behavioral responses, thereby providing a better control for differences in task difficulty across functions.

Blocked studies

LaBar et al. (1999)

One of the first functional neuroimaging studies that directly compared different cognitive functions within-subjects is probably the study by LaBar et al. (1999), which contrasted verbal working memory and visuospatial attention using fMRI. This study compared a working memory task without a spatial attention component (a letter 2-back task) to a spatial attention task without a working memory component (a Posner cuing paradigm in which the cue remained on until the target was presented). Each task

was compared to its own control task, and common regions were identified with a conjunction analysis.

As shown in Table 3, the conjunction analysis identified a common network of brain regions for verbal working memory and spatial attention, including posterior/dorsomedial PFC (BA 6), parietal (BAs 7/40), and left temporal regions. This overlap in posterior PFC and parietal regions is consistent with the results of the foregoing metaanalysis (see spatial attention and verbal working memory in Table 2). In LaBar et al.'s study, the verbal working memory tasks involved shifts between external (letters on display) and internal (letters in working memory) frames of reference, whereas the spatial attention task involved shifts to different locations in space. Thus, the authors proposed that the common network reflects shifts in attentional focus, irrespective of whether the shifts occur over space, time, or other cognitive domains.

In addition to conjunction analyses, LaBar et al. compared verbal working memory and spatial attention directly—after subtracting out their respective control conditions (see Table 3). Working memory was associated with activations in SMA, left opercular PFC (BA 44), precuneus, and inferior parietal regions (right BA 40), whereas spatial attention was associated with occipitotemporal and extrastriate cortex. The finding that SMA was more activated for verbal than for spatial stimuli is intriguing because this region was previously associated with spatial processing (e.g., Courtney, Petit, Maisog, Ungerleider, & Haxby, 1998). The finding that Broca's area (left BA 44) was more activated for working memory than for spatial attention is consistent with the metaanalysis reported in this chapter (see Table 2)

Braver et al. (2001)

The blocked fMRI study by Braver et al. (2001) compared PFC activations during working memory (2-back task), episodic encoding (intentional learning), and episodic retrieval (old/new recognition). Each task was investigated using words and unfamiliar faces. The authors made three predictions. (1) Dorsolateral PFC should be selectively activated by the working memory task. According to Braver et al., dorsolateral PFC "is critically important for tasks requiring active maintenance over intervening items and/or the monitoring and manipulation of maintained information" (p. 50), and these processes are not engaged during episodic memory encoding or retrieval. (2) Regardless of the task, ventrolateral PFC activity should be left lateralized for verbal materials and right lateralized for spatial materials (e.g., Kelley et al., 1998; McDermott, Buckner, Petersen, Kelley, & Sanders, 1999). (3) Frontopolar PFC should be selectively activated by episodic memory retrieval. The authors based this prediction on the aforementioned idea that anterior PFC

regions are involved in episodic retrieval mode (e.g., Lepage et al., 2000; Nyberg et al., 1995).

The results confirmed the first two predictions but not the third. Dorsolateral PFC regions were activated during working memory but not during episodic encoding or retrieval. Although this finding confirms Braver et al.'s first prediction, it is surprising because dozens of PET and fMRI studies of episodic memory encoding and retrieval have reported significant activations in dorsolateral PFC regions (Cabeza & Nyberg, 2000). The second prediction that ventrolateral PFC regions should be lateralized according to materials (left for words, right for faces) for both working and episodic memory was confirmed, suggesting that this lateralization pattern is a function-independent phenomenon. Finally, because anterior PFC was not differentially activated by episodic memory retrieval, the third prediction was not confirmed. On the contrary, a left anterior PFC (BA 10) was more activated for working memory than for episodic encoding and retrieval. This may have happened because the episodic retrieval task involved only retrieval processes whereas the working memory task (2-back) involved encoding, maintenance processes, and retrieval processes. Thus, it is possible that the working memory task was more complex and involved greater time-on-task activity than then episodic encoding and retrieval tasks. Since blocked designs cannot distinguish encoding, maintenance, and retrieval phases of working memory, they do not allow an appropriate comparison between episodic retrieval and the retrieval phase of working memory.

Nyberg, Forkstam et al. (2002) and Nyberg, Marklund et al. (submitted)

In two PET experiments, the neural correlates of working memory, semantic memory, and episodic memory were compared (Nyberg et al., 2002). Across the two experiments, three measures were used for each of the examined memory systems. Results were analyzed using multivariate statistical technique [Partial Lest Squares—PLS: \McIntosh, 1996 #3196] that can identify the combinations of experimental conditions that account for most variance in the brain images. In Experiment 1, both working memory and episodic retrieval were associated with activations in right anterior PFC, precuneus/cuneus, and bilateral parietal regions (see Table 3). In keeping with the results of Braver et al. (1999), right BA 47 was more activated for episodic retrieval than for working memory. Consistent with the metaanalysis previously reported, left PFC (BA 9, 45, 44) was differentially activated by semantic retrieval tasks, and posterior PFC (BA 6) by working memory tasks (see Table 3). Experiment 2 yielded an unexpected finding: an autobiographical memory task, which can be classified as episodic, activated a similar set of regions as semantic retrieval tasks, including left

ventrolateral PFC. We suggested that the cued word retrieval used in the task elicited general semantic retrieval, and therefore had a shared pattern of brain activity with tests of semantic retrieval.

In a follow-up study (Nyberg et al., submitted), the frontal regions common to working memory, episodic retrieval, and semantic retrieval were identified and the functional connectivity of these regions and the rest of the brain was investigated across tasks (e.g., McIntosh, Nyberg, Bookstein, & Tulving, 1997). This undertaking is closely related to the network view discussed in the Introduction, and to our knowledge this is the first study to consider connectivity analyses in cross-function comparisons. Three frontal regions were identified: left anterior PFC (BA 10), left ventrolateral PFC (BA 45), and dorsal anterior cingulate cortex (BA 32), (see Table 3). Of the three common regions, only the ventrolateral PFC region showed a shared pattern of functional connectivity. Thus, despite the fact that the anterior cingulate and anterior PFC regions were consistently activated across working memory, episodic retrieval, and semantic retrieval, they apparently played different roles in each of these functions. In contrast, the left ventrolateral region appeared to play the same role across the three memory functions, consistent with the idea that this region is involved in semantic generation (Fletcher & Henson, 2001) and active retrieval (Owen, Lee, & Williams, 2000) processes.

