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Imaging Cognition II: An Empirical Review of 275 PET and fMRI Studies

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Abstract

■ Positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) have been extensively used to explore the functional neuroanatomy of cognitive functions. Here we review 275 PET and fMRI studies of attention (sustained, selective, Stroop, orientation, divided), perception (object, face, space/motion, smell), imagery (object, space/motion), language (written/spoken word recognition, spoken/no spoken response), working memory (verbal/numeric, object, spatial, problem solving), semantic memory retrieval (categorization, generation), episodic memory encoding (verbal, object, spatial), episodic memory retrieval (verbal, nonverbal, success, effort, mode, context), priming (perceptual, conceptual), and procedural memory (conditioning, motor, and nonmotor skill learning). To identify consistent activation patterns associated with these cognitive operations, data from 412 contrasts were summarized at the level of cortical Brodmann's areas, insula, thalamus, medial-temporal lobe (including hippocampus), basal ganglia, and cerebellum. For perception and imagery, activation patterns included primary and secondary regions in the dorsal and ventral pathways. For attention and working memory, activations were usually found in prefrontal and parietal regions. For language and semantic memory retrieval, typical regions included left prefrontal and temporal regions. For episodic memory encoding, consistently activated regions included left prefrontal and medial-temporal regions. For episodic memory retrieval, activation patterns included prefrontal, medial-temporal, and posterior midline regions. For priming, deactivations in prefrontal (conceptual) or extrastriate (perceptual) regions were consistently seen. For procedural memory, activations were found in motor as well as in non-motor brain areas. Analysis of regional activations across cognitive domains suggested that several brain regions, including the cerebellum, are engaged by a variety of cognitive challenges. These observations are discussed in relation to functional specialization as well as functional integration. ■

INTRODUCTION

Functional neuroimaging has made possible the identification of large-scale activation patterns associated with higher-order cognitive processes. Here we review positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) studies of attention, perception, imagery, language, working memory, semantic memory retrieval, episodic memory encoding, episodic memory retrieval, priming, and procedural memory. The present review is the second edition of our review of PET studies to December 1995 (Cabeza & Nyberg, 1997), which we have extended to encompass both PET and fMRI studies up to December 1998. In the three years since the first edition, we have witnessed an explosion in the number of published papers relevant to the scope of this review from 73 to 275 articles (see Figure 1). This enlarged database has allowed us to evaluate the robustness of some of the activation patterns identified in the first edition. In general, salient activation patterns still seem to hold, but new patterns have been discovered.

The review has three main sections, Introduction, Review by Process, and Review by Region. The Introduction is concerned with the basics of functional neuroimaging methods and design, the scope of the review, the organization of the tables, and caveats of the review. The Review by Process section identifies activations patterns for processes of attention, perception, imagery, language, working memory, semantic memory, episodic memory encoding, episodic memory retrieval, priming, and procedural memory. The Review by Region section identifies the processes typically associated with different prefrontal, temporal, parietal, occipital, and subcortical regions.

Methodological Considerations

Noninvasive functional neuroimaging methods can be classified into two broad groups, electromagnetic tech-

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niques, such as ERPs (event-related potentials) and MEG (magneto-encephalography), and hemodynamic techniques, such as PET and fMRI. Electromagnetic techniques have excellent temporal resolution (a few milliseconds) but poor spatial resolution (several centimeters), whereas hemodynamic techniques have good spatial resolution (a few millimeters) but coarse temporal resolution (several seconds). A good understanding of the neural correlates of cognitive processes requires the time information provided by electromagnetic techniques (for ERP reviews, see Rugg & Coles, 1994). However, in order to limit the scope of the review, we focused on hemodynamic techniques, namely PET and fMRI. Moreover, although functional neuroimaging techniques can identify regions associated with a certain cognitive task, they cannot determine which of these regions are essential for performing the task. This information can be provided by neuropsychological studies with brain-damaged patients. Thus, PET and fMRI findings should be complemented with the data provided by electromagnetic and neuropsychological methods.

PET and fMRI are called hemodynamic techniques because they investigate neural activity by measuring changes in blood flow (for a review, see Buckner & Logan, in press). Although some issues remain to be resolved, it is generally agreed that blood flow is a good index of neural activity. The resolution of hemodynamic measures is limited both temporally and spatially. Temporal resolution is ultimately limited by the "sluggishness" of the hemodynamic response; a neural event that lasts a fraction of a second can elicit a blood flow change that lasts for 10 sec. This is a clear disadvantage when compared to the temporal resolution of electromagnetic techniques, which measure neural activity directly and can identify changes in the order of milliseconds. The spatial resolution of hemodynamic techniques is about 3–6 mm., but this depends on the smoothing filter employed. This resolution is too coarse to investigate neuronal or columnar organization, and may preclude the differentiation of nearby regions. However, PET and fMRI techniques can identify the operation of groups of columns, and are particularly useful for revealing large-scale distributed networks of brain regions.

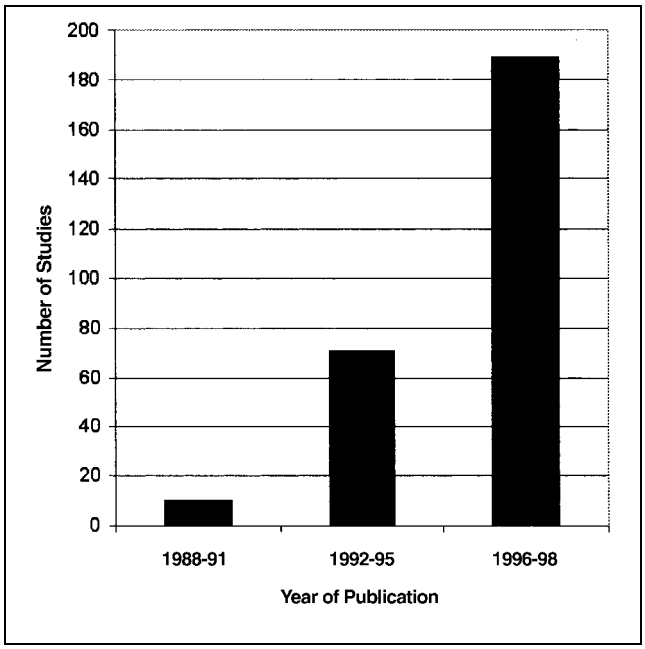


Figure 1. Increase in publication rate of cognitive PET and fMRI studies.

PET and fMRI measure blood flow changes differently. PET measures hemodynamic changes relatively directly by marking blood with a radioactive tracer (for example, $O^{15}H_2O$). In contrast, fMRI measures blood flow changes through changes in blood oxygenation. When a brain region is activated, oxy-hemoglobin in the region increases beyond the actual oxygen demands, and the associated decrease in deoxyhemoglobin concentration yields the signal detected with MRI (Blood Oxygenation Level Dependent contrast mechanism, or BOLD). Compared to PET, fMRI has both disadvantages and advantages. fMRI is more sensitive to motion artifacts, is difficult to apply to paradigms involving overt speech or soft auditory stimulation, and does not allow whole brain sampling: activations in orbito-frontal and anterior temporal regions are difficult to detect due to susceptibility artifacts (for example, Schacter & Wagner, 1999). On the other hand, fMRI is less invasive and expensive than PET, provides both structural and functional information, and allows event-related paradigms (see below).

The design of PET and fMRI studies is most crucial, as the understanding of any observed changes in brain activity is critically dependent on how well the design helps reduce the number of possible interpretations of the effect. In most studies, the design involves comparing blood flow in a target task (for example, completing word-stems with a studied word) and a reference task (for example, completing word-stems with any word). Regions showing relative increased activity in the target task compared to the reference task (so-called "activations") can then be assumed to reflect cognitive processes more engaged by the target task than by the reference task (for example, word retrieval). One problem of this subtraction method is the "pure insertion assumption" (Friston et al., 1996), the idea that the additional processes tapped by the target task (for example, word retrieval) do not alter the operations assumed to be common for both tasks (for example, word generation). Empirical evidence demonstrates that the pure insertion assumption is not always valid (Jennings, McIntosh, Kapur, Tulving, & Houle, 1997). There are at least three different ways of addressing the problem of pure insertion. One is to use a "cognitive conjunction" analysis (Price & Friston, 1997) that isolates what is common to several independent task

comparisons. The present review can be said to use this method across studies: By putting together numerous independent studies on the basis of what the comparisons are expected to isolate, we hope to reveal stable trends that are not influenced by the peculiarities of individual contrasts.

Another way of addressing the pure insertion assumption is to use a parametric design. These designs can reveal the neural correlates of a factor (for example, working memory load) by identifying those regions in which activity changes as this factor is varied across a number of measurement conditions. A somewhat related statistical approach involves computation of correlations between brain activity and some behavioral or physiological measure. The behavioral/physiological measure can be acquired at the same time that PET or fMRI measurement takes place, or can be collected at a separate point in time. As described below, this kind of approach can reveal how brain activity at time of encoding of a set of study-items relates to subsequent memory performance.

Finally, in the case of cognitive processes that can be isolated in time or have different time courses, the pure insertion assumption can be circumvented by using event-related fMRI designs. For example, in working memory studies, event-related fMRI can distinguish between brain activity associated with encoding, maintenance, and retrieval, without need of subtractions: These three processes are associated with different stages of a working memory trial (D'Esposito, in press). Event-related fMRI designs have two other advantages. First, they allow mixing of different item types (for example, old and new words in a recognition test), which is critical to ensure that cognitive strategies are constant across these item types (see Buckner & Logan, in press). Second, event-related fMRI designs allows sorting trials into separate bins according to cognitive performance and relate brain activity to these differences in performance. As mentioned below, these designs have allowed researchers to identify regions whose activity during encoding predicts successful performance in a subsequent memory test (Brewer, Zhao, Glover, & Gabrieli, 1998; Wagner et al., 1998c).

Even if conjunction, parametric, and event-related analyses ameliorate the problems of the task-comparison method, all these techniques have a general limitation: They identify brain regions associated with a certain cognitive process, but do not provide information regarding the functional relations between these regions. To investigate how different brain regions interact during cognitive performance, PET and fMRI data have been submitted to various forms of ''network analyses'' (for a discussion of pros and cons of the network approach, see Nyberg & McIntosh, in press). A common goal of various approaches to network analysis is to study how brain regions interact during task performance, and to identify task-related changes in interregional interactions. Computation of interregional correlations of brain activity are done between or within (in case of fMRI) subjects, and the correlation maps (and further analyses thereof) are used to support conclusions regarding *functional* and *effective* connectivity (Friston, 1994). Functional connectivity refers to the correlation of activity among brain regions without reference to how a correlation is mediated (a strong correlation between the activity in two regions may be driven by a shared functional relation with a third region). In the case of effective connectivity, a combination of anatomical and functional information allows conclusions about region-to-region influences. It is a matter of debate whether such influences can be taken as evidence of excitatory vs. inhibitory inter-regional interactions (Nyberg et al., 1996d).

In summary, PET and fMRI experiments can be designed in many different ways and several different statistical approaches can be adopted to identify changes in brain activity relating to the experimental question. Regardless of type of design and statistical technique, the specific location of observed changes are often expressed in the form of three-dimensional coordinates according to the atlas of Talairach and Tournoux (1988): x (left/right), y (anterior/posterior), and z (superior/inferior). The use of a common metric facilitates the identification of commonalties in a review such as this, and is a cornerstone in the creation of electronic databases such as BrainMap (http://ric.uthscsa.edu/projects/brainmap.html).

Scope of the Review

In keeping with our previous paper, the review is limited in several ways:

1. We restricted the review to include data from healthy young adults, and did not include data from studies of older adults (for a review, see Cabeza, in press) or neurological/psychiatric patients (for a review, see Price & Friston, in press). Nor did we include studies concerning the effects of alcohol or drugs.

2. We did not include studies of lower-order sensory or motor processes, but focussed on higher-order cognitive functions. In the perceptual domain, the distinction between lower-order and higher-order processes was based on whether the study focused on physical properties of the stimulus (light wavelength, sound frequency, and so forth) or on perceptual units (objects, faces, and so forth).

3. With a few exceptions (for example, Cohen, Semple, Gross, Holcomb, & et al., 1988; Cohen, Semple, Gross, King, & Nordahl, 1992), we only included PET studies that measured blood flow.

4. We limited ourselves to presentation of results on *regional* activation changes (as revealed by task comparison, parametric designs, brain-behavior correla-

tions and the like), and did not include data on changes in functional or effective connectivity (for a review of network analyses of cognitive processes, see Nyberg & McIntosh, in press).

5. We focused on domains for which we have been able to identify several relevant studies. Consequently, many studies that did not easily fit within our classification scheme are not detailed in tables. However, some of these studies, but by no means all, are presented in separate table sections (referred to as "Other"), and may be included in topical subsections in future reviews.

In our previous review, we included studies using regions-of-interest (ROI) only when the number of ROIs was large enough to provide a representative sample of the whole brain. In the present review, we relaxed this criterion and included ROI studies based on a few brain regions. The reason for this change is that the ROI approach is quite common in fMRI studies, and, in many cases, it provides a more detailed understanding of the functional role of specific brain regions. When looking at the results from ROI studies, it is important to keep in mind that the absence of activations in non-sampled regions is not informative; only the presence of activations is important. To highlight this fact, ROI studies in Tables 1 to 10 are identified by letters in *italics*. A second difference from our previous review is that we now include studies that used statistical methods other than pairwise task comparison, such as parametric analyses. The type of statistical approach taken will be evident from the study description that accompanies each paper in the tables.

As mentioned above, we cover studies published until December 1998. The studies included in our previous review (Cabeza & Nyberg, 1997) are still part of the tables, if they are still relevant to the classification employed. The studies added to this second edition were identified by computerized and manual searches, and include studies that were published after our previous deadline (December 1995), that previously did not fit the classification scheme, or that were overlooked in the previous review. In total, we present data from 275 studies yielding 412 contrasts and 2748 activation peaks. Although we have tried to include as many relevant papers as possible, we are certain that we missed several studies, including those that escaped our researchers and those that we identified, but libraries or authors failed to provide in time. Hence, the review should not be seen as exhaustive, in the sense of including all relevant papers, but empirical, in the sense that we tried to capture general trends, which, hopefully, are unaffected by the omission of some relevant studies.

Organization of the Tables

In summarizing the results of functional neuroimaging studies, the most appropriate unit is not one experiment, or one experimental condition, but one contrast. We use the word "contrast" in a very broad sense to include almost any statistical procedure that yields a set of activations. The most typical contrasts are *subtraction contrasts*, that is, a pairwise comparison between a target and a reference condition. In the tables, subtractions are identified by a minus sign between the target and reference task (T–R). As noted in our previous review, the regions identified by a subtraction cannot be attributed to the target task alone; they are also determined by the reference task. In the present review, we also included parametric, correlational, and factorial contrasts. *Parametric contrasts* involve a variable that increases across three or more conditions. For example, Price et al. (1992) investigated auditory processing by presenting words at different speeds. *Correlational contrasts* identify regions where brain activity increases or decreases as a function of cognitive performance during or after the scan. Nyberg et al. (1996c), for instance, found that activity in medial-temporal regions increased as a function of the number of words correctly retrieved during the scan. Finally, *factorial contrasts* identify regions associated with main effects or interactions within a factorial design. For example, Cohen et al. (1997) crossed working-memory load (0-back to 3-back) with time (images 1 to 4). Regions associated with time but not with load were attributed to sensorimotor processes, whereas those associated with load were attributed to working memory processes. Similarly, different regions can be associated with regressors in a multiple-regression analysis (for example, Courtney, Ungerleider, Keil, & Haxby, 1997).

In the previous review, contrasts were classified into eight categories: attention, perception, language, working memory, semantic memory retrieval/episodic memory encoding, episodic memory retrieval, priming, and procedural memory. This taxonomy is still used, but two categories were added, one for imagery studies, which were previously included within the perception category, and one for episodic memory encoding studies, which were previously treated together with semantic memory retrieval studies. We also created several new subcategories, such as a problem solving in the working memory section. These changes are detailed as the different sections are presented and discussed. As in our previous organization, we minimize redundancy by avoiding listing multiple contrasts from individual studies. Instead, we have selected the result we think best represents the study in the relevant context. Occasionally, we included multiple entries from individual studies (for example, when these contrasts isolated clearly different processes). In some cases, contrasts could be classified in more than one category. For example, contrasts involving recall of nonverbal materials in the episodic memory retrieval section could also be included in the imagery section. In those cases, we chose the category into which they

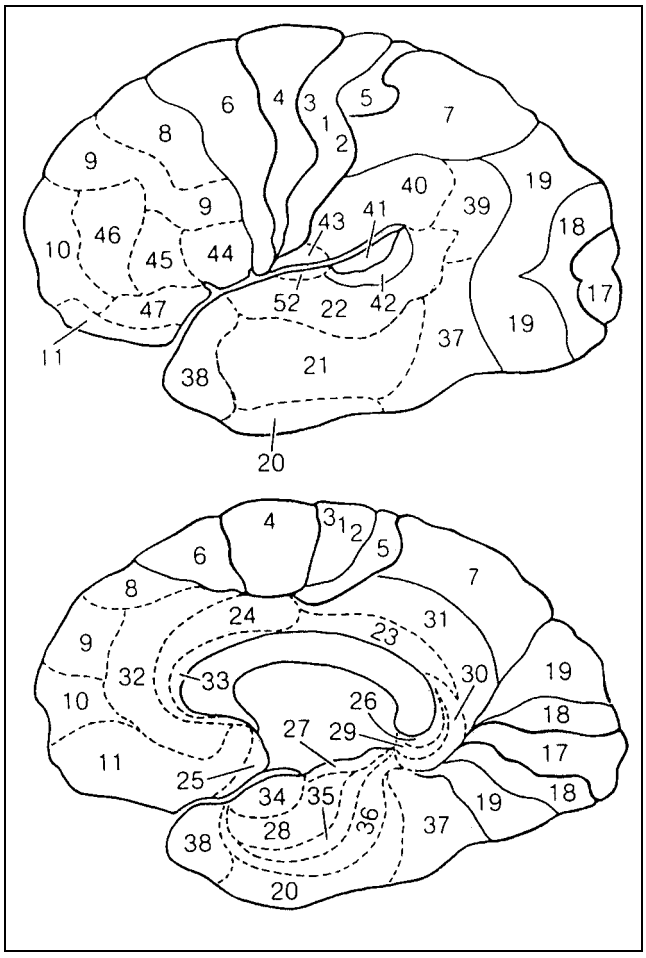


Figure 2. Brodmann's areas of the cortex (From H. Elliott, *Textbook of Neuroanatomy*. Philadelphia: Lippincott. Reprinted with permission).

seemed to fit best, in light of the other results in the category.