Event-related fMRI studies

Ranganath and D'Esposito (2001) and Ranganath, Johnson, & D'Esposito (submitted)

Ranganath and collaborators (Ranganath & D'Esposito, 2001; Ranganath, Johnson, & D'Esposito, submitted) compared brain activity during the encoding and retrieval phases of working memory and episodic memory. In PFC (Ranganath et al., submitted), bilateral posterior (BA 6) and ventrolateral (BA 44, 45, 47) regions were activated during both encoding and retrieval phases of both working memory and episodic memory. Additionally, bilateral dorsolateral PFC regions (BA 9, 46) and left anterior PFC region (BA 10/46) were activated during the retrieval phase but not during the encoding phase of both functions (see Table 3). A left ventrolateral PFC region (BA 47) was more activated during episodic retrieval than during working memory retrieval, but this region did not show a significant difference with respect to baseline in either condition. Thus, working memory and episodic memory recruited similar PFC regions, including a left anterior PFC region that was associated with the retrieval phase of both functions. According to the authors, the left anterior PFC activation reflected the "on-line" monitoring and evaluation of specific memory characteristics during retrieval.

In MTL regions, the study yielded a very interesting finding: whereas the hippocampus was activated during the maintenance phase of the working memory task, the parahippocampal gyrus was activated during the encoding and retrieval phases of both working memory and episodic memory (Ranganath & D'Esposito, 2001). A second experiment replicated these results, and additionally showed that both hippocampal and parahippocampal activations were greater for novel than for familiar faces (Ranganath & D'Esposito, 2001). The authors argued that both regions play a role in episodic memory (e.g., Aggleton & Brown, 1999). To explain why the hippocampus was not significantly activated during episodic encoding and retrieval tasks, the authors suggested that the hippocampus may use sparse representations (e.g., Fried, MacDonald, & Wilson, 1997), and as a result, its transient activity during episodic encoding and retrieval may be difficult to detect. In contrast, prolonged hippocampal activity may be easier to detect during working memory tasks, or during episodic tasks involving sustained recollective processing (e.g., Eldridge et al., 2000). More generally, the authors argued that their results cast doubts on the idea that working memory and episodic memory depend on distinct neural correlates, and endorsed the notion that working memory maintenance is the outcome of controlled activation of episodic memory networks (e.g., Fuster, 1995).

Cabeza, Dolcos, Graham, and Nyberg (in press)

In this study (Cabeza et al., in press), the neural correlates of episodic retrieval and working memory for verbal materials were compared. The trials of both tasks consisted of two phases (Phase 1 and Phase 2). In the episodic retrieval trials, Phase 1 consisted of an instruction to think back to a previous study episode, and Phase 2 consisted of a retrieval cue, to which subjects made a Remember-Know-New recognition response. Phase 1 was expected to elicit retrieval mode activity, and Phase 2 was expected to elicit cue-specific retrieval activity. In working memory trials, Phase 1 consisted of a memory set of four words in two columns, and Phase 2 consisted of a word probe, to which subjects made a Left-Right-New response. Thus, Phase 1 measured working memory encoding and maintenance activity, and Phase 2 measured working memory retrieval activity.

The fMRI data yielded two main findings (see Table 3). First, there were similarities and differences in PFC activity across tasks: (i) a left dorsolateral region (BA 9) was similarly activated for working memory and episodic retrieval tasks, (ii) anterior (BA 10) and ventrolateral (BA 47, 45) regions were more activated for episodic retrieval, and (iii) Broca's (left BA 44) and posterior/dorsal (BAs 44, 6) regions were more activated for working memory (see Table 3). (i) The finding of overlapping dorsolateral PFC activity for episodic retrieval and working memory is

consistent with the aforementioned results by Ranganath et al. (submitted). Dorsolateral prefrontal activations have been attributed to monitoring in both episodic retrieval and working memory studies, and the results were consistent with this idea. (ii) The anterior PFC activation during episodic retrieval was consistent with the hypothesis that this region is involved in retrieval mode (Cabeza & Nyberg, 2000; Düzel et al., 1999; Lepage et al., 2000; Nyberg et al., 1995). In keeping with this idea, the anterior PFC activation started during Phase 1, before the presentation of the retrieval cue and was sustained throughout the trial (see Figure 9). This time-course could explain why Braver et al. (2001) and Ranganath et al. (submitted) failed to detect differential anterior PFC activity during episodic retrieval because those studies did not differentiate between retrieval mode and cue-specific aspects of episodic retrieval. Greater ventrolateral PFC activity for episodic retrieval than for working memory is consistent with the results of Braver et al. (2001) and Nyberg et al. (2002). The fact that this activation occurred during Phase 2 following the recognition cue (see Figure 9) fits well with the notion that this region is involved in the specification of episodic retrieval cues (Henson, Shallice, & Dolan, 1999). (iii) Finally, the finding that Broca's area was differentially engaged during working memory is consistent with the results of LaBar et al. (1999), and the fact that this activation was maximal during the maintenance phase of working memory harmonizes with the idea that this region mediates phonological rehearsal (for a review, see Smith & Jonides, 1999).

-------- Figure 9 about here --------

The second main result of the study was the unexpected finding that anterior MTL was activated during both episodic retrieval and working memory. Although consistent with the aforementioned study by Ranganath and D'Esposito (2001), this finding is surprising because MTL has been strongly associated with episodic retrieval but not with working memory. We speculated that the MTL overlap might reflect the indexing functions of this region, which could play a role not only during the access of stored long-term memory traces but also during the maintenance of short-term memory representations. As discussed below, however, more recent findings show that anterior MTL is also activated during an attention task without a mnemonic component, suggesting that the representations indexed by MTL are not necessarily mnemonic.

Cabeza, Dolcos, Prince, et al. (submitted)

In a recent event-related fMRI study, the neural correlates of episodic memory retrieval and visual attention were compared. The motivation for comparing these two functions was that many of the brain regions typically activated during episodic retrieval tasks (for reviews, see

Cabeza, 1999; Rugg & Henson, in press), such as prefrontal, parietal, anterior cingulate and thalamic areas, are also frequently activated during visual attention tasks (for reviews, see Handy, Hopfinger, & Mangun, 2001; Kanwisher & Wojciulik, 2000). Thus, although the involvement of these regions during episodic retrieval has been attributed to episodic retrieval processes (e.g., postretrieval monitoring), it may actually reflect attentional operations. To investigate this idea, the previously described episodic retrieval task with retrieval mode and cue-specific retrieval phases (Cabeza et al., in press) was compared to a visual attention task with an important sustained attention component. In the visual attention task, participants stared at a letter in the center of the screen to determine whether it blipped once, twice, or never during a 12 sec interval.