The results of the different contrasts are reported in Tables 1–10, one for each category. The activation peaks of these contrasts, as identified by *xyz* coordinates in the articles, are plotted in Figures 2 to 11. The first column of the tables identifies the articles in which each contrast was reported. When the same contrast was reported in more than one publication, the most recent report is referenced. The second column includes descriptions of each contrast. These descriptions are too brief to allow a proper account of the conditions involved, but should allow the interested reader to identify the contrast within the corresponding article. The rest of the tables report the activations identified by each contrast in terms of Brodmann's areas (BAs; see Figure 2). Different symbols are used to indicate whether an activation is left-lateralized, right-lateralized, or bilateral, and whether it is lateral or medial (defined as less than 12 mm. from midline, unless otherwise stated in the source). If BAs were not provided in the paper, we determined them by locating coordinates in Talairach and Tournoux's (1988) atlas. If neither BAs nor coordinates were provided (and we did not feel that we could extract the relevant information from figures, and so forth), the study was not included in the table, but sometimes mentioned in the accompanying text section.

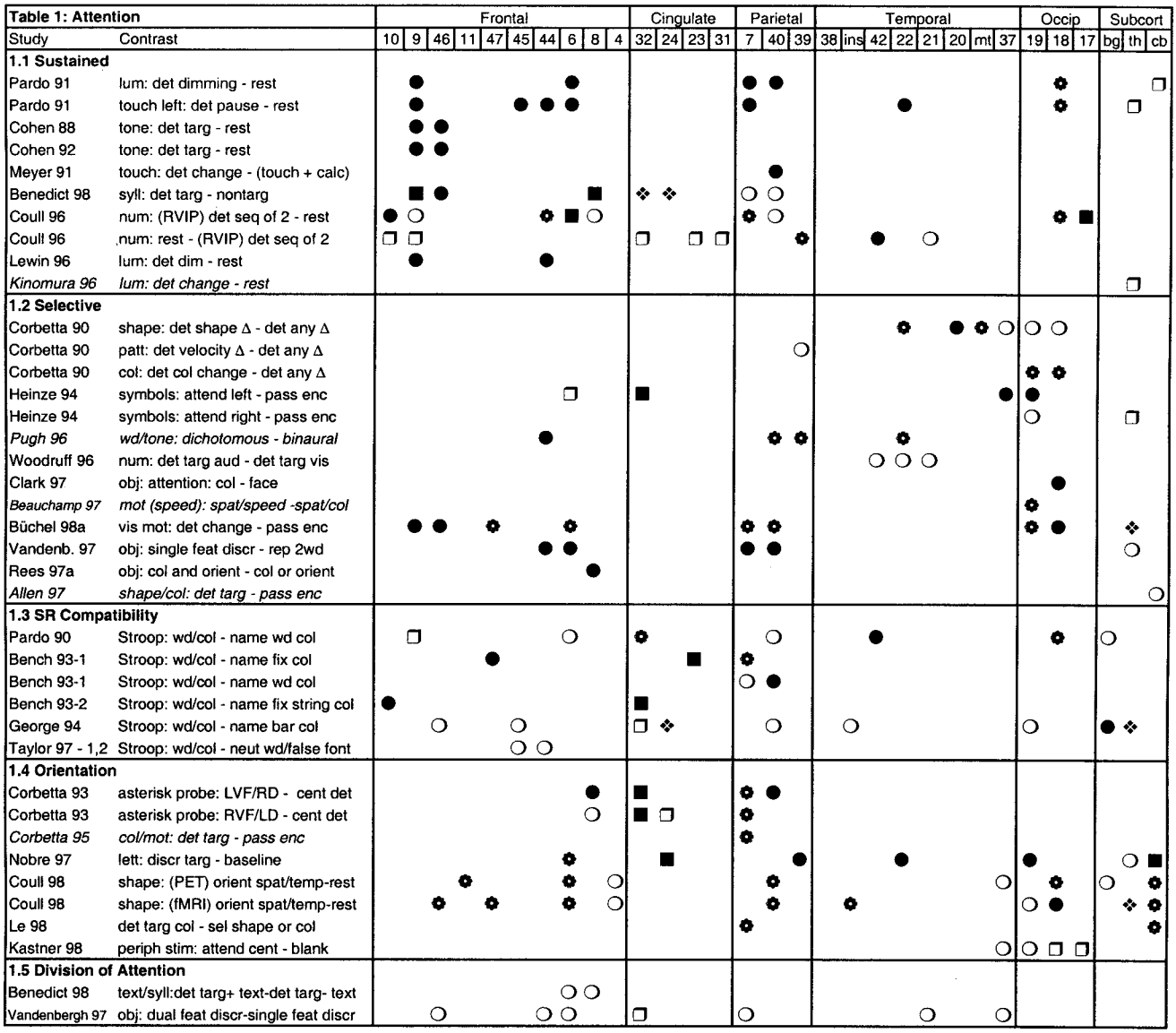
The rationale for choosing BAs instead of other kinds of anatomical description, such as a gyrus-plus-qualifier description (for example, anterior middle temporal gyrus), was twofold. First, the average size of BAs is appropriate for the spatial resolution of hemodynamic techniques and the variability of cognitive activations. Second, since BAs have different cytoarchitectonic structure and connectivity, they are also likely to differ in terms of functions. Having said that, it is worth noting that the tables do not exactly follow the Brodmann system. First, activations in some BAs (for example, 3/1/2, 5, 33, 43) were very scarce and, hence, were not included in the table. Second, to reduce the number of table columns, some BAs were collapsed: area 41 is treated with area 42, area 30, with area 31. Third, activations in medial-temporal regions are treated as a unit, even though different cortical (areas 36, 35, 28, and so forth) and subcortical (hippocampus, amygdala) areas are likely to have different functions. We did so because these regions are small, and the localization of activations was not always clear, and, as well, to increase the probability of finding consistencies across studies. Finally, BAs are not available for insular regions and subcortical structures, such as basal ganglia, thalamus, and cerebellum. Even if each of these regions consists of different subregions or nuclei, we treated them as units for the same reasons as we did for medial-temporal regions. In general, we have maintained a relatively coarse level of analysis that emphasized consistencies rather than inconsistencies across studies.

Caveats of the Review

In our previous review, we noted several issues in functional neuroimaging of cognition, including (1) limitations in spatial and temporal resolution and whole-brain sampling, (2) problems with the subtraction method; (3) difficulties applying the subtraction method; (4) limitations in statistical power; and (5) problems summarizing the results of different studies. These problems are still relevant and apply to PET as well as to fMRI, but, to avoid reiteration here, we will focus only on the last issue. That is, we would like to underscore some of the difficulties of the "between-study approach" that forms the basis for this review.

One obvious limitation is that the identification of general activation patterns is critically related to our organization of the results from individual studies. Indeed, the classification we have used may be imperfect at the level of major sections, as well as at the level of subsections. Moreover, while we have tried to stay close to how the authors defined their comparisons, it can always be questioned

Table 1: Attention		Frontal										Cingulate				Parietal			Temporal								Occip			Subcort		
Study	Contrast	10	9	46	11	47	45	44	6	8	4	32	24	23	31	7	40	39	38	ins	42	22	21	20	mt	37	19	18	17	bg	th	cb
1.1 Sustained																																
Pardo 91	lum: det dimming - rest		●						●							●	●											✪				❒
Pardo 91	touch left: det pause - rest		●				●	●	●							●						●						✪			❒	
Cohen 88	tone: det targ - rest		●	●																												
Cohen 92	tone: det targ - rest		●	●																												
Meyer 91	touch: det change - (touch + calc)																●															
Benedict 98	syll: det targ - nontarg		■	●						■		❖	❖			○	○															
Coull 96	num: (RVIP) det seq of 2 - rest	●	○					✪	■	○						✪	○											✪	■			
Coull 96	num: rest - (RVIP) det seq of 2	❒	❒									❒		❒	❒			✪			●		○									
Lewin 96	lum: det dim - rest		●					●																								
Kinomura 96	*lum: det change - rest*																														❒	
1.2 Selective																																
Corbetta 90	shape: det shape Δ - det any Δ																					✪		●	✪	○	○	○				
Corbetta 90	patt: det velocity Δ - det any Δ																	○														
Corbetta 90	col: det col change - det any Δ																										✪	✪				
Heinze 94	symbols: attend left - pass enc								❒			■														●	●					
Heinze 94	symbols: attend right - pass enc																										○				❒	
Pugh 96	*wd/tone: dichotomous - binaural*							●									✪	✪				✪										
Woodruff 96	num: det targ aud - det targ vis																				○	○	○									
Clark 97	obj: attention: col - face																											●				
Beauchamp 97	*mot (speed): spat/speed -spat/col*																										✪					
Büchel 98a	vis mot: det change - pass enc		●	●		✪			✪							✪	✪										✪	●			❖	
Vandenb. 97	obj: single feat discr - rep 2wd							●	●							●	●														○	
Rees 97a	obj: col and orient - col or orient									●																						
Allen 97	*shape/col: det targ - pass enc*																															○
1.3 SR Compatibility																																
Pardo 90	Stroop: wd/col - name wd col		❒						○			✪					○				●							✪		○		
Bench 93-1	Stroop: wd/col - name fix col					●								■		✪																
Bench 93-1	Stroop: wd/col - name wd col															○	●															
Bench 93-2	Stroop: wd/col - name fix string col	●										■																				
George 94	Stroop: wd/col - name bar col			○			○					❒	❖				○			○							○			●	❖	
Taylor 97 - 1,2	Stroop: wd/col - neut wd/false font						○	○																								
1.4 Orientation																																
Corbetta 93	asterisk probe: LVF/RD - cent det									●		■				✪	●															
Corbetta 93	asterisk probe: RVF/LD - cent det									○		■	❒			✪																
Corbetta 95	*col/mot: det targ - pass enc*															✪																
Nobre 97	lett: discr targ - baseline								✪				■					●				●					●				○	■
Coull 98	shape: (PET) orient spat/temp-rest				✪				✪		○						✪									○		✪		○		✪
Coull 98	shape: (fMRI) orient spat/temp-rest			✪		✪			✪		○						✪			✪							○	●			❖	✪
Le 98	det targ col - sel shape or col															✪																✪
Kastner 98	periph stim: attend cent - blank																									○	○	❒	❒			
1.5 Division of Attention																																
Benedict 98	text/syll:det targ+ text-det targ- text								○	○																						
Vandenbergh 97	obj: dual feat discr-single feat discr			○				○	○			❒				○							○			○						



Symbols and abbreviations in Tables 1-11: ○ = left lateral; ● = right lateral; ✪ = bilateral lateral; ❒ = left medial; ■ = right medial; ❖ = bilateral midline; abstr = abstract; aud = auditory; bg = basal ganglia; cat = category; cb = cerebellum; cent = central; col = color; comp = completion; concr = concrete; cond = conditioning; conj = conjunction; dec = decision; dens = density;det = detect; diff = different; discr = discrimination; distr = distraction; enc = encoding; feat = feature; gen = generate; ima = imagine; ins = insula; inst = instance; K = know; lett = letter(s); liv = living;lum = luminance; LVF = left visual field; MCST = Modified Card Sorting Test; mot = motion; mt = medial temporal; nonfam = nonfamiliar; nonliv = nonliving; nontarg = nontarget(s); nonwd = nonword(s);norm = normal; num = number; obj = object(s); ortho = orthographic; pass = passive; patt = pattern(s); periph = peripheral; phonol = phonological; pseudocond = pseudoconditioning;R = remember; Rc = recall; Rn = recognition; rot = rotation; RVF = right visual field ; RVIP = Rapid Visual Information Processing Task; sacc = saccades; sel = select; sem = semantic;sent = sentence(s); sm = sensorimotor control; SOP = self ordered pointing; S-R = stimulus - response; STM = short term memory; syll = syllable; temp = temporal; th = thalamus; WCST = Wisconsin Card Sorting Test; delta = change

Abbreviated names: Vandenb. = Vandenberghe

whether a particular data point fits well in its context. We can only hope that most readers will find our organization acceptable. If the reader does not agree with our classification system, s/he can always treat the review as a database, and reclassify the results in a different way.

A second point to notice is that we do not support the identification of general activation patterns by any quantitative indices. Rather, we simply try to extract and discuss what we find emerges from different tables as salient results. As such, there is a risk that "reviewer bias" influenced the detected patterns. The remedy for this, of course, is to ignore our discussions of what each table suggests and inspect the table "as is". This being said, we must acknowledge that tables may not be entirely "objective" either. Most importantly, studies differ widely in their statistical power and in the criteria they use for defining significant results. They may also differ in several ways related to the preprocessing of the data. Such factors may have affected the results considerably, although it seems reasonable to expect that significant results from several independently conducted studies should be reliable data.

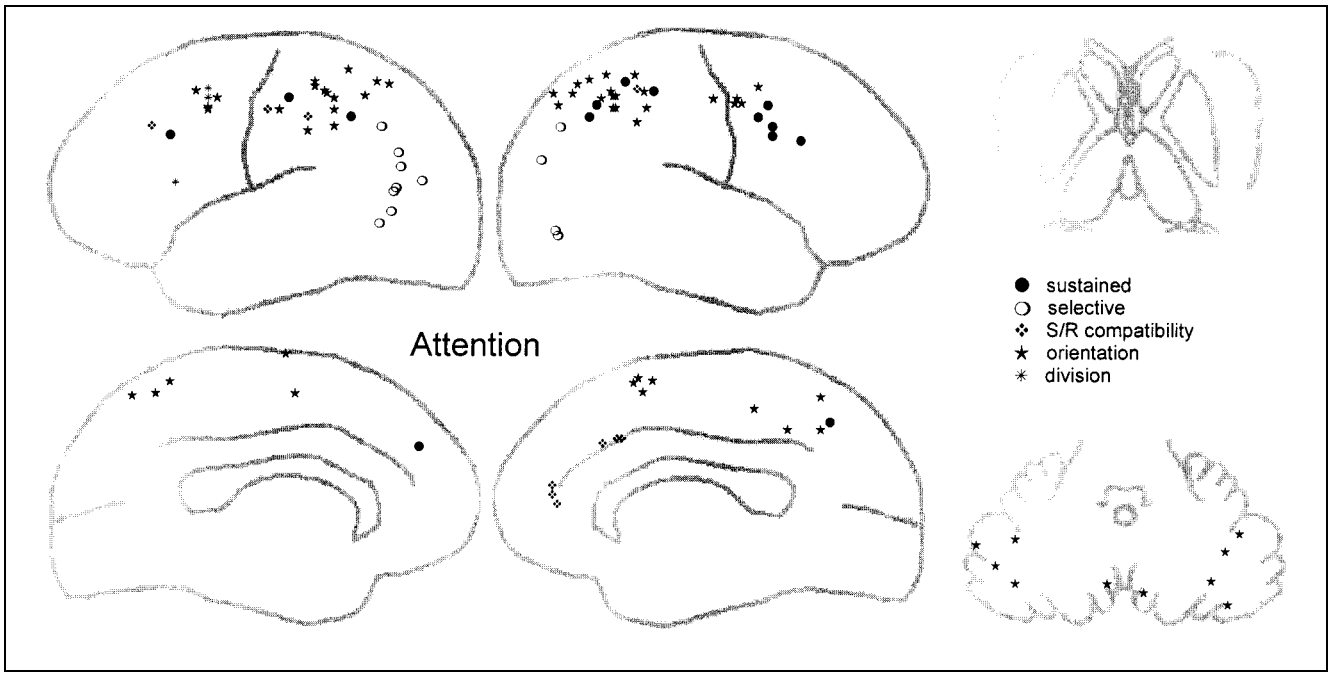


Figure 3. Representative peaks (published coordinates) associated to processes of attention. In this and following figures, only peaks in Brodmann's areas activated by at least 40% of the studies in each subcategory are plotted (see Table 11). Peaks are projected to the closest cortical surface: the lateral or medial surfaces of the left or right hemispheres. Peaks on the ventral surface of the temporal lobe and in hippocampal/parahippocampal regions are displayed in medial views. Peaks in the thalamus, basal ganglia, and insula are projected to a transverse slice at $Z=4$ (top-right corner) and peaks in cerebellum projected to a transverse slice at $Z=-24$ (bottom-right corner).

REVIEW BY FUNCTION

Attention

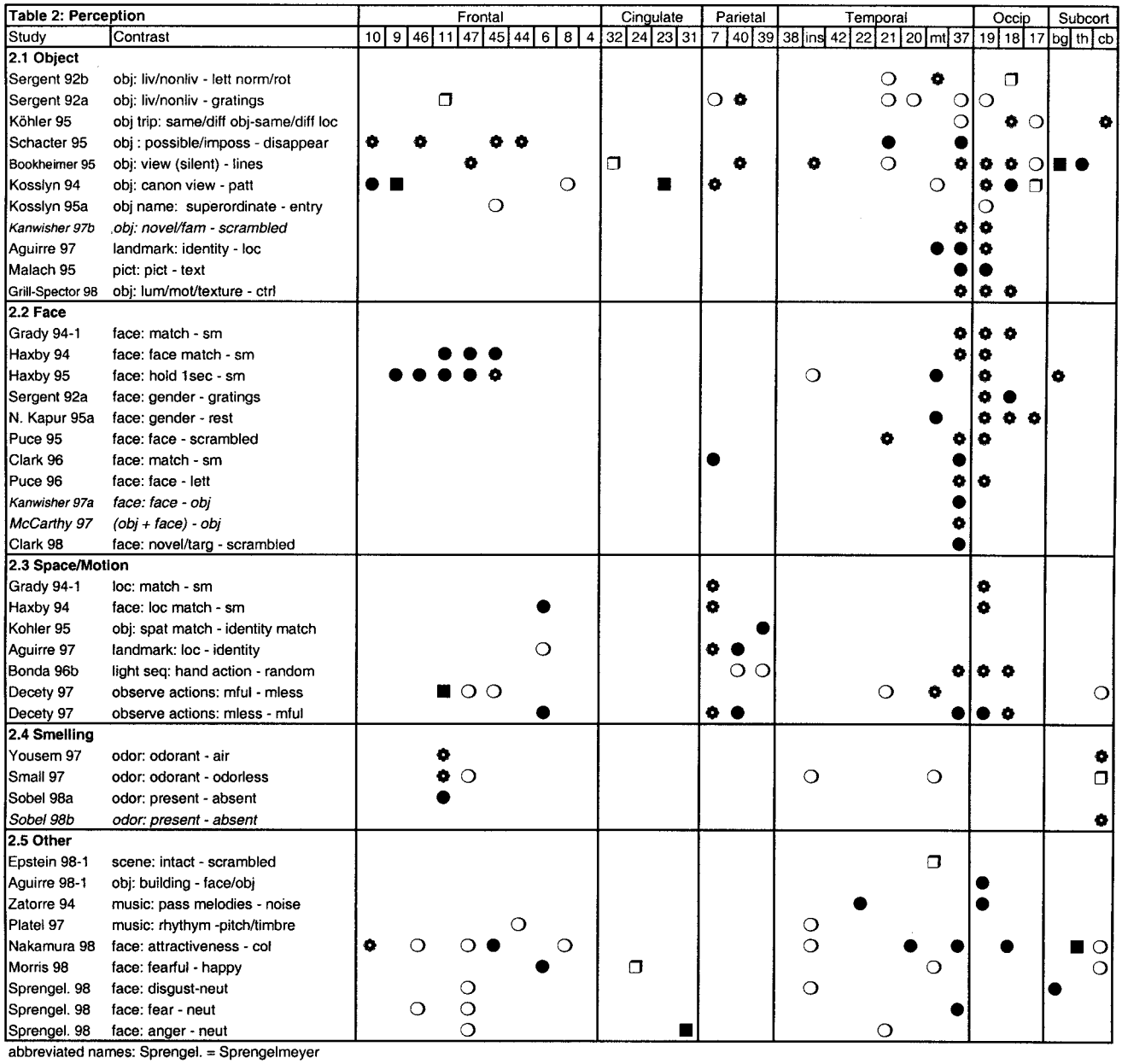
Results concerning attention processes are shown in Table 1 and Figure 3, and are divided into five categories: sustained attention, selective attention, SR compatibility, orientation of attention, and division of attention. The tasks included in the sustained attention section involved continuous monitoring of different kinds of stimuli (for example, somatosensory stimulation). The selective attention section includes studies in which subjects selectively attended to different attributes of the same set of stimuli (for example, attend to color only for stimuli varying with respect to both color and shape). The stimulus-response (SR) compatibility section also includes studies examining selective attention, with the important difference that they involve a "conflict component". In all cases, this is implemented by employing the Stroop task.

Starting with the category of sustained attention, we noted in our previous review that prefrontal and parietal areas, preferentially in the right hemisphere, are frequently engaged. The more recent studies support this conclusion. The fMRI study by Lewin et al. (1996) is of special interest, since it involved the same visual vigilance task that was included in the early study by Pardo et al. (1991). The results were in close agreement with the PET data reported by Pardo and colleagues, showing predominantly right-sided prefrontal and parietal activation (the latter activation did not reach significance at the group level and is, therefore, not shown in the table). Coull et al. (1996) concluded that their data is consistent with a right fronto-parietal network for sustained attention. In agreement with Haxby et al.'s (1994) conclusion that selective attention to one sensory modality is correlated with suppressed activity in regions associated with other modalities (for a related finding, see Ghatan, Hsieh, Petersson, Stone-Elander, & Ingvar, 1998), Coull et al. (1996) also found deactivations in the auditory cortex. Taken together, the results suggest the existence of a fronto-parietal network underlying sustained attention. Direct support for fronto-parietal interactions during sustained attention was provided by Büchel and Friston (Buchel & Friston, 1997) using structural equation modeling of fMRI data. Finally, Kinomura et al. (1996) focused on the effects of attention on thalamic (intralaminar nuclei) and brain stem (midbrain tegmentum) activity. Their demonstration of attentional effects was interpreted as evidence that these areas may control the transition from relaxed wakefulness to high general attention.

Selective attention is characterized by increased activity in posterior regions involved in stimulus processing. Different regions seem to be involved depending on the specific attribute that is attended to (for example, Corbetta, Miezin, Dobmeyer, Shulman, & Petersen, 1990). Recent examples of attentional modulation of auditory regions are provided in Woodruff et al. (1996) and Pugh et al. (1996), and modulation of activity in the lingual and fusiform gyri during a color attention task was demonstrated by Clark et al. (Clark et al., 1997).

Beauchamp, Cox, & De Yoe (1997) showed that attending to motion activated a region in occipito-temporal cortex, and Buchel et al. (1998b) extended these findings by showing that, in addition to extrastriate regions, attention to motion increased activity in several higher-order areas as well. It was argued that activity in extrastriate regions may be modulated by prefrontal, parietal and thalamic regions. Similarly, Heinze et al. (1994) suggested that modulation of activity in specific posterior regions is mediated by regions in parietal and anterior cingulate cortices, as well as the pulvinar. A role of parietal cortex, especially the inferior parietal lobe, in control of selective attention is suggested by the findings of Pugh et al. (1996; see also Vandenberghe, Duncan, Dupont, Ward, & et al., 1997). Rees et al.'s (1997a) study pointed to a role of prefrontal cortex in attentional modulation. Collectively, these studies indicate that quite an extensive network of brain regions is mediating selective attention, and the study by Allen et al. (Allen, Buxton, Wong, & Courchesne, 1997) suggest that cerebellum may be part of this network as well (see also Rees et al., 1997a). Finally, a critical issue in studies on selective attention is the degree to which the nonselected information is processed. A study by Rees et al. (1997b), not shown in the table, indicated that as long as attentional load is low, task-irrelevant stimuli are perceived and elicit neural activity. However, when the attentional load is increased, irrelevant perception and its associated activity is strongly reduced.

The stimulus-response compatibility panel includes selective attention studies on the Stroop test. In our previous review, the Stroop test was clearly associated



abbreviated names: Sprengel. = Sprengelmeyer

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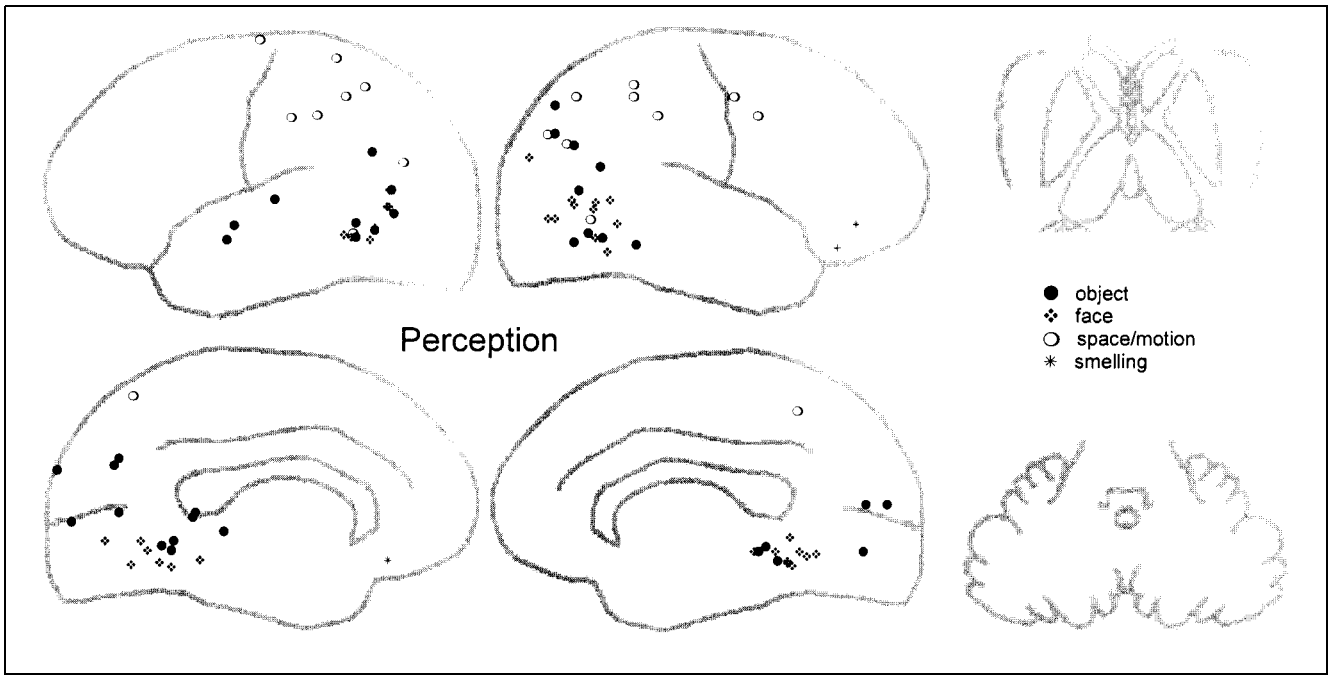

Figure 4. Representative activation peaks (published coordinates) associated to processes of perception.

with activations in the anterior cingulate cortex. Interestingly, in the single study that has been added to this section, Taylor et al. (1997) questioned the importance of this region for overcoming Stroop interference. Instead, the Taylor study underscored the importance of the left prefrontal cortex. Taken together, SR compatibility studies point to a role of both the anterior cingulate and the left prefrontal cortex.

The category ''orientation of attention'' includes the comprehensive study by Corbetta, Miezin, Shulman, & Petersen (1993), which associated shifts of spatial attention to parietal and prefrontal regions. In a subsequent study (Corbetta, Shulman, Miezin, & Petersen, 1995), Corbetta and collaborators found activations in superior parietal regions during a visual search for conjunction of features. Based on the similarities in activation patterns, Corbetta et al. (1995) suggested that serial shifts of attention took place during the search task. Nobre et al. (1997) provided evidence supporting the existence of a large-scale neural system for visuospatial attention that includes the right posterior parietal cortex. Coull and Nobre (1998) used both PET and fMRI to study attentional orienting to spatial locations (left vs. right) and to time intervals (short vs. long stimulus onset times). Both spatial and temporal orienting were found to activate a number of brain regions, including prefrontal and parietal brain regions. More detailed analyses (not shown in the table) revealed that activations in the intraparietal sulcus were right-lateralized for spatial attention and left lateralized for temporal attention. Moreover, simultaneous spatial and temporal attention activated mainly parietal regions, suggesting that parietal cortex, especially in the right hemisphere, is a site for interactions between different attentional processes. Parietal activation was, furthermore, demonstrated in an fMRI study of nonspatial attention shifting (Le, Pardo, & Hu, 1998). In addition, in the study by Le at al., the cerebellum was implicated in attention shifting, and the authors related this aspect of their findings to the demonstration by Allen et al. (1997 see above) of attentional activation of the cerebellum. Finally, Kastner et al. (1998) showed that spatial direction of attention can influence the response of the extrastriate cortex. Specifically, it was demonstrated that while multiple stimuli in the visual field interact with each other in a suppressive way, spatially directed attention partially cancels out the suppressive effects.

In the final subsection, two studies are included which seem to have isolated neural responses related to division of attention. Both studies indicate that activity in the left prefrontal cortex increases under divided-attention conditions (Benedict et al., 1998; Vandenberghe et al., 1997). In this context, it is also relevant to mention the suggestion by Klingberg and Roland (1997—not in table) of a physiological basis for dual task interference. Klingberg and Roland argued that if two tasks activate overlapping brain areas, there will be significant interference effects when the tasks are performed simultaneously.

Perception

Results concerning perception processes are shown in Table 2 and Figure 4, and divided into object, face, space/motion, smell and ''other'' sections. In our previous review, we concluded that object perception

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was associated with activations in the ventral pathway (ventral BAs 18, 19, and 37). The ventral occipito-temporal pathway is associated with object information, whereas the dorsal occipito-parietal pathway is associated with spatial information (Ungerleider & Mishkin, 1982). The results from more recent studies support and extend this general conclusion (for a review, see Kanwisher, Downing, Epstein, & Kourtzi, in press). Kanwisher et al. (1997b) found that viewing novel, as well as familiar, line drawings, relative to scrambled drawings, activated a bilateral extrastriate area near the border between the occipital and temporal lobes. Based on their findings, Kanwisher et al. suggested that this area is concerned with bottom-up construction of shape descriptions from simple visual features. Related work by Malach and colleagues (Grill-Spector, Kushnir, Edelman, Itzchak, & Malach, 1998; Malach et al., 1995) supports and extends this conclusion by showing that a region termed the ''lateral occipital complex'' (LO) is selectively activated by different kinds of shapes (for example, shapes defined by motion, texture, and luminance contours). Aguirre and D'Esposito (1997) found greater activity in lingual gyrus (area 19) and/or inferior fusiform gyrus (area 37) when subjects made judgements about appearance than when they made judgments about locations, thereby providing additional support that object identity preferentially activates regions in the ventral pathway. Kraut et al. (1997 not included in the table due to lack of coordinates and Brodmann's areas) found both ventral and dorsal activations during shape-based object recognition, and suggested that visual object processing involves both pathways to some extent (for a similar conclusion based on network analysis of PET data, see McIntosh et al., 1994).

In our previous review, we suggested that face perception involves the same ventral pathway as object perception, but we noted a tendency for right-lateralization of activations for faces, but not for objects. These impressions were supported by several new studies. For example, Puce et al. (1996) found bilateral fusiform gyrus activation for faces, but with more extensive activation in the right hemisphere. Further data from the same group were interpreted as evidence that faces are perceived, at least in part, by a separate processing stream within the ventral object pathway (McCarthy, Puce, Gore, & Allison, 1997). Additional support for selective regional activation within the ventral pathway was provided by Kanwisher et al. (1997a). These authors used fMRI to identify a region more responsive to faces than to objects, which they termed the ''fusiform face area'' or FF area, and subsequently tested the specificity of this region by manipulating different variables (for a review, see Kanwisher et al., in press). Results (not shown in the table) from studies by Wojciulik et al. (1998) and Kanwisher et al. (1998) provide evidence on the specific nature of the neural response in area FF.

Whereas perception of objects and faces tends to preferentially activate regions in the ventral visual pathway, perception of spatial location tends to selectively activate more dorsal regions located in parietal cortex. This tendency was quite clear in our previous review, and it is now supported by additional observations. Aguirre and D'Esposito (1997) found greater activity in the superior parietal lobe (area 7) as well as in premotor cortex during location judgments than during object judgments. The dorsal pathway is not only associated with space perception, but also with action (for reviews, see Goodale & Humphrey, 1998; Goodale & Milner, 1992). For example, Bonda, Petrides, Ostry, and Evans (1996b) found that perception of scripts of goal-directed hand action engaged parts of the parietal cortex. Decety et al.'s (1997) study suggests that the nature of the actions is a critical factor. They compared meaningful actions (for example, pantomime of opening a bottle) and meaningless actions (for example, signs from the American Sign Language that were unknown to subjects). Whereas meaningless actions activated the dorsal pathway, meaningful actions activated the ventral pathway. They argued that meaningless actions are decoded in terms of spatiotemporal layout, while meaningful actions are processed by areas that allow semantic processing and memory storage. Thus, as object perception, location/action perception may involve both dorsal and ventral pathways to some extent.

Turning now to an instance of nonvisual perception, Panel 2.4 summarizes data from four studies on smell perception. Yousem et al.'s (1997) and Small et al.'s (1997) studies found activations in the orbitofrontal cortex (where secondary olfactory cortex is located, see Zatorre, Jones-Gotman, Evans, & Meyer, 1992), particularly in the right hemisphere, and the cerebellum. Small et al. also observed increased activity in primary olfactory cortex (piriform cortex). The two studies by Sobel and colleagues extended these findings. Sobel et al. (1998b) showed that odorants (regardless of sniffing) activated the posterior lateral cerebellum, whereas sniffing (non-odorized air) activated anterior parts of the cerebellum. The authors proposed that the cerebellum receives olfactory information for modulating sniffing. Sobel et al. (1998a) found that odorants (regardless of sniffing) activated anterior and lateral orbitofrontal cortex whereas sniffing (even in the absence of odorants) activated the piriform and medial/posterior orbitofrontal cortices (results not shown in table). In sum, smell perception involves primarily the orbitofrontal cortex and parts of the cerebellum and its neural correlates can be dissociated from those of sniffing.

In the last subsection (''Other''), we included studies from different perceptual domains. Epstein and Kanwisher (1998) used fMRI to define a ''parahippocampal place area'' (PPA). This conclusion was based on findings that this region responds selectively to passively

Table 3: Imagery		Frontal										Cingulate				Parietal			Temporal								Occip			Subcort		
Study	Contrast	10	9	46	11	47	45	44	6	8	4	32	24	23	31	7	40	39	38	ins	42	22	21	20	mt	37	19	18	17	bg	th	cb
3.1 Object																																
Kosslyn 93-3	lett: ima large - ima small																						○						■			
Kosslyn 95b	obj: ima small - pass listen																											✿	●			
Kosslyn 96a	pict/wd: ima neg - ima neut		○							○										✿								✿	●			
Roland 95	patt: ment Rc - vis learn	○																												■		
D'Esposito 97	wd: ima concr - ima abstr								○				❒													○						
Mellet 98	wd def: ima concr - ima abstr								○		○						○							✿		✿						
Ghaem 97	landmark: visualize - rest								○					■									○	○	✿							
Howard 98	col: ima - ctrl																			○					●	●						
3.2 Space-Motion																																
Cohen 96	shape: ment rot - match			✿				✿		✿						✿		✿									✿					
Alivisatos 97	alphanumeric: rot - lett/num discr			○			●									■	○									✿		✿		■		
Alivisatos 97	alphanumeric: rot - norm/mirr discr						●			●						○	○													■		
Kosslyn 98	cube: ment rot - baseline															✿	✿										✿					
Kosslyn 98	hands: ment rot - baseline		○						○		○					○	○			○							○		■			
Mellet 95	imagery - rest								❖																		●					❖
Ghaem 97	route: ima - rest	○	●						✿						❖	○									✿	○	○					
3.3 Other																																
Sugishita 96	ment writing - rest										✿						✿	○									✿					
Zatorre 96a	wd pair: ima pitch change-wd length	○	✿			○	✿		■							○	○					✿	✿									
McGuire 96	wd: ima other voice-read adjective						○	○	○											●		○	○									

viewed scenes. Aguirre, Zarahn, and M (1998) showed that a region probably overlapping with PPA responded selectively to buildings, and they proposed that this brain region may respond to stimuli that have orienting value (isolated landmarks as well as scenes). Zatorre et al. (1994) studied the neural correlates of music perception, and found evidence that specialized neural systems in the right superior temporal cortex participated in perceptual analysis of melodies. Subsequent work by Platel et al. (1997) identified different components of music perception. For example, as summarized in the table, they found that attention to changes in rhythm activated Broca's/insular regions in the left hemisphere, pointing to a role of this area in the sequencing of auditory input. Finally, examples of "emotional perception" are taken from three different studies. In agreement with the conclusion by Sprengelmeyer et al. (1998), inspection of the table suggests that perception of different kinds of emotion are based on separate neural systems, with a possible convergence in prefrontal regions (area 47). Consistent with the role of the amygdala in fear conditioning (for a review, see Maren & Fanselow, 1996), Morris et al. (1998) found the amygdala to be more activated for fearful faces relative to happy faces. To account for the lack of amygdalar activation in their study, Sprengelmeyer et al. (1998) made reference to the rapid habituation of the amygdala in response to fearful faces (see Breiter et al., 1996).