The study yielded three main findings. First, consistent with previous functional neuroimaging evidence, the study identified a common fronto-parietal-cingulate-thalamic network for episodic retrieval and visual attention. This finding suggests that many of the PFC and parietal activations frequently found during episodic retrieval reflect basic attentional processes rather than complex mnemonic operations. Actually, some of the memory-related interpretations proposed in episodic retrieval studies can be easily rephrased in terms of simpler attentional processes. For example, right dorsolateral PFC activations during episodic retrieval have been attributed to postretrieval monitoring (Henson et al., 1999), but since monitoring involves sustained attention and sustained attention is associated with right PFC activations (for reviews, see Coull, 1998; Sarter, Givens, & Bruno, 2001), then right PFC activations during episodic retrieval may be described as sustained attention to the retrieval output.

Second, several subregions were differentially involved in episodic retrieval vs. visual attention. For example, left PFC was more activated for episodic retrieval than for visual attention, possibly reflecting semantically-guided information production, whereas right PFC was more activated for visual attention than for episodic retrieval, possibly reflecting monitoring processes (Cabeza, Kester, & Anderson, submitted). Consistent with Cabeza et al. (in press), anterior PFC (BA 10) was differentially involved in episodic retrieval, possibly reflecting retrieval mode. The precuneus and neighboring regions were more activated for episodic retrieval than for visual attention, suggesting that these areas are involved in processing internally generated information.

-------- Figure 10 about here --------

Finally, the study yielded an unexpected finding: anterior MTL regions were similarly activated during episodic retrieval and during visual attention (see Figure 10). If one assumes that MTL has an indexing function (e.g., MClelland, McNaughton, & O'Reily, 1995), then this finding suggests that MTL indexes not only episodic memory and working memory representations (Cabeza et al., in press), but also perceptual representations. In other words, anterior MTL may index representations in the focus of consciousness, regardless of whether the representations originate in episodic memory, working memory, or the senses. This idea is consistent with Moscovitch's proposal that MTL is a module specialized in automatically registering the conscious experience (Moscovitch, 1992). Also, the idea is coherent with evidence that MTL activity during episodic retrieval differs for old items associated with different forms of consciousness (remembering vs. knowing: Eldridge et al., 2000) but is similar for old and new items associated with similar forms of consciousness (veridical vs. illusory recognition: Cabeza, Rao, Wagner, Mayer, & Schacter, 2001; Schacter, Reiman et al., 1996). Since MTL lesions do not usually impair working memory and attention tasks, but sometimes disrupt implicit tasks (e.g., Chun & Phelps, 1999), one has to conclude that MTL activity may reflect processing the contents of consciousness but is neither necessary nor sufficient for this processing.

Conclusions

To summarize the main findings of comparing different cognitive functions across studies (Figures 3-8, Table 2) and within-subjects (Table 3), we performed the drastic simplification shown in Table 4. First, we collapsed over verbal, object, and spatial stimuli because the modulatory effects of stimulus type can be summarized in two simple statements: differences between object and spatial stimuli generally follow the ventral/dorsal pathway distinction (Ungerleider & Mishkin, 1982), and differences between verbal and nonverbal stimuli follow hypothetical hemisphere specializations (e.g., Milner, 1971). Second, we only considered activation overlaps supported by both cross-study (Table 2) and within-subjects (Table 3) analyses. Thus, Table 4 does not include the perception domain, which has not been investigated by direct cross-function studies. Finally, we focused on the most consistent activation patterns and did not emphasize exceptions to these patterns or theoretical controversies.

As illustrated by Table 4, anterior PFC (BA 10) plays a prominent role in episodic retrieval and, to a lesser degree, in working memory. The involvement of this region in episodic retrieval is consistent with the retrieval mode hypothesis (Cabeza et al., in press) and the overlap between episodic retrieval and working memory (Nyberg et al., 2002; Ranganath et al., submitted) is consistent with a more general role in monitoring internally generated information (Christoff & Gabrieli, 2000). Dorsolateral PFC (BA 9/46) is most strongly associated with working memory and episodic retrieval, possibly reflecting a role in monitoring (Cabeza et al., in press). Anterior ventrolateral

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PFC (BA 47/45) is also involved in working memory and episodic retrieval, but in the left hemisphere it plays a major role in episodic encoding/semantic retrieval, possibly reflecting semantic processing (e.g., Gabrieli et al., 1998). Ventrolateral PFC is also known to play an important role in inhibitory control (D'Esposito, Postle, Jonides, & Smith, 1999; Jonides et al., 1998), and this function could account for its involvement in Stroop tasks. In the left hemisphere, posterior ventrolateral PFC (BA 44) is strongly associated with verbal working memory, consistent with a hypothetical role in phonological rehearsal (Cabeza et al., in press; Kapur et al., 1996; Poldrack et al., 1999). Finally, posterior-dorsal PFC (dorsal BA 6) seem primarily associated with attention and working memory, consistent with a hypothetical role in top-down selection (Corbetta & Shulman, 2002)

Table 4 shows that whereas parietal regions (BAs 40, 7) were primarily associated with attention and working memory, left temporal regions (particularly BA 21) were primarily associated with semantic and episodic memory. The involvement of parietal regions in attention and working memory, as well as in episodic retrieval, can be explained if one assumes that these regions are involved in shifting attention not only among external events (spatial and nonspatial attention), but also among internal events (working memory and episodic retrieval). The involvement of left temporal regions in both semantic and episodic memory tasks (Nyberg et al., 2002) can be explained by a general role in semantic processing.

Finally, the MTL seems to be involved in all four cognitive functions. Although the cross-study metaanalysis did not link MTL to working memory, two cross-function fMRI studies found the MTL to be activated for both episodic retrieval and working memory (Cabeza et al., in press; Ranganath & D'Esposito, 2001). Overlapping MTL activations for episodic retrieval and visual attention have been found and suggests that this region indexes representation within the focus of consciousness (Cabeza, Dolcos et al., submitted). This hypothesis fits well a popular cognitive neuroscience model (Moscovitch, 1992) and can account for the involvement of these regions in several different cognitive functions.