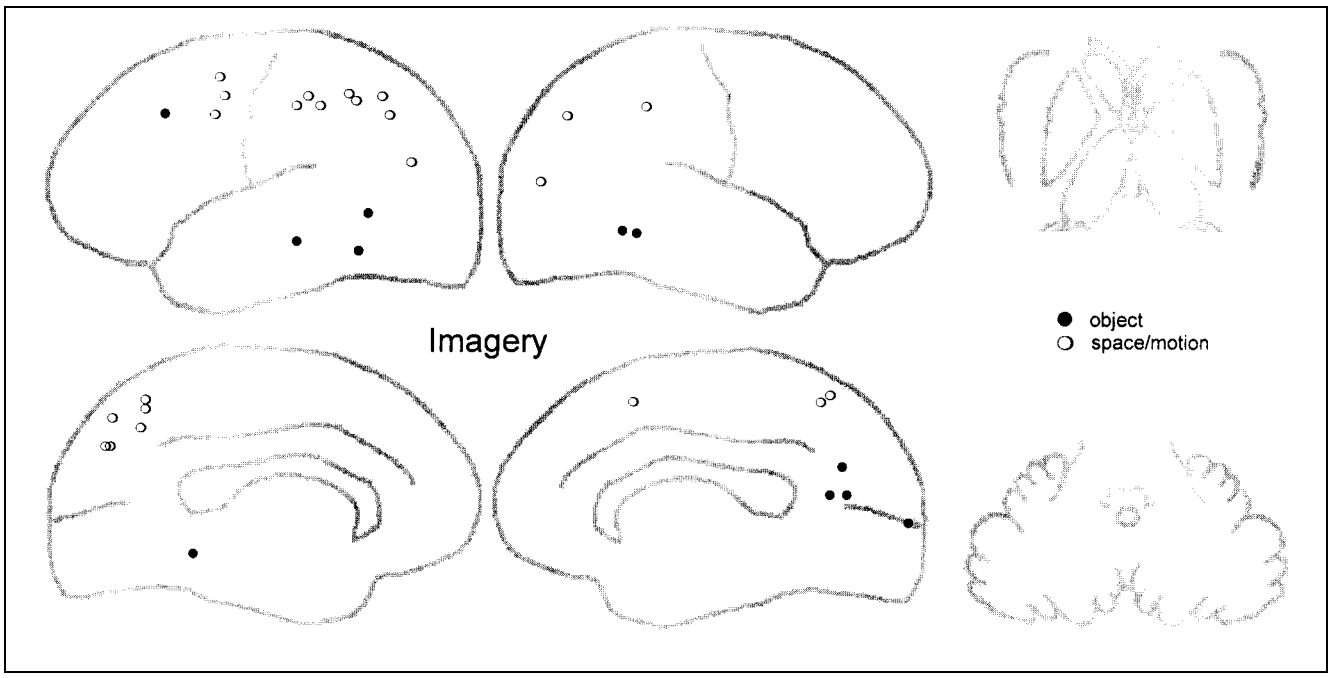

Figure 5. Representative activation peaks (published coordinates) associated to processes of imagery.

Imagery

Results concerning imagery processes are shown in Table 3 and Figure 5. Imagery can be defined as manipulating sensory information that comes not from the senses, but from memory. The memory representations manipulated can be in working memory (for example, holding three spatial locations for 3 sec), episodic memory (for example, retrieving the location of an object in the study phase), or semantic memory (for example, retrieving the shape of a bicycle). Thus, imagery-related contrasts could be classified within working memory, episodic retrieval, and semantic retrieval sections. Although we did so in many cases, we kept some imagery contrasts in a separate imagery section, primarily because some imagery-related issues (for example, the engagement of visual cortex) are more related to perception than to memory. At any rate, the reader should keep in mind that imagery contrasts can be described as visuospatial retrieval contrasts, and vice versa.

A central issue in the field of imagery has been whether those visual areas that are involved when an object is perceived are also involved when an object is imagined (for discussions on the imagery controversy, see Moscovitch, Behrmann, & Winocur, 1994; Roland & Gulyas, 1994). In its strictest form, this idea would imply activation of primary visual cortex in the absence of any visual input. A series of PET experiments by Kosslyn and colleagues provided support for similarities between visual perception and visual imagery by showing increased blood flow in area 17 during imagery (Kosslyn et al., 1993). In particular, by comparing tasks involving image formation for small and large letters, respectively, their Experiment 3 provided evidence that imagery activates topographically mapped primary visual cortex. A subsequent PET study, involving objects of three different sizes, provided additional information that visual imagery activates primary visual cortex (Kosslyn, Thompson, & Alpert, 1997; Kosslyn, Thompson, Kim, & Alpert, 1995b; for further discussion of similarities, see Kosslyn, Thompson, Kim, Rauch, & et al., 1996b).

Other studies, however, have suggested that primary visual cortex is not activated during visual imagery. Roland and Gulyas (1995) found no evidence for increased activity, as indicated by PET, in occipital cortex when subjects attempted to recall (that is, imagine) previously studied visual patterns. Similarly, in an fMRI study of neural activity related to generation of visual images of cue words, D'Esposito, Detre, Aguirre, Stallcup, & et al. (1997) found no support for increased activity in primary visual cortices; none of seven subjects showed evidence for increased activation in area 17. Importantly, though, this latter study agrees with the findings by Kosslyn and colleagues by showing increased activation in extrastriate visual regions. The left inferior temporal lobe (area 37) was most reliably activated across subjects (for some subjects the activation extended into area 19 of the occipital lobe). Compared with rest (not shown in the table), a left posterior-inferior temporal region was also activated in the study by Roland and Gulyas. Moreover, mental imagery of spoken-concrete words has been shown to activate inferior-temporal gyrus/fusiform gyrus bilaterally (Mellet, Tzourio, Denis, & Mazoyer, 1998). According to these authors, right temporal activation may be related to more complex visual imagery.

Taken together, although revealing similarities between imaging and perceiving, several of the studies discussed so far have pointed to significant differences as well. Further support for differences comes from two additional studies. Howard et al. (1998) studied color imagery and color perception. These processes were found to engage overlapping networks anterior to region V4 (an area specialized for color perception), whereas areas V1–V4 were selectively activated by color perception. Kosslyn et al. (1996a) examined whether emotional content (neutral vs. aversive pictures) affects neural information processing in the same way in perception and imagery. The results showed striking differences between negative-minus-neutral imagery and negative-minus-neutral perception contrasts, hence, pointing to fundamental differences in the way emotion affects perception and imagery. Another interesting result of this study was an increase in primary visual-cortex activity during negative imagery, as compared to neutral imagery. This finding adds to the other data presented by Kosslyn and colleagues on a role of the primary visual cortex in visual imagery, and indicates that emotion affects the quality of the image representations.

The studies falling into the category of imaging space-motion can be further subdivided into those concerned with mental rotation of visual stimuli (Cohen et al., 1996; Alivisatos & Petrides, 1997; Kosslyn et al., 1998; see also Tagaris et al., 1997), and those concerned with mental "exploration" of maps or routes (Ghaem et al., 1997, Mellet et al., 1995). Starting with the former type of task, the results converge on consistent involvement of lateral parietal areas (BA47 and BA40). Cohen et al. (1996) used fMRI to explore mental imagery with the famous Shepard and Mtezler (1971) task, and based on their findings they suggested that the bulk of the computation for this kind of mental rotation is performed in the superior parietal lobe. Alivisatos and Petrides (1997) used PET to study a mental-rotation task in which subjects were asked to decide whether letters and digits, tilted in 120°, 180°, or 240°, were in normal or mirror image form. Their results strongly implicated the left parietal cortex in this task. Kosslyn et al. (1998) studied two mental-rotation tasks, involving (i) figures or (ii) drawing of human hands. Mental rotation of both kinds of

stimuli activated parietal areas, although the data pointed to significant differences in activation patterns as well.

Turning to the second class of test, imaging maps/routes, Mellet, Tzourio, Denis, & Mazoyer (1995) used PET to study mental exploration of a map. They found that this task was associated with increased activity in right superior occipital cortex, the supplementary motor area (SMA) and the cerebellar vermis. The latter two activations were related to eye movements, and it was concluded that the superior occipital cortex has a specific role in generation and maintenance of visual mental images. In a subsequent PET study by Ghaem et al. (1997) occipital activation was again observed, although this time the peak was in left middle occipital gyrus. This activation was specific to a task involving mental navigation—static visual imagery was not associated with occipital activation. It is quite likely that mental navigation tasks tap visual memory to a high extent, and it has been speculated that feedback influences from areas involved in visual memory activate visual (occipital) areas during certain imagery tasks (compare, Cohen et al., 1996, p. 96).

Taken together, the results of the studies in this section can be summarized as showing that visual mental imagery is a function of visual association cortex (compare, D'Esposito et al., 1997), although different association areas seem to be involved depending on the task demands (compare, Charlot, Tzourio, Zilbovicius, Mazoyer, & et al., 1992). It remains an open issue whether primary visual cortex is activated, and we have chosen not to draw any definite conclusions (for recent evidence in support of the view that primary visual cortex is activated, see Kosslyn et al., 1999). In this regard, it may be crucial to consider factors related to the choice of reference task (compare, Kosslyn et al., 1995a,b) and type of imagery task (compare, Mellet et al., 1995). In addition, prefrontal areas have been activated in many of the reported comparisons. Partly, these effects may be driven by eye movements (especially for areas 6

Table 4: Language

		Frontal										Cingulate				Parietal			Temporal								Occip			Subcort		
Study	Contrast	10	9	46	11	47	45	44	6	8	4	32	24	23	31	7	40	39	38	ins	42	22	21	20	mt	37	19	18	17	bg	th	cb
4.1 Spoken word Rn - spoken response																																
Howard 92	wd: (hear+rep)-(hear rev+ "crime")																						○						●			
Muller 97	sent: hear - rest					○																✿	✿									
Price 96-4	wd: rep - rest								❒		✿									✿	✿	✿	✿								○	❒
4.2 Spoken word Rn - no spoken response																																
Price 92	wd: hear - rest																					✿										
Petersen 89	wd: hear - fix											❒	❒								✿	✿										
Schlosser 98	sent: (listen) native lang - Turkish					○																	○									
Tzourio 98	*story: hear - rest*																		✿			✿	✿									
Grady 97	wd: hear - rest																				○	○										
Price 96-4	wd: hear - rest																					✿	✿									
Perani 96	story: (listen) native lang - att rest						○								■			○	✿			✿	✿									●
Hirano 97	sent: hear right - ctrl						○														○	✿										●
Binder 96	wd: wd > tone		○				○	○										○					○	○								
4.3 Written word Rn - spoken response																																
Howard 92	wd:read aloud-(false font + "crime")												❒										○									
Bookheimer 95	wd: name - ctrl					○			✿				❒				✿	○		✿	○	✿	○	○	○	○	✿	✿		✿	✿	✿
Small 96	*wd: read aloud-false font + "range"*																					○	○									
Rumsey 97	wd: (lexical dec) ortho - fix										✿	❒								○	○	●	●								✿	✿
Price 94-1	wd: read aloud - feat dec		○					○		○		❖									○	○			○				❒	✿		
Hirano 96	sent: read aloud - rest							○	✿													○						■				■
4.4 Written word Rn - no spoken response																																
Menard 96	wd: read - 5X baseline		○				○											○		○		○					○					
Menard 96	wd: read - fix baseline		✿			○	○		■							●		○				○										
Bookheimer 95	wd: read - ctrl					○				○			❒					○		○		○	○	○		○	✿	✿				
Bottini 94	sent: literal - lexical dec	❒			✿	✿	○		○	○		❒			❒		○		○			○	○	○	●							
Price 94-2	wd: read silent - false font					○		○	❒	❖	✿				❒					✿		✿	✿					○			■	✿
Petersen 90	wd: read silent - fix	○													❒												✿	○				
Beauregard 97	wd: concr - flashing "+"	❒		○								❒										○	○	○	○	○	○	○		❒	❒	❒
Hirano 96	sent: read silent - rest								❖																			○				
Gabrieli 98	wd: sem - phonol					○	○																									
4.5 Other																																
Büchel 98b	wd/nonwd: (feat det) braille - ctrl						○																			○						
Perani 96	story: (listen) native - unknown														●			○	✿													
Kim 97	vis cue: ment description - fix							○														○										
Calvert 97-2	num: mouthing - still																	✿			✿	✿				●	✿					
Soderfeldt 97	wd: sign - speech																									✿	○	■	■			
Sakurai 92	*wd: read (Kanji) aloud - fix*					✿	✿		✿			❖									✿	✿	✿			✿		✿		✿	✿	✿
Sakurai 93	*wd: read (Kana) aloud - fix*					✿	✿		✿												✿	✿	✿			✿		✿	✿	✿	●	●
Nichelli 95	fables: moral comp - sem comp					●																	●				○	●	●			
Caplan 98-1	sent: right-branch-cent-embedded							○	■			❒																				

Note: BAs in Sakurai et al. (1993) were estimated from area names.

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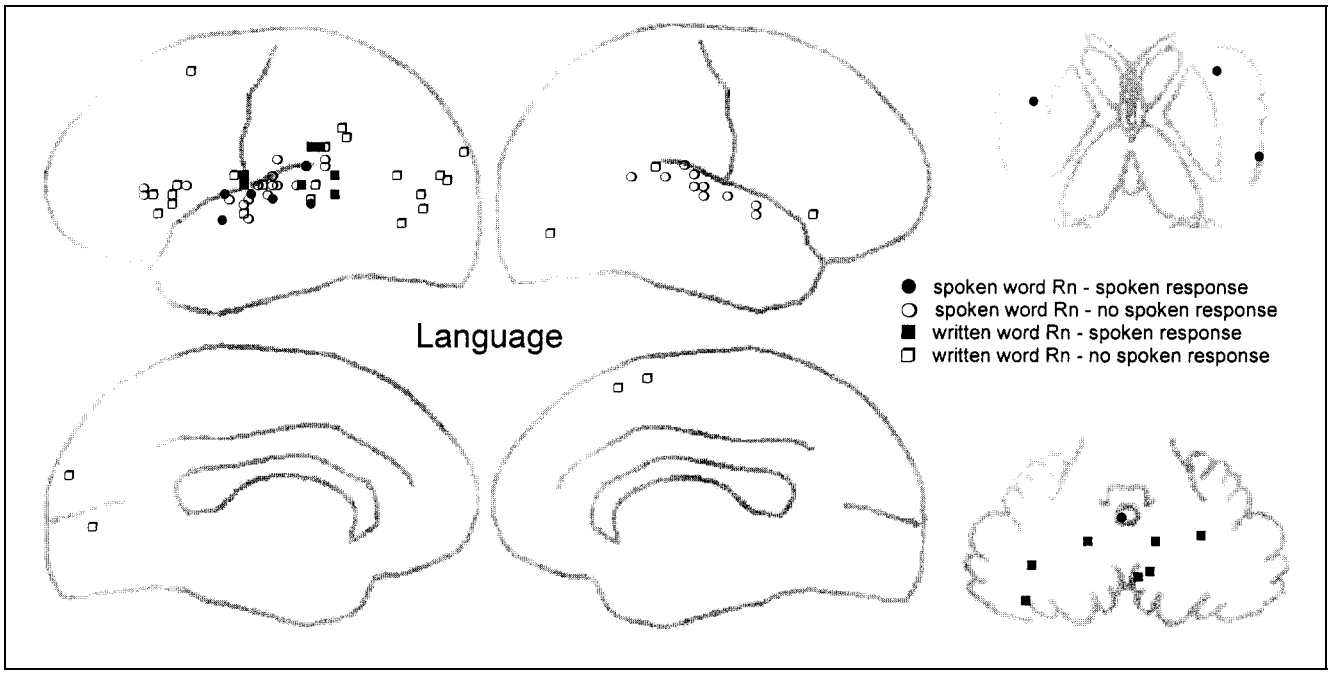

Figure 6. Representative activation peaks (published coordinates) associated to processes of language.

and 8), but other factors, such as image generation and combination of parts into a whole, may be accounting for some activations as well.

The section ''other'' includes some examples of non-visual imagery. Sugishita et al. (1996) explored neuroanatomical correlates of motor imagery by having subjects perform a mental writing task. The results most strongly implicated a left parietal region in motor imagery, and, more generally, the authors noted that their results pointed to similarities between mental writing and actual writing. Similarities between perception and imagery were revealed in a study of musical imagery and perception (Zatorre, Halpern, Perry, Meyer, & Evans, 1996a). In particular, it is of interest to note that relative to a visual baseline condition, the imagery task was associated with increased activity in bilateral secondary auditory cortex. This was so despite the fact that the contrast included two entirely silent conditions. Similarly, a comparison of a task involving imaging a sentence being spoken in another person's voice with a visual control task (McGuire et al., 1996) revealed left temporal activation. Both studies also revealed activation of the supplementary motor area, suggesting that both input and output speech mechanisms are engaged in auditory mental imagery (compare, Zatorre et al., 1996a,b).