As noted above, Table 4 shows an extremely simplified (almost simplistic) description of typical activation patterns, which does not acknowledge exceptions to the patterns or theoretical controversies about the functions of different brain regions. For example, although anterior PFC tends to play a more important role in episodic retrieval than in working memory, Ranganath et al. (submitted) found similar anterior PFC activity across these functions and Braver et al. (2001) found greater activity for working memory. Even if Ranganath et al.'s findings reflect a lack of power and Braver et al.'s results reflect the lack of differentiation between working memory

encoding and retrieval, further research is clearly warranted. Also, there are inconsistencies about the lateralization of overlapping PFC activations. For instance, overlapping anterior PFC activations for episodic retrieval and working memory have been found in the right hemisphere (Nyberg et al., 2002), in the left hemisphere (Ranganath et al., submitted), and bilaterally (Cabeza et al., in press). Moreover, Table 4 collapsed over regions is likely to have different roles in cognition, such as inferior (BA 40) and posterior (BA 7) parietal regions. For example, we recently found that the posterior parietal cortex was similarly involved in working memory and episodic retrieval, whereas the anterior parietal cortex in the left hemisphere was differentially involved in working memory (Cabeza et al., in press; see also Ranganath et al., submitted). If there is disagreement about the activation patterns in Table 4, there is of course much more disagreement about the theoretical interpretations of these activations. For instance, a recent fMRI study (Bush et al., 2002) pointed out that if one considers only research with humans subjects, the list of cognitive processes attributed to the anterior cingulate cortex include the following: attention-for-action/target selection, motivational valence assignment, motor response selection, error detection/performance monitoring, competition monitoring, anticipation, working memory, novelty detection, and reward assessment. Cross-functions comparisons could help decide among these different functional interpretations

Cross-function comparisons provide important constraints to functional interpretations, particularly if one assumes the sharing view. For example, although we have attributed MTL activity to the recovery of episodic memory traces (e.g., Cabeza et al., 2001; Nyberg, McIntosh, et al., 1996), the involvement of these regions in attention, working memory, and semantic memory suggest a much more general function in cognition. Cross-function comparisons work against the natural tendency to interpret activations in terms of our favorite cognitive function (episodic memory in our case). They help us overcome function-chauvinism and see the "big picture." In other words, cross-function comparisons allow us to see the forest through the trees.

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Figure Captions

Figure 1. Illustration of within-function and cross function approaches to functional neuroimaging.

Figure 2. Brodmann's areas (From H. Elliott, *Textbook of Neuroanatomy*. Philadelphia: Lippincott. Reprinted with permission).

Figure 3. Percentage of activations in anterior and dorsolateral prefrontal regions in five cognitive domains. Notes: BA = Brodmann Area; V = verbal; O = object; S = spatial.

Figure 4. Percentage of activations in ventrolateral and posterior prefrontal regions in five cognitive domains. Notes: BA = Brodmann Area; V = verbal; O = object; S = spatial.

Figure 5. Percentage of activations in midline regions in five cognitive domains. Notes: BA = Brodmann Area; V = verbal; O = object; S = spatial.

Figure 6. Percentage of activations in parietal regions in five cognitive domains. Notes: BA = Brodmann Area; V = verbal; O = object; S = spatial.

Figure 7. Percentage of activations in temporal regions in five cognitive domains. Notes: BA = Brodmann Area; V = verbal; O = object; S = spatial.

Figure 8. Percentage of activations in medial temporal lobe regions in five cognitive domains. Notes: BA = Brodmann Area; V = verbal; O = object; S = spatial.

Figure 9. Time-courses of brain activity during episodic retrieval and working memory in three prefrontal regions (after Cabeza et al., in press).

Figure 10. Time-courses of brain activity during episodic retrieval (ER) and visual attention (VA) in a left anterior medial temporal lobe region (after Cabeza, Dolcos et al., submitted).

Table 1. Number of activations (reported peaks) in 136 PET/fMRI studies according to the cognitive function and type of stimulus involved.

	Verbal	Object	Spatial	Total
1. Attention	37	60	83	180
2. Perception	106	109	27	242
3. Working Memory	238	85	177	500
4. Semantic Retrieval/Episodic Encoding	171	124	60	355
5. Episodic Retrieval	216	49	45	310
Total	768	427	392	1587

Table 2. Typical activation patterns in PET and fMRI studies of five cognitive functions

		Prefrontal							Midline			Parietal			Temporal				MTL
		10	9	46	47	45	44	6	32	24	31	7	40	39	22	21	20	37	
Attention	verbal	●			●	○	●		❖	❖			✿						
	object			✿				✿				✿	✿		✿		●		●
	spatial			✿				✿	❖	❖		✿	✿						
Perception	verbal								❖	❖				○	○	○	○		
	object					✿										○		✿	✿
	spatial							✿				✿	✿	✿				✿	
Working Memory	verbal		✿	✿			○	✿		❖			✿						
	object		●	✿	✿		○		❖				✿			✿		✿	
	spatial	✿	✿	●	✿			✿		❖	❖	✿	✿						
SemRet/EpiEnc	verbal		○	○	○	○	○		❖					○	○	○			○
	object						✿									○	○	✿	✿
	spatial			○		●					❖	✿	○				✿	○	✿
Episodic Retriev.	verbal	●	●		●	✿			❖	❖		✿					✿		✿
	object	●			●				❖	❖				✿		○	✿		✿
	spatial	○	●		●			●			❖	✿		●				✿	●

Notes: ○ = left lateral; ● = right lateral; ✿ = bilateral lateral; ❖ = midline. For each brain region (e.g., BA 10), a symbol is shown if the frequency of activations for a particular stimuli/cognitive function cell (e.g., verbal episodic retrieval) was higher than the average frequency for the region. The size of the symbol approximately corresponds to relative proportion of activations for each function compared to the rest of the functions. Activations are shown as lateralized when the frequency for one hemisphere was at least double than in the other hemisphere.

Table 3. Results of PET/fMRI studies that compared different cognitive functions within-subjects

Study / Contrast	Prefrontal							Midline			Parietal			Temporal				MTL
	10	9	46	47	45	44	6	32	24	31	7	40	39	22	21	20	37	
Blocked paradigms																		
LaBar et al. (1999)																		
Both WM & spatial attention							❀				❀	❀		○		○		
WM > spatial attention						○	❀				❀	●						
Spatial attention > WM																	❀	
Braver et al. (2001): PFC																		
WM > other tasks	○	❀	❀				●											
Episodic enc. > other tasks	❖			○														
Episodic ret. > other tasks*			●															
Nyberg et al. (2002): task PLS																		
Exp. 1: Both WM & episodic ret.	●									❖	❀	❀						
Episodic ret. > other tasks	●		●							❖	○	❀			○			
Semantic ret. > other tasks		○		○	○							○			○			
WM > other tasks		❀	❀				●				❖	❀				●		
Exp. 2: both autobio. m. & sem. ret.				●	○	○	❀								○			
Nyberg et al. (submitted): seed PLS																		
WM, episod. ret. & sem ret.	○			○				❖										
Even-related paradigms																		
Ranganath et al. (submitted): PFC																		
Ranganath & D'Esposito (2001): MTL																		
Both WM enc & episodic enc.			❀	❀	❀	❀											❀	❀
Both WM ret & episodic ret.	○	❀	❀	❀	❀	❀	❀	❖				❀	●				❀	❀
WM > episodic m.												○		○				❀
Episodic m. > WM				○													❀	❀
Cabeza et al. (2002)																		
Both vorking m. & episodic ret.		○		❀			❀	❖			❀							❀
Episodic ret. > WM	❀	❀		❀	❀		●	❖		❖			❀	❀	●			
WM > episodic ret.						○	❀				❀	○		❀	❀		❀	
Cabeza et al. (submitted)																		
Both episodic ret. & visaul attention		●		●			❀	❖			❀							
Episodic ret. > visual attention	○	○	○	○	○					❖	❖	○	❀		○			
Visaul attention > episodic ret.	●		●		●	●	❀				●	❀		❀			●	

Notes: ○ = left lateral; ● = right lateral; ❀ = bilateral lateral; ❖ = midline. E1 = Experiment 1; enc = encoding; ret = retrieval; sem. = semantic; WM = working memory; * the activation did not meet the significance criteria used for other contrasts.

Table 4. Common regions for four cognitive functions and their hypothetical role in cognition

Function / region/BA	PFC					ACC: 32,24	pCun: 31	Pariet: 40,7	Temp: 21	MTL
	ant: 10	DL: 9,46	aVL: 47,45	pVL: 44	postDors: 6					
Attention			● 1,7		✻ 1,2,7	❖ 1,7		✻ 1,2,7		✺ 1,7
Working Memory	✺ 1,3,4,5	✻ 1,3,4,5,6	✻ 1,4,5,6	◯ 1,2,5,6	✻ 1,3,4,5,6	❖ 1,4,5,6	❖ 1,4	✻ 1,4,5,6		✺ 5,6
Epi Enc/Sem Ret		◯ 1,4	◯ 1,4,5	◯ 1,4,5		❖ 1,4			◯ 1,4	✺ 1
Episodic Retrieval	✻ 1,4,5,6,7	✻ 1,4,5,6,7	✻ 1,4,5,6,7			❖ 1,4,5,6,7	❖ 1,4,6,7	✺ 1,4,5,7	◯ 1,4,7	✻ 1,5,6
Hypothetical processes	retrieval mode and/or monitoring of internally generated information	monitoring	semantic processing & inhibitory control	in left hemisphere: phonological rehearsal	top-down selection	initiation of action and/or conflict monitoring	orienting attention to internally generated information	shifts of attention among external or internal events	semantic processing	indexing of representations within the focus of consciousness

Abbreviations: Epi. = episodic; Enc = encoding; Ret = retrieval; BA = Brodmann Area; PFC: prefrontal cortex; ACC = anterior cingulate; Precun = precuneus; Pariet = parietal cortex; Temp = temporal cortex; MTL = medial temporal lobes; ant = anterior; DL = dorsolateral; aVL = anterior ventrolateral; VLp = posterior ventrolateral-posterior; postDors = posterior dorsal

Numbers: 1 = present metanalysis (see Table 2); 2 = LaBar et al. (1999); 3 = Braver et al. (2001); 4 = Nyberg et al. (2002) and Nyberg et al. (submitted); 5 = Ranganath & D'Esposito (2001) and Ranganath et al. (submitted); 6 = Cabeza et al. (2002); 7 = Cabeza et al. (submitted).
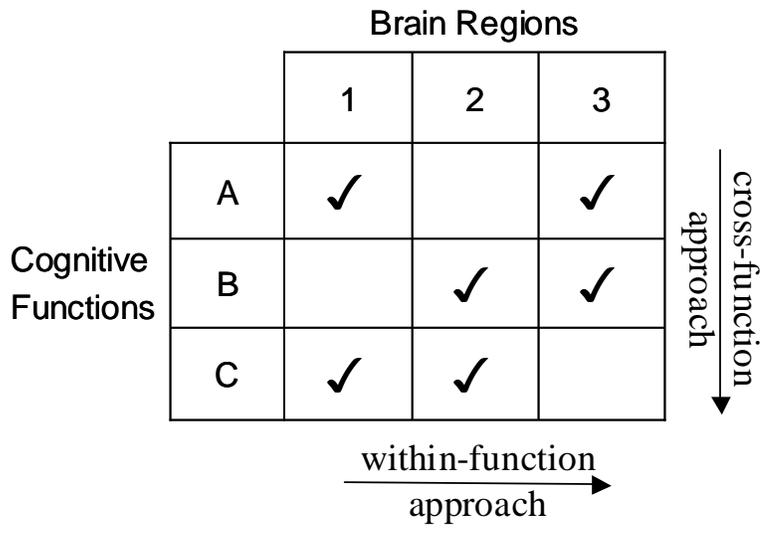
Fig. 1
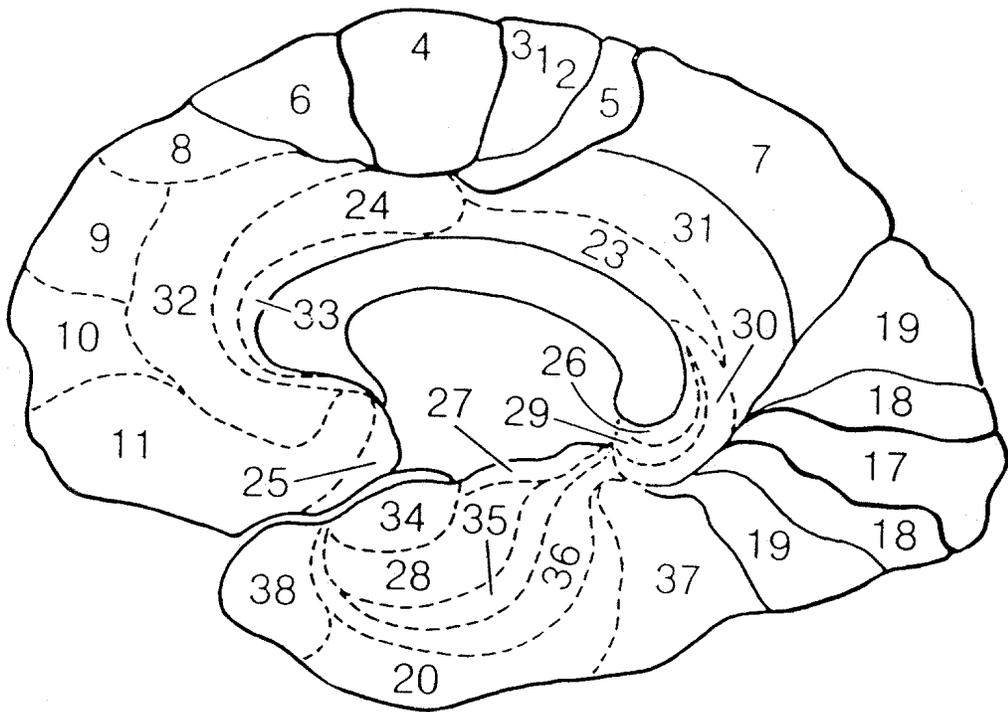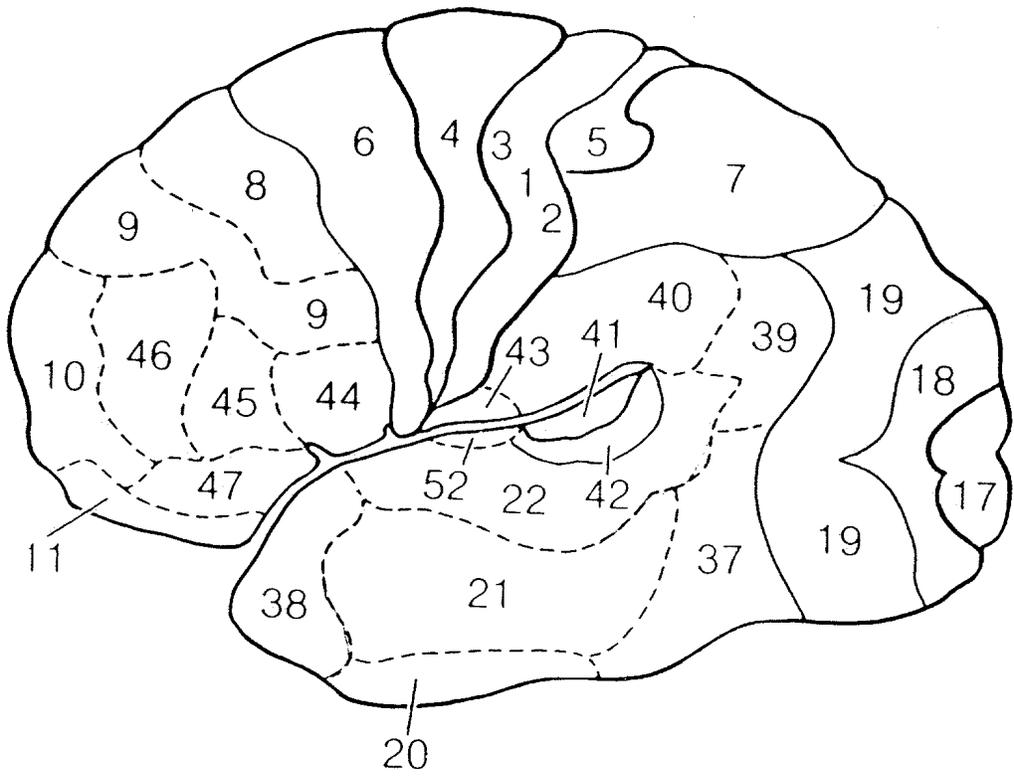
Fig. 2