Language

Results concerning language processes are shown in Table 4 and Figure 6, and divided into four categories: spoken and written word recognition crossed with spoken or no-spoken response. On basis of this ''factorial design'', we will attempt to identify brain activity related to language comprehension and production. Most of the reviewed studies have included single words as stimuli, but full sentences have been studied as well (see also Bavelier et al., 1997; Mazoyer et al., 1993; for example, Muller et al., 1997; Tzourio, Nkanga-Ngila, & Mazoyer, 1998).

As can be seen in the table, word recognition, regardless of input modality and whether or not a spoken response is required, has consistently been found to activate areas 21 and 22 in temporal cortex (see also Binder et al., 1994; Mazoyer et al., 1993). In general this activation tends to be bilateral, although in the category of written word recognition all activations were left-lateralized. The cortical surface covered by these areas is most likely made up by several distinct regions that can be functionally dissociated (see for example, Fiez, Raichle, Balota, Tallal, & et al., 1996a; Zatorre, Meyer, Gjedde, & Evans, 1996b). Involvement of left superior temporal gyrus/Wernicke's area in word recognition is in agreement with the traditional view implicating this area in comprehension. However, it has been argued that Wernicke's area is not the primary location where language comprehension occurs, but other left temporo-parietal regions may be more critical for comprehension of auditory as well as visual material at a linguistic-semantic level (Binder, Frost, Hammeke, Cox, & et al., 1997).

Whereas left temporal brain regions have strongly been related to word comprehension, left inferior prefrontal cortex/Broca's area has traditionally been linked to word production. However, comparing conditions involving spoken response with conditions involving no spoken response do not suggest that (left) prefrontal

involvement is greater when spoken responses are required. Instead, the major difference between these two classes seems to be that conditions involving spoken responses tend to activate cerebellum to a higher extent. Consistent with the impression from the table, in a comprehensive study, Price et al. (1996) concluded that Broca's area is involved in word perception, as well as in word production, and Binder et al. (1997) suggested that, in addition to having an output function, left prefrontal areas may participate in receptive language processing in the uninjured state (see also Fiez, Raichle, Miezin, Petersen, & et al., 1995). With regard to the possible role of the cerebellum in production, it is interesting to note that a recent fMRI study provided evidence that cerebellar activation is related to the articulatory level of speech production (Ackermann, Wildgruber, Daum, & Grodd, 1998).

Our classification of studies, furthermore, permits evaluation of differences in activation patterns between written and spoken word recognition. In addition to the fact that visual areas are more frequently involved in the case of written word recognition, inspection of the table suggests that, regardless of output (spoken/no spoken), written word recognition tends to differentially activate left prefrontal and anterior cingulate regions. We have no explanation for this trend, but note that left inferior prefrontal activation has been related to semantic processing (see Price, 1998).

In Section 4.5 ("Other"), a study by Buchel et al. (1998a,b) provides evidence that a posterior left tem-

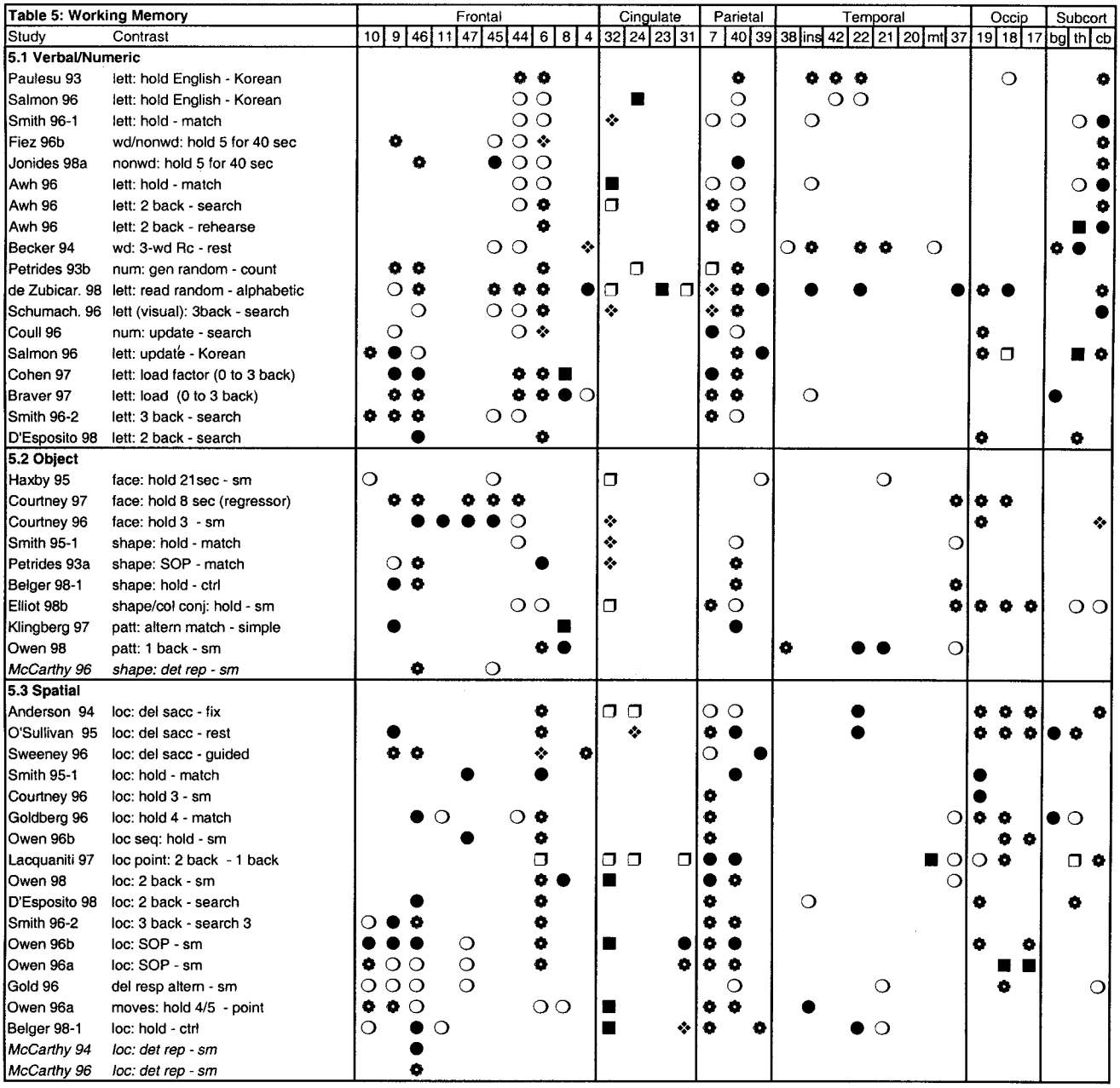

Table 5: Working Memory

		Frontal										Cingulate				Parietal			Temporal								Occip			Subcort		
Study	Contrast	10	9	46	11	47	45	44	6	8	4	32	24	23	31	7	40	39	38	ins	42	22	21	20	mt	37	19	18	17	bg	th	cb
5.1 Verbal/Numeric																																
Paulesu 93	lett: hold English - Korean							✪	✪								✪			✪	✪	✪						○				✪
Salmon 96	lett: hold English - Korean							○	○				■				○				○	○										
Smith 96-1	lett: hold - match							○	○			❖				○	○			○											○	●
Fiez 96b	wd/nonwd: hold 5 for 40 sec		✪				○	○	❖																							✪
Jonides 98a	nonwd: hold 5 for 40 sec			✪			●	○	○								●															✪
Awh 96	lett: hold - match							○	○			■				○	○			○											○	●
Awh 96	lett: 2 back - search							○	✪			❒				✪	○															✪
Awh 96	lett: 2 back - rehearse								✪							✪	○														■	●
Becker 94	wd: 3-wd Rc - rest						○	○			❖								○	✪		✪	✪		○					✪	●	
Petrides 93b	num: gen random - count		✪	✪					✪				❒			❒	✪															
de Zubicar. 98	lett: read random - alphabetic		○	✪			✪	✪	✪		●	❒		■	❒	❖	✪	●		●		●				●	✪	●				✪
Schumach. 96	lett (visual): 3back - search			○			○	○	✪			❖				❖	✪															●
Coull 96	num: update - search		○					○	❖							●	○										✪					
Salmon 96	lett: update - Korean	✪	●	○													✪	●									✪	❒			■	✪
Cohen 97	lett: load factor (0 to 3 back)		●	●				✪	✪	■						●	✪															
Braver 97	lett: load (0 to 3 back)		✪	✪				✪	✪	●	○					✪	✪			○										●		
Smith 96-2	lett: 3 back - search	✪	✪	✪			○	○								✪	○															
D'Esposito 98	lett: 2 back - search			●					✪																		✪				✪	
5.2 Object																																
Haxby 95	face: hold 21sec - sm	○					○					❒						○					○									
Courtney 97	face: hold 8 sec (regressor)		✪	✪		✪	✪	✪																		✪	✪	✪				
Courtney 96	face: hold 3 - sm			●	●	●	●	○				❖															✪					❖
Smith 95-1	shape: hold - match							○				❖					○									○						
Petrides 93a	shape: SOP - match		○	✪					●			❖					✪															
Belger 98-1	shape: hold - ctrl		●	✪													✪									✪						
Elliot 98b	shape/col conj: hold - sm							○	○			❒				✪	○									✪	✪	✪	✪		○	○
Klingberg 97	patt: altern match - simple		●							■							●															
Owen 98	patt: 1 back - sm								✪	●									✪			●	●			○						
McCarthy 96	*shape: det rep - sm*			✪			○																									
5.3 Spatial																																
Anderson 94	loc: del sacc - fix								✪			❒	❒			○	○					●					✪	✪	✪			✪
O'Sullivan 95	loc: del sacc - rest		●						✪				❖			✪	●					●					✪	✪	✪	●	✪	
Sweeney 96	loc: del sacc - guided		✪	✪					❖		✪					○		●														
Smith 95-1	loc: hold - match					●			●								●										●					
Courtney 96	loc: hold 3 - sm															✪											●					
Goldberg 96	loc: hold 4 - match			●	○			○	✪							✪										○	✪	✪		●	○	
Owen 96b	loc seq: hold - sm					●			✪							✪												✪	✪			
Lacquaniti 97	loc point: 2 back - 1 back								❒			❒	❒		❒	●	●								■	○	○	✪			❒	✪
Owen 98	loc: 2 back - sm								✪	●		■				●	✪									○						
D'Esposito 98	loc: 2 back - search			●					✪							✪				○							✪				✪	
Smith 96-2	loc: 3 back - search 3	○	●	✪					✪							✪	✪															
Owen 96b	loc: SOP - sm	●	●	●		○			✪			■			●	✪	●										✪		✪			
Owen 96a	loc: SOP - sm	✪	○	○		○			✪						✪	✪	✪											■	■			
Gold 96	del resp altern - sm	○	○	○		○											○						○					✪				○
Owen 96a	moves: hold 4/5 - point	✪	✪	○					○	○		■				✪	✪			●												
Belger 98-1	loc: hold - ctrl	○		●	○							■			❖	✪		✪				●	○									
McCarthy 94	*loc: det rep - sm*			●																												
McCarthy 96	*loc: det rep - sm*			✪																												

Table 5: Working Memory (continued)		Frontal										Cingulate				Parietal			Temporal								Occip			Subcort		
Study	Contrast	10	9	46	11	47	45	44	6	8	4	32	24	23	31	7	40	39	38	ins	42	22	21	20	mt	37	19	18	17	bg	th	cb
5.4 Problem Solving																																
Rao 97	conceptual reasoning - ctrl	●		●		●			✿	●		❖				✿		✿					●			●	✿	✿		●	●	✿
Nagahama 96	card sorting (MCST) - rest								✿		○	□		■	■		✿	○									●					✿
Goldberg 98	card sorting (WCST) - ctrl	●	✿	✿			○	✿				■					✿	●									●	❖	□	○	□	○
Berman 95	card sorting (WCST) - ctrl	●		✿	✿	○	○	✿		●		❖				○	✿	○					✿	●		○	✿	✿				✿
Goel 97	sent: deduction - understand					○	○																				○					
Goel 97	sent: induction - understand	○	□			○				□		□	□											○			○					
Owen 96a	Tower London (hard) - ctrl		○						●	✿						✿	●										●	●	❖	○		
Baker 96	Tower London - ctrl	●	✿				●		✿			■	□			✿	✿										✿	✿			■	○
Elliot 97	Tower London - guess					✿	●		✿																		✿		●	●	●	
Flitman 97	covered maze - sm ctrl	●								●																	●					
Prabhakar. 97	Raven figural - match		●	●								■				✿	✿									●	●					
Prabhakar. 97	Raven analytical -match	●	✿	✿			✿	✿	✿			❖				✿	✿	✿					✿			✿	✿	✿				
D'Esposito 95	*dual task - single tasks*		✿	✿																												
Klinberg 98	dual task - ctrl	○		●					○								✿		○			●										✿
Goldberg 98	dual task - single tasks								●		○							●	○		○	●					●	●	✿			✿
Goldberg 98	single tasks - dual task	○	○	○		○				○													○									
5.5 Other																																
Barch 97	delay (8 sec > 1 sec)		○	○				○	○							○	○															
Barch 97	difficulty (interaction w/scan)					●	●	●		■		■																		●		
Jonides 98b	lett: hold & inhibit prepot resp - hold						○																									
Bonda 96a	tactual identity - ctrl															✿	●															✿
Zatorre 94	melody: compare notes - listen		✿	✿		●	✿		○	□		❖				✿	✿		✿				●							■		■

abbreviated names: de Zubicar. = de Zubicaray; Prabhakar. = Prabhakaran; Schumach. = Schumacher

poral region (BA 37) is a multimodal language region. Both blind and sighted subjects were found to activate this area during tactile vs. visual reading (compared to non-word letter strings). It was suggested that this area may not contain linguistic codes per se, but may promote activity in other areas that jointly lead to lexical or conceptual access. Relating this finding to the pattern in Table 4, it is interesting to note that area 37 has been activated in several studies of written word recognition but not in studies of spoken word recognition. The study by Calvert et al. (1997) demonstrated that lipreading activates the auditory cortex in the absence of auditory speech sounds. The activation was observed for silent speech as well as pseudo-speech, but not for nonlinguistic facial movements, suggesting that lipreading modulates the perception of auditory speech at a prelexical level.

A study by Soderfeldt et al. (1997) examined perception of signed and spoken language. The results revealed few differences between sign language and spoken language, and the authors concluded that sign language in bilingual persons activates a similar network as that underlying spoken language (for a similar conclusion based on a study of visual sentence processing in English and in American sign language, see Bavelier et al., 1998). The difference in activation in ventral temporal cortex (area 37) related to sign language was interpreted in terms of an attention mechanism that assigns importance to signing hands and facial expressions. A related set of studies compared brain regions involved in processing of native and foreign languages. Perani et al. (1996) found that native-language processing, relative to processing of a foreign language, selectively activated several brain regions, and similar results were observed by Dehaene et al. (1997). Perani et al. concluded that some brain areas are shaped by early exposure to the maternal language, and these regions may not be activated when people process a language that they have learned later in life. This conclusion was extended by Kim et al. (1997). They showed that in Broca's area, second languages acquired in adulthood are spatially separated from native languages, whereas second languages acquired at an early age tend to activate overlapping regions within Broca's area. In Wernicke's area, no separation based on age of language acquisition was observed. An additional study exploring the influence of subject-related differences in the activation pattern was reported by Shaywitz et al. (1995, not shown in table). In this study, fMRI was used to determine brain activity related to aspects of language processing. It was found that during phonological tasks, brain activation in males was lateralized to left inferior frontal gyrus, whereas the pattern was more diffuse for females.

A final set of studies explored activation patterns related to the processing of particular aspects of information. Nichelli et al. (1995) contrasted a task involving monitoring a fable for its moral with a task involving monitoring the fable for a specific semantic feature. The results indicated that a set of brain regions in the right hemisphere was selectively activated when subjects tried to appreciate the moral of a story. Caplan, Alpert, and Waters (1998; see also Just, Carpenter, Keller, Eddy, & Thulborn, 1996; Stromswold, Caplan, Alpert, & Rauch, 1996) studied brain activation related to syntactic complexity of sentences. The results indicate that parts of Broca's area increases their activity when sentences increase in syntactic complexity.

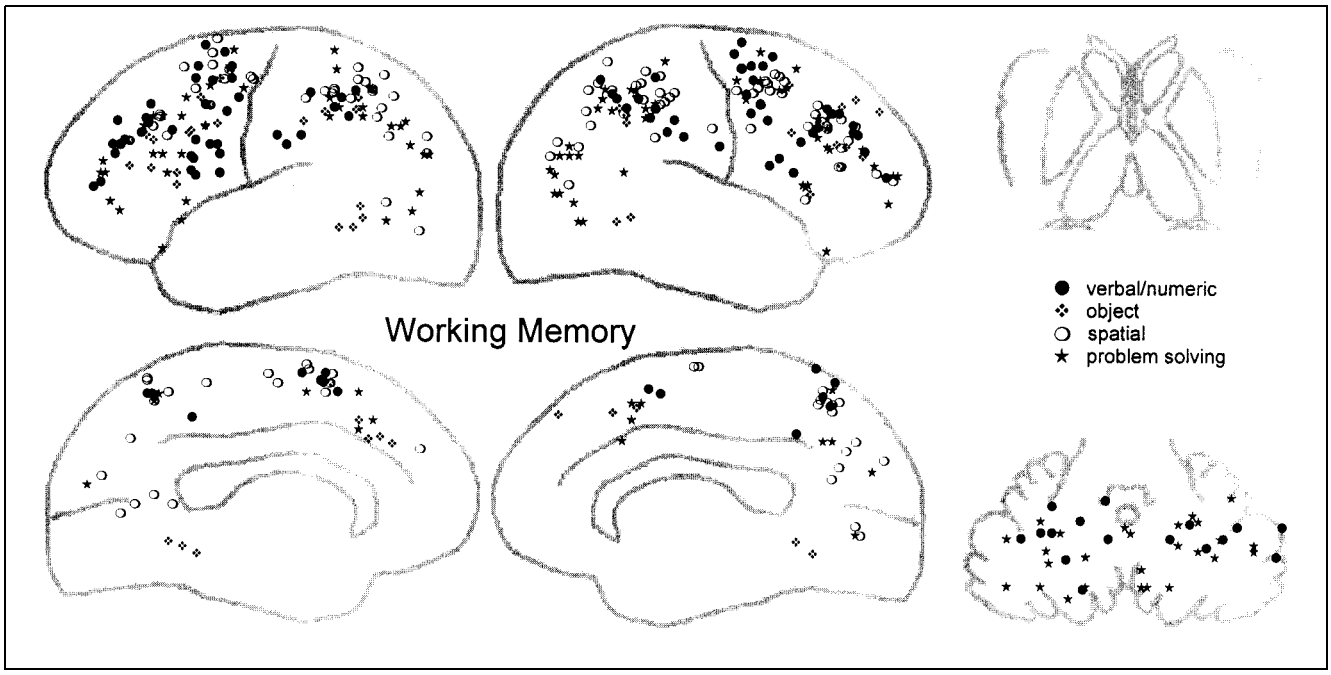

Figure 7. Representative activation peaks (published coordinates) associated to processes of working memory.