Anterior and Dorsolateral Prefrontal Regions

BA 10
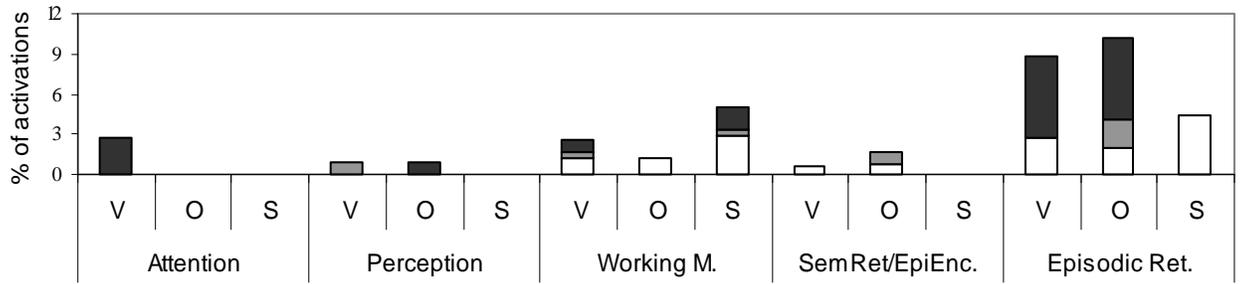
BA 9
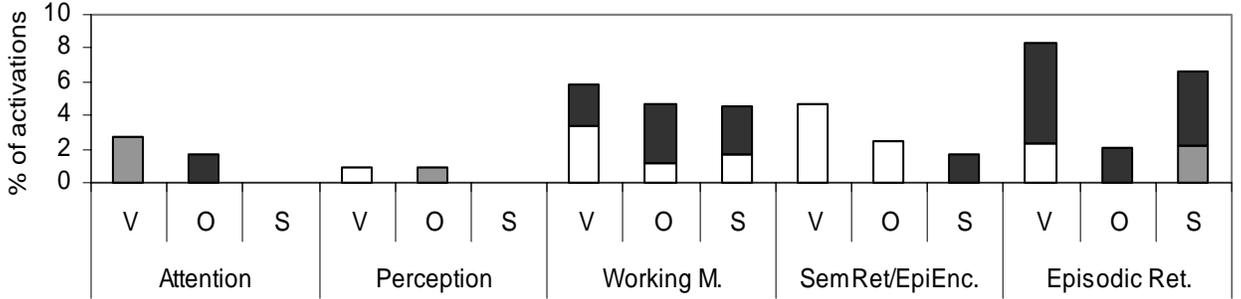
BA 46
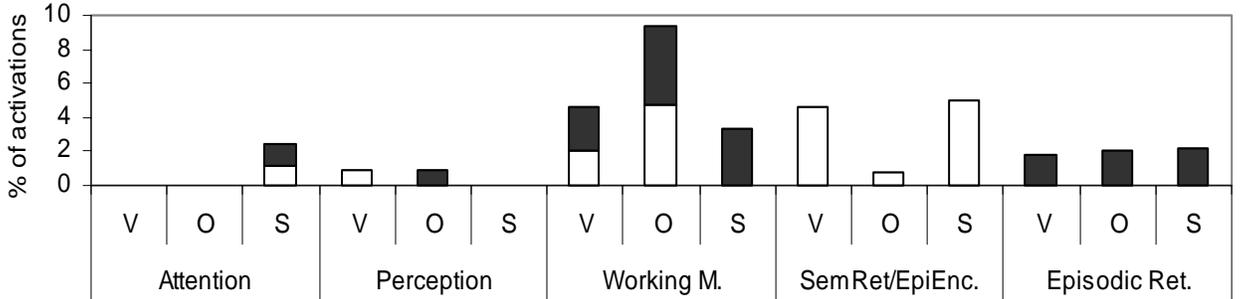
Fig. 3

Ventrolateral and Posterior Prefrontal Regions

BA 47
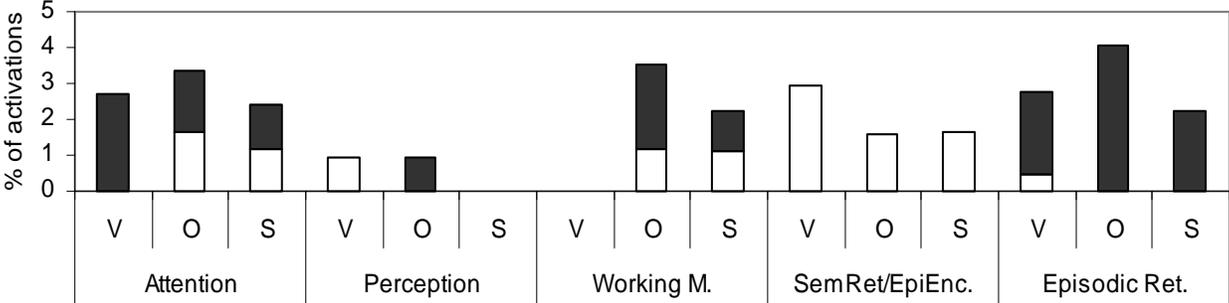
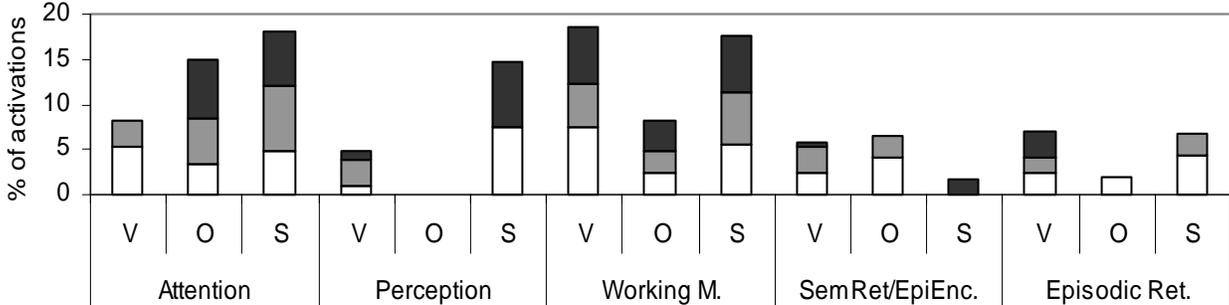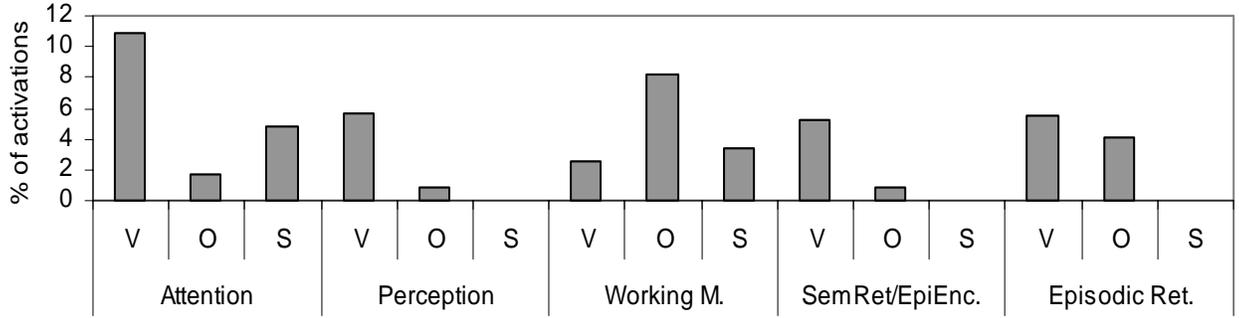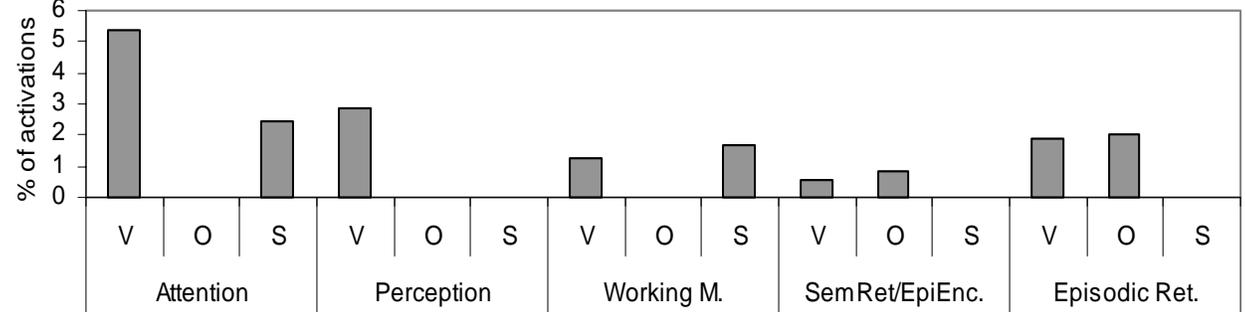**BA 45**
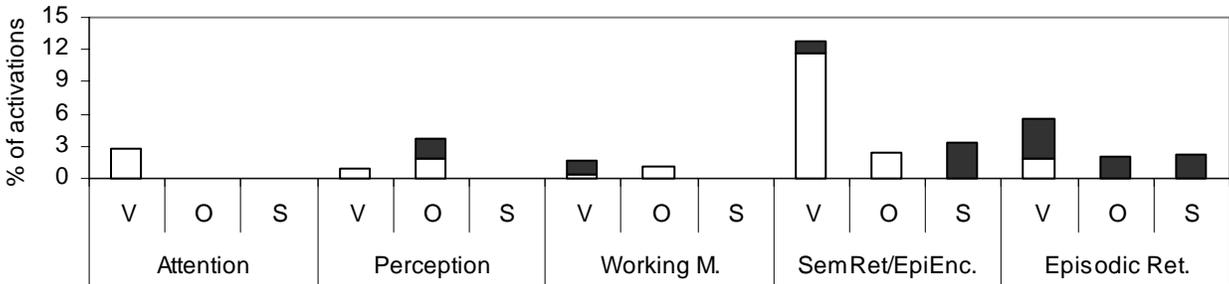
BA 44