Working Memory

Results concerning working memory processes are shown in Table 5 and Figure 7. According to Baddeley's model (Baddeley, 1986; Baddeley, 1998), working memory consists of three main components: a phonological loop for the maintenance of verbal information, a visuospatial sketchpad for the maintenance of visuospatial information, and a central executive for attentional control. In our previous review, the working memory table consisted of only eight contrasts related to the phonological loop and the visuospatial sketchpad. During the last three years, however, dozens of functional neuroimaging studies of working memory have been published (for a recent review, see D'Esposito, in press), so now the working memory table (Table 5) includes more than 60 contrasts. Contrasts involving central executive processes are included in all subsections of the Table, but they are the main focus of the ''Problem Solving'' subsection. Contrasts associated with the visuospatial sketchpad are now separated into those involving object processing and those involving spatial processing. Our previous working memory table associated working memory with activations in prefrontal, parietal, and cingulate regions. While confirming this basic pattern, the present table suggests the involvement of other areas (for example, occipital and cerebellar regions), as well as finer discriminations between different Brodmann's areas.

Most working memory studies have employed three types of tasks: delayed response, *N*-back, and self-ordered response. In each trial of delayed response tasks, subjects are presented with one or more items (for example, letters, numbers, shapes), hold them in short-term memory for a few seconds, and then make a response to a probe (for example, whether the probe matches one of the items). This task requires primarily maintenance operations, and the short-term memory store is emptied after each trial. In *N*-back tasks, subjects must indicate whether or not each item in a continuous stream of item matches an item that occurred one, two, or more items back in the series (1 back, 2 back, and so forth). *N*-back tasks involve not only short-term maintenance (for example, two items in the 2-back task) but also constant updating, which is an operation attributed to the central executive (for example, Morris & Jones, 1990). In self-ordered response tasks, subjects have to generate motor or verbal responses following a rule (for example, response alternation) or avoiding repetition (for example, self-order pointing, random generation). These tasks require monitoring of the contents of working memory, as well as inhibition of inappropriate responses. The contrasts in the Problem Solving section employed four main paradigms: card sorting (for example, Wisconsin Card Sorting Test—WCST), Tower of London (a simplified version of the Tower of Hanoi), Raven Progressive Matrices, and dual tasks. Dual tasks are included in this section, not because they are problem solving tasks per se, but because they require allocating of attentional resources to different simultaneous operations, which is one of the main roles of the central executive (see D'Esposito, Detre, Alsop, & Shin, 1995).

Working memory is almost always associated with increased activity in the prefrontal cortex. As indicated by Table 5, this activity is typically found in areas 6, 44,

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9 and 46. Area 44 activations are more prevalent for verbal/numeric tasks than for visuospatial tasks, and tend to be lateralized to the left hemisphere (that is, Broca's area), suggesting that they reflect phonological processing. Area 6 activations were common for verbal, spatial, and problem-solving tasks, and, hence, they are probably related to general working memory operations (that is, they are not material- or task-specific). In contrast, the activations in areas 9 and 46 seem to occur for certain kinds of working memory tasks but not others. As noted by D'Esposito et al. (1998), activations in these two areas tend to be more prevalent for tasks that require manipulation of working memory contents, such as *N*-back, than for tasks that require only uninterrupted maintenance, such as delayed response tasks (D'Esposito, in press). In Table 5, this difference can be seen by comparing the top half and the bottom half of the verbal and spatial subsections. This pattern is consistent with Petrides' model (Owen, 1997; Petrides, 1994; Petrides, 1995), which proposes that ventrolateral prefrontal regions are involved in simple short-term operations, whereas middorsal prefrontal regions perform higher-level executive operations, such as monitoring. In contrast, the data in Table 5 provide little support for the idea that object working memory engages ventrolateral prefrontal regions while spatial-working memory engages dorsolateral prefrontal regions (for example, Goldman-Rakic,

Table 6: Semantic Memory Retrieval

		Frontal										Cingulate				Parietal			Temporal								Occip			Subcort		
Study	Contrast	10	9	46	11	47	45	44	6	8	4	32	24	23	31	7	40	39	38	ins	42	22	21	20	mt	37	19	18	17	bg	th	cb
6.1 Categorization																																
Kapur 94	wd: living/nonliv - graphem	○		○		○	○																									
Jennings 97	wd: living/nonliv - graphem				○		○					■																	○			■
Price 97	wd: living/nonliv - phonol																○		○											❐		
Wagner 98c-1	wd: abstr/concr - upper/lower		○	○			○	○																	○	○						
Demb 95	*wd: abstr/concr - ascen/desc*			○		○	○			○																						
Vandenb. 96	wd/pict: meaning - ctrl				○	○	○										○						○	○	○	○	○					●
ThompsonS 97	obj: sem attributes - similarities						○	✪	❐	❐						○										○						
Perani 95	pict: match tools - sm		○	○			○																		✪		○	○				
Sergent92a	face: famous - nonfam				○														✪				○		✪	✪		●				
Tempini 98	face/wd: famous - nonfam	❐	❐		❐										❐	❐		○					○	○								
Demonet 94	wd: wd - phoneme									○					❐			✪					○									
Wise 91	pair: categ-instance check - rest																			✪	✪	✪										
6.2 Generation																																
Fletcher 95b	gen instance - rep											❐																		✪		
Buckner95b	stem comp - fix						○	○	❐												○					○	✪			■		✪
Petersen 89	gen verb - rep					○						❐	❐																			✪
Nath.James 97	wd: sentence comp - read						○					■										○	○									
Zelkowicz 98	obj: name obj - ctrl (wd/nobj)																		●								✪					■
Martin 96	obj: name obj - view nobj							○											○							✪			■		○	❖
Martin 95	obj: gen action wd - name obj	○	○			○	○	○	○								○	○					○			○						●
Klein 95	wd: gen synonym - rep		○	○		○	○			○		■	■			○								○		○		❖	❖			✪
Wise 91	wd: verb fluency - rest		○				○	○	❖													○	○								
Warburt. 96-3	wd: verb fluency - rest		○				✪	○	○									○	●			✪	○							✪	❖	
Warburt. 96-3	wd: noun fluency - rest		○	○			○	○	✪			❐						○				✪	✪			○				○	✪	
Frith 91b	wd: sem/ortho fluency - ctrl		○	○									❖		❐			○														
Frith 91a	wd: ortho fluency - rep			○								■																				
Paulesu 97	sem fluency - rest						○								❐															❐		
Paulesu 97	ortho fluency - rest						○	○	○										○											❐		
McCarthy 93	wd: gen verb - rep	✪				✪																										
Phelps 97	*wd: ortho fluency - rep*			○			○			○		❖	❖																			
Friedman 98	*wd: covert ortho fluency - rest*						○	○															○			○			❐	❐		
Buckner 95b	*gen verb - read*	○		○		○	○	○																								
Buckner 95b	*stem comp - fix*					○	○	○																								
6.3 Domains																																
Perani 95	pict: match animals - tools																										○	❐				
Perani 95	pict: match tools - animals						○																									
Martin 96-2	silhouette: name animals - tools																											❐				
Martin 96-2	silhouette: name tools - animals							○	○																	○						
Damasio 96	*pict: name animals - tools*																						○									
Damasio 96	*pict: name tools - animals*																									○						
Martin 95-1	pict: gen col - action																									✪						
Martin 95-1	pict: gen action - col						○															○	○									
6.4 Other																																
Desmond 98	stem comp: many - few	✪	○	○								❐	❐				○													❐		○
Desmond 98	stem comp: few - many					●				❖																✪	✪					●
Paulesu 97	sem fluency - ortho fluency														❐																	
Paulesu 97	ortho fluency - sem fluency							○	○																							
Maguire 97	loc: Rc route - rep num														❐	✪			○						✪		✪					○
Partiot 96	script verification - ctrl		○						❐			❐	❐						○													

abbreviated names: Nath. James = Nathaniel James; ThompsonS = Thompson-Schill; Vandenb. - Vandenberghe; Warburt. = Warburton

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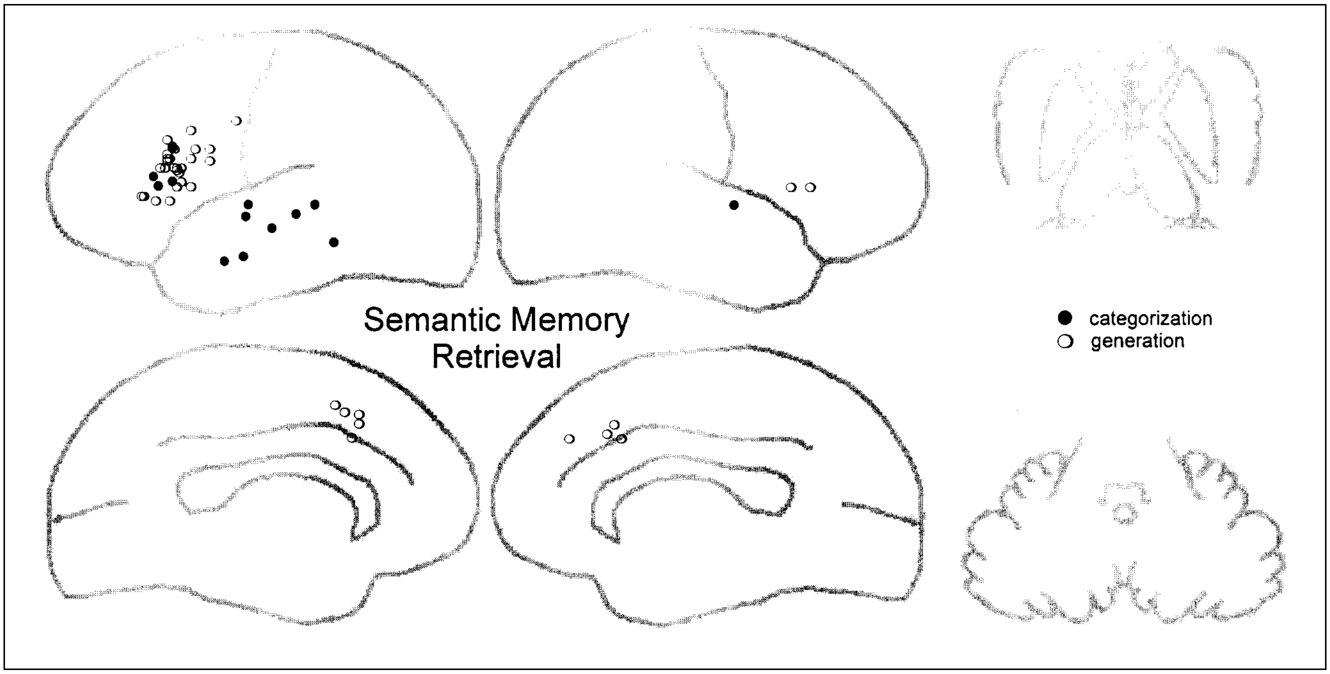

Figure 8. Representative activation peaks (published coordinates) associated to processes of semantic memory retrieval.

1996). This dissociation was found in a few studies (for example, Courtney, Petit, Maisog, Ungerleider, & Haxby, 1998; Courtney, Ungerleider, Keil, & Haxby, 1996), but it is not apparent in the general pattern of the data. An alternative proposal is that object working memory is left-lateralized while spatial working memory is right-lateralized (Smith, Jonides, Koeppe, Awh, & et al., 1995). Again, although a tendency was observed in some studies (Belger et al., 1998; Smith, Jonides, & Koeppe, 1996; Smith et al., 1995), the pattern is not obvious in Table 5.

In addition to prefrontal activations, working memory studies normally show activations in parietal regions, particularly areas 7 and 40. In the case of verbal/numeric tasks, these activations tend to be left-lateralized, suggesting that they are related to linguistic operations. According to Baddeley's model, the phonological loop consists of a phonological store, where information is briefly stored, and a rehearsal process, which refreshes the contents of this store. It has been suggested that left parietal activations reflect the phonological store (Awh, Jonides, Smith, Schumacher, & et al., 1996; Paulesu, Frith, & Frackowiak, 1993), whereas left prefrontal activations in area 44 (Broca's area) reflect the rehearsal process (Awh et al., 1996; Fiez et al., 1996a; Paulesu et al., 1993). When nonverbal materials are employed, parietal activations, particularly those in area 7, tend to be bilateral, and to occur for spatial but not for object working memory. This last pattern suggests that the distinction between a ventral pathway for object processing and a dorsal pathway for spatial processing (Ungerleider & Mishkin, 1982) may also apply to working memory.

Working memory tasks are also associated with anterior cingulate, occipital, and cerebellar activations. Anterior cingulate activations are often found in area 32, but they may not reflect working memory operations per se. Barch et al. (1997) manipulated working memory by varying the delay between the cue and the probe, and task difficulty by varying the readability of the letters presented on the screen. Whereas activity in dorsolateral prefrontal regions (areas 9 and 46) varied as a function of delay, but not of readability, activity in the anterior cingulate (and in some right ventrolateral prefrontal regions) varied as a function of readability but not of delay. Thus, the anterior cingulate activation seems to be related to task difficulty, rather than to working memory, per se. Occipital activations are usually found for visuospatial tasks, and may reflect increased visual attention under working memory conditions. As for cerebellar activations, they were common during verbal working memory tasks, particularly for tasks involving phonological processing (for example, holding letters) and that engaged Broca's area (left area 44).

Given that most problem-solving tasks were highly spatial (for example, Tower of London, WCST), it is not surprising that the pattern of activations in the Problem Solving subsection were very similar to that of the Spatial subsection. Consistent with the aforementioned idea that mid-dorsal areas 9/46 are involved in higher-level working memory operations, activations in these areas were prominent in the Reasoning/Planning subsection. area 10 activations were also quite prevalent, and may be related to episodic memory aspects of problem-solving tasks (see episodic memory retrieval section). Tasks involving sequential decisions, such as

conceptual reasoning, card sorting and Tower of London tasks (first six contrasts of the Problem Solving subsection), consistently engaged basal ganglia, thalamic, and cerebellar regions. These regions are typical skill learning regions (see Procedural Memory section), and may reflect the skill-learning aspects of sequential problem-solving tasks. Also, basal ganglia, thalamus, and prefrontal cortex are intimately linked (Alexander & Freedman, 1984) and dysfunction of this circuitry could underlie planning deficits in Parkinson disease (for example, Owen et al., 1995).

Finally, dual task studies have yielded inconsistent results. D'Esposito et al. (1995) found that two tasks, which did not activate prefrontal regions when performed individually, engaged the mid-dorsal prefrontal cortex when performed simultaneously, suggesting that this area is involved in executive control operations. However, other studies have shown that when the two tasks activate prefrontal regions individually, prefrontal activity during dual-task performance may not increase (Klingberg, 1998) or even decrease (Goldberg et al., 1998). To account for these results, D'Esposito (in press) hypothesized that prefrontal activity follows an inverted-U function: under dual-task conditions, prefrontal activity increases to meet processing demands until an asymptote level, but then the capacity of executive control is exceeded, and activity starts to decrease. An alternative hypothesis is that dual performance enhances activity in some prefrontal regions (for example, those associated with attentional control) but attenuates activity in other prefrontal regions (for example, those associated with operations tapped by each individual task).

Semantic Memory Retrieval

Results concerning semantic-memory retrieval processes are shown in Table 6 and Figure 8. Semantic memory refers to knowledge we share with other members of our culture, such as knowledge about the meaning of words (*A banana is a fruit*), the properties of objects (*Bananas are yellow*), and facts (*Bananas grow in tropical climates*). So far, most functional neuroimaging studies of semantic memory have focused on knowledge of words and objects, and paid little attention to knowledge of facts (see, however, Partiot, Grafman, Sadato, Flitman, & Wild, 1996; Tulving, 1989; Wood, Taylor, Penny, & Stump, 1980). In Table 6, the semantic memory tasks investigated were divided into two broad groups: categorization and generation. In categorization tasks, subjects classify words into different categories (for example, living vs. nonliving), whereas in generation tasks, they produce one (for example, word stem completion) or several (for example, fluency tasks) words in response to a cue. The panel ''Domains'' includes studies that compared semantic retrieval for different types of knowledge, such as information about animals and information about tools. An inspection of Table 6 indicates that semantic memory retrieval is associated with activations in prefrontal, temporal, anterior cingulate, and cerebellar regions.

Prefrontal activity during semantic memory tasks has been almost always found in the left hemisphere but not in the right. This happened even when the stimuli were nonverbal materials, such as objects (Martin, Haxby, Lalonde, Wiggs, & et al., 1995; Martin, Wiggs, Ungerleider, & Haxby, 1996; Thompson-Schill, M, Aguirre, & Farah, 1997; Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996) and faces (Sergent, Ohta, & MacDonald, 1992a; Tempini et al., 1998). This striking left-lateralization is in sharp contrast with the right-lateralization of prefrontal activity typically observed during episodic memory retrieval. This asymmetric pattern has been conceptualized in terms of a hemispheric encoding/retrieval asymmetry (HERA) model (Nyberg, Cabeza, & Tulving, 1996a; Nyberg, Cabeza, & Tulving, 1998; Tulving, Kapur, Craik, Moscovitch, & Houle, 1994a). This model consists of three hypotheses: (1) the left prefrontal cortex is differentially more involved in semantic memory retrieval than is the right prefrontal cortex; (2) the left prefrontal cortex is differentially more involved in encoding information into episodic memory than is the right prefrontal cortex; and (3) the right prefrontal cortex is differentially more involved in episodic memory retrieval than is the left prefrontal cortex. Thus, the left-lateralization of prefrontal activations in Table 6 supports the first hypothesis of the model. The second and third hypotheses are discussed in the episodic memory encoding and episodic memory retrieval sections, respectively.