BA 6

Fig. 4

Midline Regions

BA 32

BA 24

BA 31
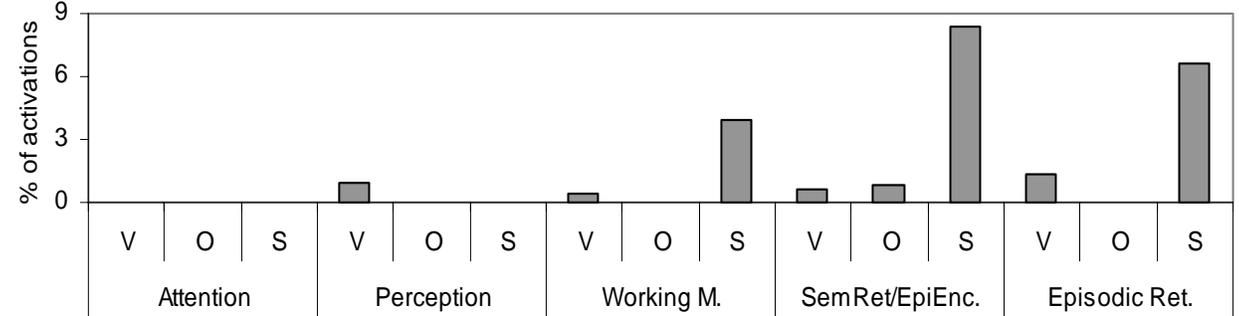
Fig. 5

Parietal Regions

BA 7
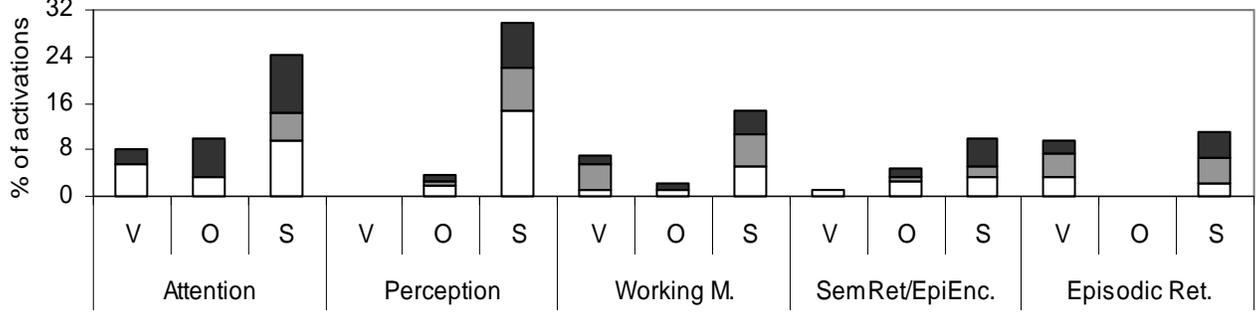
BA 40

BA 39
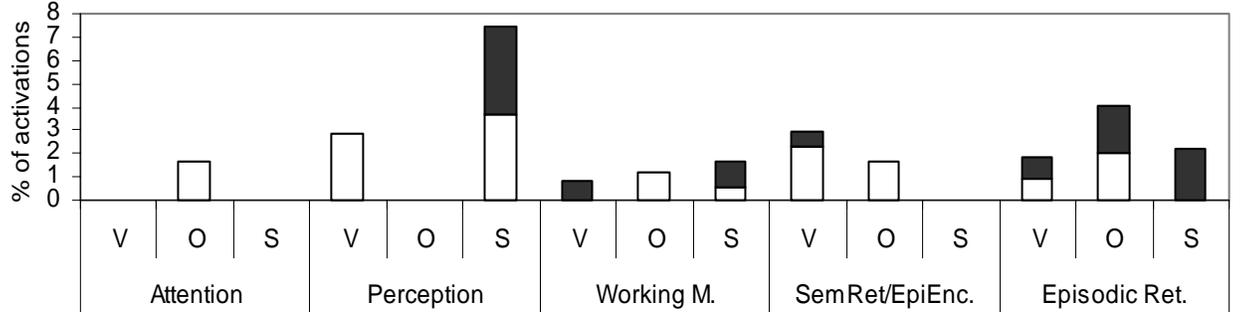
Fig. 6

Temporal Regions

BA 22
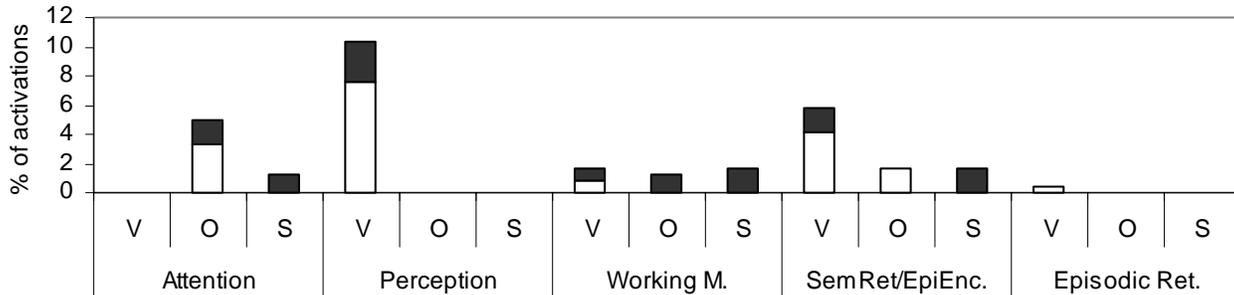
BA 21
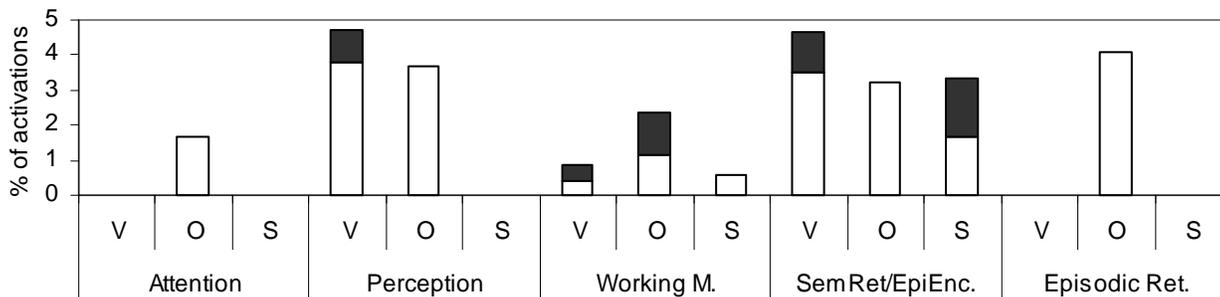
BA 20

BA 37

Fig. 7

Medial Temporal Lobe Regions

MTL

% of activations

	Attention			Perception			Working M.			SemRet/EpiEnc.			Episodic Ret.		
	V	O	S	V	O	S	V	O	S	V	O	S	V	O	S

Fig. 8

Fig. 9

Fig. 10