Within the frontal lobes, activations were found in most prefrontal regions, including ventrolateral (areas 45 and 47), ventromedial (area 11), posterior (areas 44 and 6), and mid-dorsal (areas 9 and 46) regions. Activations in ventrolateral regions occurred during both classification and generation tasks and under a variety of conditions, suggesting that they are related to generic semantic retrieval operations. In contrast, area 11 activations were more common for classification than for generation tasks, and could be related to a component of classification tasks, such as decision-making. Conversely, activations in posterior and dorsal regions are more typical for generation tasks than for classification tasks. Many posterior activations (areas 44 and 6) occurred at or near Broca's area, and, hence, they may reflect overt or covert articulatory processes during word generation. Activations in dorsal regions (areas 9 and 46) were particularly frequent for fluency tasks. Since fluency tasks require the monitoring of several items in working memory (see Working Memory section), these activations may reflect working memory, rather than semantic memory per se. Consistent with this idea, Desmond et al. (1998, see ''Other'' subsection) found that when subjects completed word stems,

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Table 7: Episodic Memory Encoding		Frontal									Cingulate				Parietal			Temporal							Occip			Subcort		
Study	Contrast	10	9	46	11	47	45	44	6	8	4	32	24	23	31	7	40	39	38	ins	42	22	21	20	mt	37	19	18	17	bg	th	cb
7.1 Verbal																																
Nyberg 96b	wd: enc - retrieval (LV2)		○	○			○																					○				
Jonides 98a	wd: enc - nonwd																											○				
Kelley 98	wd: enc - fix		○				○	○	❐							○	○							○	⊙			⊙	○			
Kopelman 98	wd (old/new): enc - read			○							○								○			○		○				❖	○		⊙	
Kopelman 98	wd: new - old					○	○		○															○	⊙			⊙				●
Grady 98	wd/obj: enc wd - enc obj		○														○	○			●		○									
Wagner 98b	wd: wd - textures		○		○	○	○	○	○	○																						
Wagner 98c-2	wd: confident subsequent Rn - miss					○	○	○	○																○	○						
Fletcher 95b-1	pair: aud enc - ctrl			○								❐		❐	❐							○	●									
S. Kapur 96	pair: enc - read			○			○	○	○			❐	❐										○		○							
Dolan 97	pair: new/new - old/old																						○		○							
Dolan 97	pair: new/old + old/new - old/old		○	○																												
Fletcher 98a	wd-list: organize - blocked		○																													
Fletcher 98a	wd-list: less distraction	○		○						❐		❐																				
Kopelman 98	covariate w/ wds recalled																								○			❐			●	
Fernandez 98	correlate w/ wds recalled									⊙											○	○			⊙						●	
Busatto 97	wd: enc - read numbers						⊙							■			○										❖	❖	❖			○
Halsband 98	pair: enc - read pseudo words	○	○				●					❐	❐															❖	❖			
7.2 Objects/Faces																																
Haxby 96	face: enc - match		○	○	○	○				○		●												○	●	○			❐			
Kelley 98	face: enc - fix							●	●							⊙	⊙								●	⊙	●	⊙	❖			
Kelley 98	obj: enc - fix		○				○	⊙	❐			❐				⊙	⊙								⊙	⊙	●	⊙	⊙			
Grady 98b	obj/wd: enc obj - enc wd																								⊙		●	■				
Owen 96c	obj-feat: enc - retrieval		○	○				○							❐							○	○	○							
Wagner 98b	texture: enc texture - enc wd	■					●		●			❐																				
Roland 95	visual pattern: encode - rest	⊙		○			○																									
Rombouts 97	*obj: enc - same pict*																								⊙							
7.3 Spatial (ego- and allocentric)																																
Brewer 98	*scene: subsequent R>K>miss*							●																	⊙							
Stern 96	*scene: enc - same pict*																								⊙	⊙	⊙					
Gabrieli 97	*scene: enc - same pict*						●																		⊙							
Nyberg 96b	loc (wd): enc - enc item/time															●	●															
Owen 96d	obj-loc: enc - retrieval			○	○	○	○										○							○		○						
Owen 96d	loc: enc - retrieval		●	○	●										❐		○					●	⊙			○						●
Aguirre 96	virtual environ: explore - forward								●						❖		○								⊙	○	⊙	○				■
Maguire 96	film: navigation - nonnavigation															■									⊙							
Maguire 98b-1	virtual environ: explore - images															○									●		⊙	⊙				⊙

Note: Area 45 in Gabrieli et al. (1997) was estimated from gyral description in the text.

areas 9/10 were more active for stems with many completions than for stems with few completions. They proposed that these areas are involved in selecting among competing candidate responses (for selection-related activations in the inferior frontal gyrus, see Thompson-Schill et al., 1997).

Semantic retrieval tasks are also commonly associated with temporal, anterior cingulate, and cerebellar regions. Temporal activations occurred mainly in the left middle temporal gyrus (area 21) and in bilateral occipito-temporal regions (area 37). Left area 21 was activated not only for words but also pictures (Martin et al., 1995; Martin et al., 1996; Vandenberghe et al., 1996) and faces (Sergent et al., 1992a; Tempini et al., 1998), suggesting it is involved in higher-level semantic processes that are independent of input modality. In contrast, area 37 activations were more common for objects and faces, so they could be related to the retrieval of visual properties of these stimuli. Anterior cingulate activations were typical for generation tasks. In Desmond et al.'s (1998) study, the anterior cingulate—like the dorsal prefrontal cortex—was more active for stems with many than with few completions, whereas the cerebellum showed the opposite pattern. According to Desmond et al., this suggests that the anterior cingulate is involved in selecting among candidate responses, while the cerebellum is involved in memory search processes. Consistent with this last idea, cerebellar activations were found during single-word generation, but not during fluency tasks (see Table 6).

The "Domains" section includes studies comparing the neural correlates of different kinds of knowledge. Three studies compared the retrieval of information about animals and tools (see also Spitzer, Kwong, Kennedy, Rosen, & et al., 1995), which are forms of knowledge dissociated by brain damage (for a review, see Caramazza & Shelton, 1998). Perani et al. (1995) and Martin et al. (1996) associated the retrieval of animal information with left occipital regions and the retrieval of tool information with left prefrontal regions. Occipital activations could reflect the processing of the subtle differences in physical features that distinguish animals (Martin et al., 1996; Perani et al., 1995), whereas prefrontal activations could be related to linguistic (Perani et al., 1995) or motor (Martin et al., 1996) aspects of tool utilization. Damasio et al. (1996) focused on the inferior

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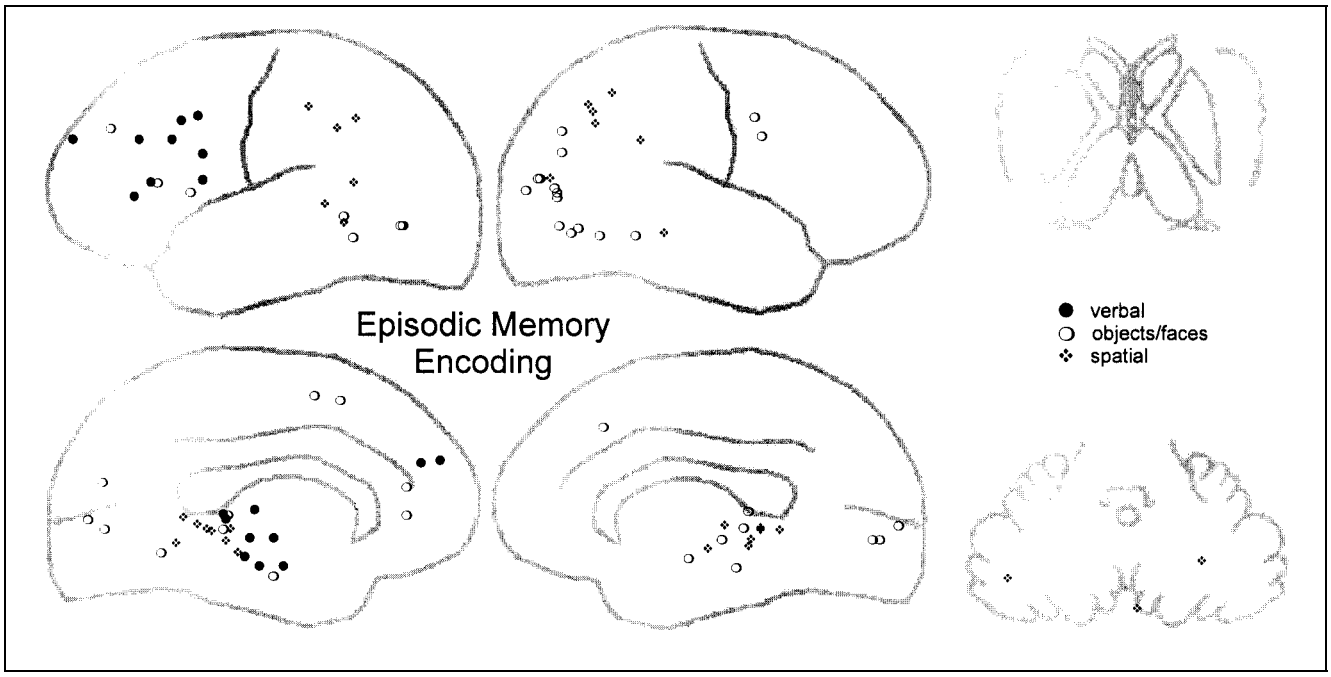

Figure 9. Representative activation peaks (published coordinates) associated to processes of episodic memory encoding.

temporal lobe, and found that animal knowledge engaged a more anterior region (area 21) than the one associated with tool knowledge (area 37). This last posterior inferotemporal activation replicates a finding by Martin et al. (1996). Another distinction investigated was knowledge about the colors and actions associated with objects (Martin et al., 1995). While generating color words engaged fusiform areas close to color perception regions, generating action words recruited a left temporo-occipital area close to motion perception regions. These results are consistent with the idea that knowledge about object attributes is stored close to the regions involved in perceiving these attributes (for example, Damasio, 1989; Squire, Knowlton, & Musen, 1993). This idea is likely to fuel further semantic memory research.

Episodic Memory Encoding

Results concerning episodic memory encoding processes are shown in Table 7 and Figure 9. Episodic memory refers to memory for personally experienced past events (Tulving, 1983), and it involves three successive stages: encoding, storage, and retrieval. Encoding refers to processes that lead to the formation of new memory traces. Storage designates the maintenance of memory traces over time, including consolidation operations that make memory traces more permanent. Retrieval refers to the process of accessing stored memory traces. Encoding and retrieval processes are amenable to functional neuroimaging research, because they occur at specific points in time, whereas storage/consolidation processes are not, because they are temporally distributed (Buckner & Koutstaal, 1998). It is very difficult to differentiate the neural correlates of encoding and retrieval on the basis of the lesion data, because impaired memory performance after brain damage may reflect encoding deficits, retrieval deficits, or both. In contrast, functional neuroimaging allows separate measures of brain activity during encoding and retrieval. This explains why the HERA pattern was not discovered before the advent of functional neuroimaging.

Episodic encoding can be intentional, when subjects are informed about a subsequent memory test, or incidental, when they are not. Incidental learning occurs, for example, when subjects learn information while performing a semantic retrieval task, such as making living/nonliving decisions. In this section, we focus on intentional episodic memory encoding, that is, conditions in which subjects were explicitly instructed to commit information to memory. Brewer et al. (1998) and Wagner et al. (1998c) used incidental encoding but they are included here because they isolated activity associated with successful encoding from activity associated with semantic processing. Even though we do not consider incidental episodic encoding in this section, it should be emphasized that semantic memory retrieval and incidental episodic memory encoding are so closely associated that they can be seen as two sides of the same coin. First, semantic processing of information (semantic retrieval) usually leads to successful storage of new information (episodic encoding; for example, Craik & Lockhart, 1972). Second, when subjects are instructed to learn information for a subsequent memory test (intentional encoding), they tend to elaborate the meaning of the information and make associations on the basis of

their knowledge (semantic retrieval). Thus, most of the regions (for example, left prefrontal cortex) associated with semantic retrieval tasks (Sections 6.1–6.2) are also associated with episodic memory encoding.

There are two basic ways in which the neural correlates of encoding can be studied. The most common method is to compare a condition assumed to involve more encoding, such as memorizing word pairs, to a condition assumed to involve less encoding, such as reading word pairs (for example, Kapur et al., 1996). Since encoding is presumed to decrease as the familiarity of the information increases, the amount of encoding in the reference task can be further reduced by presenting old items (for example, Dolan & Fletcher, 1997), or by presenting the same items again and again (for example, Stern et al., 1996). The second method to investigate encoding is to identify regions whose activation during encoding is associated with successful performance in a subsequent memory test. This could be done using scan/performance correlations in blocked PET and fMRI studies (for example, Fernandez et al., 1998; Kopelman, Stevens, Foli, & Grasby, 1998). However, the comparison of encoding activity for items that were subsequently remembered to items that were subsequently forgotten (Brewer et al., 1998; Wagner et al., 1998c) is a more powerful method than recent event-related fMRI designs has allowed. It is worth noting that the activations identified by the two methods have a different meaning. In the first method, activations are related to cognitive processes that subjects performed while trying to learn new information, whereas in the second case, they are related to the subset of operations that were actually successful in achieving this goal. In other words, the first method identifies a ''realistic'' activation pattern of encoding activity (that is, all regions activated), while the second, identifies an ''ideal'' pattern (that is, activations associated with successful encoding).

Table 7 suggests that episodic encoding is associated primarily with prefrontal, cerebellar, and medial-temporal brain regions. In the case of verbal materials, prefrontal activations were always left lateralized. This pattern contrasts with the right lateralization of prefrontal activity during episodic retrieval for the same kind of materials (see Table 8), and is consistent with the second hypothesis of the HERA model. In contrast, encoding conditions involving nonverbal stimuli sometimes yielded bilateral and right-lateralized activations during encoding (Brewer et al., 1998; Kelley et al., 1998; Wagner et al., 1998b)[1]. This is puzzling because semantic memory retrieval tasks, which involve episodic memory encoding, consistently yielded left-lateralized activations (see Table 6) for both verbal and nonverbal materials (Martin et al., 1995; Martin et al., 1996; Sergent et al., 1992a; Tempini et al., 1998; Thompson-Schill et al., 1997; Vandenberghe et al., 1996). Right-lateralized encoding activations could reflect the use of non-nameable stimuli, such as unfamiliar faces (Kelley et al., 1998) and textures (Wagner et al., 1998b), but encoding of non-nameable stimuli has been also associated with left-lateralized activations (unfamiliar faces: Haxby et al., 1996; locations: Owen, Milner, Petrides, & Evans, 1996d). Here it is important to note that contrasting encoding of verbal materials with encoding of nonverbal materials (for example, Wagner et al., 1998b) informs about the neural correlates of different materials rather than about the neural correlates of encoding per se. In sum, it is unclear why prefrontal activity during encoding of nonverbal stimuli is sometimes left-lateralized and sometimes right-lateralized (for discussion, see Nyberg et al., 1998). Nonetheless, it is fair to conclude that the second hypothesis of the HERA model is not as well supported by functional neuroimaging evidence as the first (see Semantic Retrieval section) and the third (see Episodic Retrieval section).

The prefrontal areas most commonly activated for verbal materials are areas 44, 45, and 9/46. Kapur et al. (1996) suggested that encoding activations in left area 45 reflects semantic processing while those in left area 44 reflects rote rehearsal. Areas 9/46 might reflect higher-order working memory processes during encoding. Fletcher et al. (1998a) found that activation in left area 9 increased as a function of organizational processes during encoding, and was attenuated by distraction during highly organizational tasks. Cerebellar activations occurred only for verbal materials and showed a tendency for right lateralization. The left-prefrontal/right-cerebellum pattern during language, verbal-semantic memory, and verbal-episodic encoding tasks is consistent with the fact that fronto-cerebellar connections are crossed.

In our previous review, we did not include medial-temporal activations as part of the typical activation pattern of episodic memory encoding because only a minority of studies showed them. Now, however, about half of the contrasts show these activations. Moreover, event-related fMRI studies have recently demonstrated that the strength of medial-temporal activity during encoding predicts not only what items will be remembered (Brewer et al., 1998; Wagner et al., 1998c), but also how well they will be remembered (Brewer et al., 1998). Medial-temporal activations showed a clear lateralization pattern: They were left-lateralized for verbal materials and bilateral for nonverbal materials. Grady et al. (1998b) found that, under similar conditions, medial-temporal activity was stronger during the encoding of pictures than during the encoding of words, and suggested that this difference could account for the fact that pictures are usually remembered better than words. In the case of nonverbal materials, medial-temporal activity seems to be more pronounced for spatial than for nonspatial information (Maguire, Frackowiak, & Frith, 1996; Maguire, Frith, Burgess, Donnett, & J, 1998b), consistent with the strong link between the hippocampus and

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Table 8: Episodic Memory Retrieval		Frontal										Cingulate				Parietal			Temporal								Occip			Subcort		
Study	Contrast	10	9	46	11	47	45	44	6	8	4	32	24	23	31	7	40	39	38	ins	42	22	21	20	mt	37	19	18	17	bg	th	cb
8.1 Verbal																																
Jonides 98a	nonwd: Rn - read	●	○	●								❖					●											✿				
Andreas. 95a	wd: Rn overlearnt - read	✿	●	●		●						□				□	✿															□
Andreas. 95c	wd: free Rc overlearnt - rest						●		✿		✿		□						✿	●											❖	✿
Rugg 96	wd: Rn (hi/med/low) - percep	✿	●	●						■		■																				
Cabeza 97b	wd: Rn - read	●				●	●					□						✿														
Schacter 97a	wd: true/false Rn - fix	✿				✿	✿		■		●	■				□	✿								✿		✿					
Buckner 98b	wd: Rn - fix	●	✿				✿	✿	✿		●	■				✿								○		✿	✿	✿	✿		●	✿
Fujii 97-2	wd: rep old - rep every other						●		○						■			○		○					✿	✿	○	●	■			
Buckner 95a-1	wd stem: cued Rc - comp	●	✿							✿						□									●							
Backman 97	wd stem: cued Rc - comp	✿		✿								❖										○			✿							○
Fletcher 95b-2	wd pair: cued Rc - rep	●		●								□				❖															❖	
Petrides 95	wd pair: cued Rc - rep		●	●	●				●						■	✿																□
Cabeza 97b	wd pair: cued Rc - read					●						□																		●	□	❖
Fletcher 98b	wd pair: ext cued Rc - rep		●	●			●						■			✿															❖	
Petrides 95	wd: free Rc - rep		✿	✿			○		✿			■	■			❖											✿	●			□	
Fletcher 98b	wd: free Rc - rep		●	●			●									✿																
Busatto 97	wd: Rn - read / press			○											❖											●	✿	✿	✿		✿	
Nolde 98a	wd: Rn - fix (all subjects)	○	●																													
Halsband 98	wd pair: enc - read pseudowd	✿										■				❖											❖					■
8.2 Nonverbal																																
Andreasen 96a	face: Rn - gender dec	●	●	●	✿	●						❖	❖				●										✿					○
Haxby 96	face: Rn - match	●	●				●	●		✿		□				✿		✿										✿				✿
Kapur 95a	face: det rep - rest																								●		✿	✿	■			
Roland 95	abstr patt: Rn - enc	✿								●																				●		
Schacter 95	abstr 3D obj: Rn - perc	✿		✿			✿	✿																	✿							
Henke 97	image pairs: Rn old - ctr									●														●						●		
Kohler 98	obj (feat/loc): Rn > perc/enc	✿	✿	●				✿	✿						■		●										●	□			□	
Owen 96d	loc: Rn - enc		●			●	●	●								●											○	●	❖			
Owen 96d	obj loc: Rn - enc		■		●	●									■													■	■			
Owen 96c	obj feat: Rn - enc					●																						□	■			
Moscovitch 95	obj loc: Rn - match			●			●	●									●	●						●		✿	✿	✿				✿
Maguire 98a	route: Rc - follow arrows	○																							●			○		○		
Klingberg 94	*patt: cued Rc - STM*																								●							
Aguirre 96	*route: recall - ctrl*																								✿							
8.3 Retrieval success																																
Tulving 94b	wd: Rn high targ - low	●		●				●	●			□	□			○	✿															
Tulving 96	pict: Rn high targ - low	✿	✿	✿			○	✿	✿	○		❖	❖		□	○		●										●	✿			
Andreas. 95c	wd: Rc overlearnt - learnt								●				□		■																	
Andreas. 95b	story: Rc overlearnt - learnt										●				■	□																
Kapur 95b	wd: Rn high targ - low														■																	
Rugg 96	wd: increase w/ targ dens	✿		●								■				○											○	●	●			
Rugg 97b	wd: intent Rn deep - shallow		○					○		□	○	□			■							○			○		●			●	○	
Rugg 98	wd: Rn high targ - zero targ	●													□	✿	○										○					
Nyberg 96c	wd: + correlat w/ Rn perf					✿							□												○							
Schacter 96a	wd: cued Rc deep - shallow																								●							
Heckers 98	wd: cued Rc deep - shallow														□						●	●			●			●	○			
Buckner 98b	*wd: Rn deep - shallow*	●																														
Wagner 98a-2	*wd: Rn (biasing): high - new*	●	●	●	●																											
8.4 Retrieval effort																																
Schacter 96	wd: cued Rc shallow - deep	○		○									□														■					
Andreas. 95c	wd: Rc learnt - overlearnt				●	○				○							●															●
Andreas. 95b	story: Rc learnt - overlearnt					○							□																			✿
Rugg 98	wd: cued Rc zero targ - high targ	✿													■		○															●
Buckner 98b	*wd: Rn shallow - deep*		○				✿	✿																								
8.5 Retrieval mode																																
Nyberg 95/98	wd: Rn deep - read	●					●					□	□															○				❖
Nyberg 95/98	wd: Rn new - read	●					●					❖	❖															❖				❖
Kapur 95b	wd: Rn high targ - sem	✿	●	●						❖		❖						●														
Kapur 95b	wd: Rn low targ - sem	✿	●	●						❖		❖						●														
Wagner 98a-1	wd: Rn deep/high - read	✿	✿	●	●	✿		✿	□	✿		□																				
Wagner 98a-1	wd: Rn low - read	●	✿	●	●	✿		○	□	✿		□																				
Rugg 97a	wd: Rn deep - sem		✿	●				○						□	❖	○												■		■		■
Rugg 97a	wd: Rn shallow - sem	●	●	●											■	✿																●
Buckner 98c	wd: Hits - fix (hypothesis testing)	●					✿	○																								
Buckner 98c	wd: Correct rejection - fix (hyp. test)	●					✿	○																								

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Table 8: Episodic Memory Retrieval (contd.)		Frontal									Cingulate				Parietal			Temporal							Occip			Subcort		
Study	Contrast	10	9	46	11	47	45	44	6	8	4	32	24	23	31	7	40	39	38	ins	42	22	21	20	mt	37	19	18	17	bg	th	cb
8.6 Content vs. Context																																
Moscovitch 95	obj: identity - loc																									●						
Moscovitch 95	obj: loc - identity																●															
Owen 96c	obj: feat - loc					✪																		✪		✪		✪	✪			
Owen 96c	obj: loc - feat								●	●					❐	❖	○										○	○	❖			
Kohler 98	obj: identity > loc			○		○																			○							
Kohler 98	obj: loc > identity																															○
Aguirre 97	landmark: identity - loc																								●	●	✪					
Aguirre 97	landmark: loc - identity								○							✪	●															
Nyberg 96b	wd: item Rn - loc					●																	●									
Nyberg 96b	wd: loc - item Rn									○																						
Nyberg 96b	wd: time (list) - item Rn											❐	❐																			
Eyler Zorilla 96	wd: recency - ctrl	✪							❐							○																
Cabeza 97c	wd: recency - item Rn	●							✪						■			●									✪					
Cabeza 97c	wd: item Rn - recency																		●					○	✪					■		
8.7 Other																																
Cabeza 97b	pair: cued Rc - assoc Rn											❐																				
Cabeza 97b	pair: assoc Rn - cued Rc																●	●									●					
Fletcher 98b	wd free Rc - pair cued Rc		●	●												■																
Fletcher 98b	pair cued Rc - wd free Rc								●						❖				●													
Fletcher 96	wd: imageable - nonimage											❐			■	❖						●		●								
Wagner 98b	*wd: Rn wd - Rn texture*	✪	✪	●	❖	○	○	○	○	❐																						
Wagner 98b	*texture: Rn texture - Rn wd*				●		✪	●	●																							
Buckner 96	obj: Rc obj - Rc wd																						○			○				●		●
Petersson 97	*obj: draw learnt - overlearnt*																							○	✪	✪						
Schacter 97b	obj: Rn same orient - diff orient																								○							
Schacter 96b	wd: Rn true targ - fix																○					○	○		○							
Schacter 96b	wd: Rn false targ - fix																								○							
Schacter 96b	wd: Rn false targ - ctrl	●			✪																											
Fink 96	Ima autobiographical event - rest								■					■	■				●				●								❐	

abbreviated names: Andreas. = Andreasen

spatial mapping found in animal research (for a review, see Nadel, 1991). The localization of encoding-related activations within the medial-temporal lobes is discussed in the next section, in relation to the localization of retrieval-related activations.

Episodic Memory Retrieval

Results concerning episodic memory retrieval processes are shown in Table 8 and Figure 10. Episodic memory retrieval refers to the search, access, and monitoring of

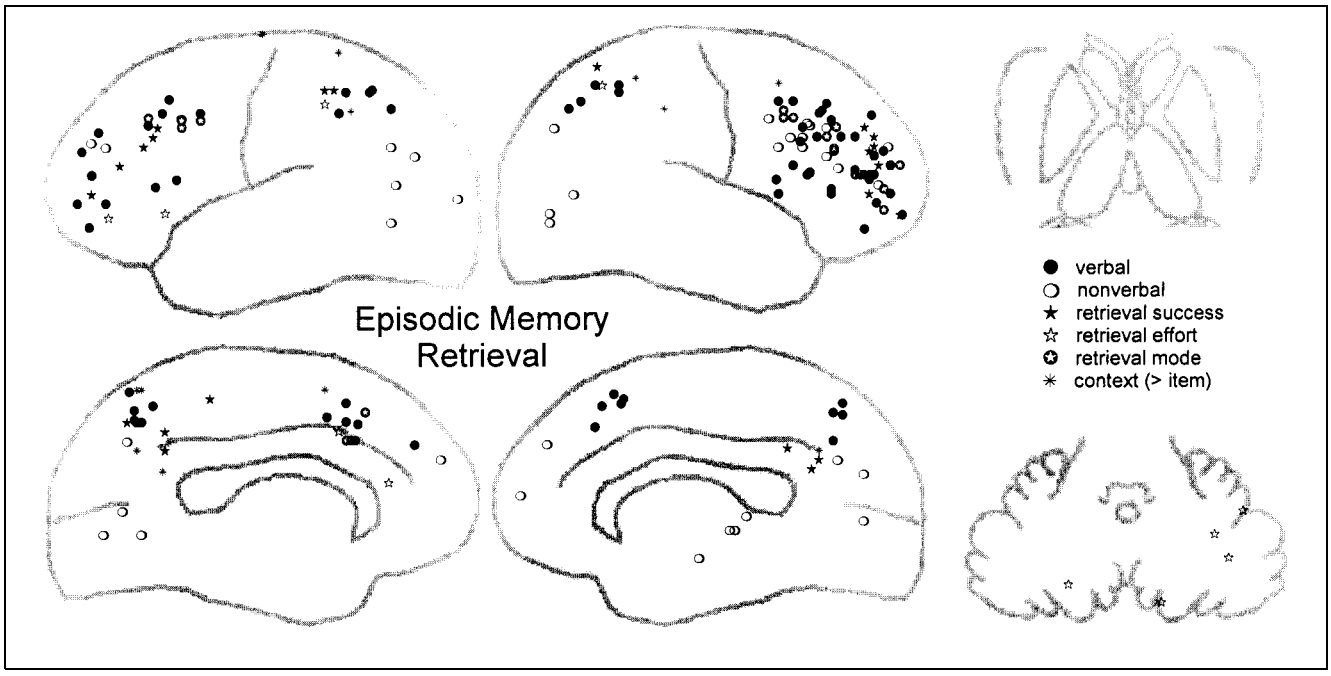

Figure 10. Representative activation peaks (published coordinates) associated to processes of episodic memory retrieval.

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stored information about personally experienced past events, as well as to the sustained mental set underlying these processes (or retrieval mode, Tulving, 1983). In the laboratory, episodic memory retrieval has been typically studied by exposing subjects to *miniature events*, such as the appearances of words or pictures, and subsequently testing them for the information stored. Traditionally, two large classes of tests have been used to study episodic memory retrieval: recall or recognition. In a recall test, the subjects' task is to produce the names of studied items (for example, words, objects), either to general instructions alone (free recall) or to specific cues (cued recall). In a typical recognition test, studied and nonstudied items are presented in a mixed sequence, and the person's task is to decide which items are *old* (studied) and which are *new* (nonstudied). An important distinction in the episodic memory domain is the one between content and context memory (for a review, see Johnson, Hashtroudi, & Lindsay, 1993). *Content memory* refers to *what* items were presented, while *context memory* refers to *where* (spatial memory), *when* (temporal memory), and *how* (source memory) they were presented.

Table 8 has seven panels. Panels 8.1 and 8.2 include basic contrasts between episodic retrieval conditions (that is, recall or recognition) vs. nonmemory conditions (for example, rest, perceptual matching). Panels 8.3 to 8.5 consist of studies that investigated changes in neural activity during retrieval as a function of the amount of old information accessed during the scan. Panel 8.6 includes a few studies comparing content memory with different aspects of context memory. Finally, the *Other* section includes contrasts between different types of episodic retrieval, such as recall vs. recognition, and other contrasts that did not fit within the previous panels. As suggested by the data in Panels 8.1 and 8.2, episodic memory retrieval is associated with seven main regions: prefrontal, medial-temporal, medial parieto-occipital, lateral parietal, anterior cingulate, occipital, and cerebellar regions.

Prefrontal activations during episodic memory retrieval are sometimes bilateral, but they show a clear tendency for right-lateralization (see Panels 8.1 and 8.2). As previously discussed, the right lateralization of prefrontal activity during episodic memory retrieval (see Table 8) contrasts with the left lateralization of prefrontal activity during semantic memory retrieval (see Table 6) and episodic memory encoding (see Table 7), a pattern specified by the HERA model (Nyberg et al., 1996a; Tulving et al., 1994a). Since this model describes a tendency across studies, it is not invalidated by a few individual studies showing encoding-related activity in the right prefrontal or retrieval-related activity in the left prefrontal cortex (for discussion, see Nyberg et al., 1998). At the same time, it is important to account for these exceptions, and some interesting ideas have been proposed. For example, Nolde, Johnson, & Raye (1998b) suggested that left prefrontal activations during episodic retrieval tend to occur for tasks that require more reflectively complex processing. Another possibility is that these activations are related to semantic retrieval processes during episodic retrieval (Cabeza et al., 1997a). Semantic retrieval can aid episodic retrieval particularly during recall, and bilateral activations tend to be more frequent during recall than during recognition. Moreover, left prefrontal activity during episodic retrieval is associated with retrieval effort (see Panel 8.4), and is more common in older adults than in young adults (Cabeza, Anderson, Mangels, Nyberg, & Houle, in press; Cabeza et al., 1997a; Grady et al., 1998a; Madden et al., 1999). Left prefrontal activations in older adults has been interpreted as compensatory (for a review, see Cabeza, in press; Cabeza et al., in press; Cabeza et al., 1997a).

Besides the lateralization issue, it is critical to understand the role of specific prefrontal regions on episodic retrieval. One approach to this problem has been to investigate whether prefrontal activity changes as a function of the amount of information retrieved during the scan. In general, this amount has been manipulated by varying encoding conditions (for example, deep vs. shallow, Buckner et al., 1998b; Nyberg et al., 1995; Schacter, Alpert, Savage, Rauch, & Albert, 1996a) or by altering the proportion of old items (targets) during the scan (Kapur, Craik, Jones, Brown, et al., 1995b; Rugg, Fletcher, Frith, Frackowiak, & Dolan, 1996; Tulving et al., 1994b; Tulving & Kroll, 1995; Wagner, Desmond, Glover, & Gabrieli, 1998a). As illustrated by Panels 8.3 to 8.5, all three possible outcomes have been observed. As more information is retrieved during the scan, prefrontal activity may increase (retrieval success), decrease (retrieval effort), or remain constant (retrieval mode). These three outcomes are not necessarily contradictory. Actually, they could correspond to three different aspects of retrieval: maintaining an attentional focus on a particular past episode (retrieval mode), performing a demanding memory search (retrieval effort), and monitoring retrieved information (retrieval success).

It is quite likely that these different aspects of retrieval are represented in distinct prefrontal regions. The contrasts in Panels 8.3–8.5 suggest some functional differentiation, although the contrasts in each panel are too few to allow strong conclusions. The region most strongly associated to retrieval mode is the right anterior prefrontal cortex (area 10). This idea was recently supported by a combined PET/ERP study that associated a right area 10 activation with task-related rather than item-related activity during episodic retrieval (Düzel et al., 1999). Activations associated with retrieval effort show a tendency to be left lateralized, in particular left areas 47 and 10. This pattern is consistent with the complexity (Nolde et al., 1998b) and compensatory (Cabeza et al., in press; Cabeza et al., 1997a) accounts of prefrontal activity during episodic retrieval. Finally, bilateral areas 10, 9, and 46 were sometimes

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associated with retrieval success (see Panel 8.3). The fact that the same areas did not show differences as a function of retrieval performance in other studies (see Panel 8.5) could reflect weaker manipulations and/or statistical power, but differences in these respects are not obvious. Another alternative, suggested by Wagner et al. (1998a), is that the difference depends on the particular strategies used at test (see also Buckner et al., 1998c). For example, they found that prefrontal activity increased with success activations when subjects were warned about the proportion of old and new items during the scan (biasing). Thus, it is a challenge for future episodic retrieval studies to differentiate between prefrontal regions associated with retrieval mode, effort, and success, and to understand the modulatory effects of retrieval strategies.

In our previous review, only a couple of studies had reported medial-temporal activations, and, hence, we did not include them as part of the typical pattern of episodic retrieval. In the last few years, however, several PET and fMRI studies have shown these activations for both verbal and nonverbal materials. In contrast with medial-temporal activations during episodic encoding (see Table 7), those during episodic retrieval tend to occur in both hemispheres, regardless of the materials employed. The fact that they were sometimes found in association with retrieval success, but never in association with retrieval effort or retrieval mode, suggest that they are related to the level of retrieval performance. Actually, Nyberg et al. (1996c) found that medial-temporal activity increased as linear function of correct old word recognition (r=.82), and suggested that this activity reflected successful access to stored-memory representations. Likewise, Schacter et al. (1996a) related hippocampal activity to conscious recollection. Hippocampal activity was also found to be sensitive to the match between study and test conditions, such as the orientation of study and test objects (Schacter et al., 1997b, see Panel 8.7). Yet, the recollective experience does not have to be veridical: Schacter et al. (1996b) found significant hippocampal activations during the recognition of false targets. In this study, verdical recognition yielded additional activations in a left temporo-parietal region, possibly reflecting the retrieval of sensory properties of auditorily studied words. Finally, intentional retrieval is not a precondition for hippocampal activity; activations in this area were found for old information encountered during a non-episodic task, suggesting they can also reflect spontaneous reminding of past events (Rugg, Fletcher, Frith, Frackowiak, & Dolan, 1997a).

After the right prefrontal cortex, the most typical region in PET/fMRI studies of episodic retrieval is the medial parieto-occipital area that includes retrosplenial (primarily areas 29 and 30), precuneus (primarily medial area 7 and area 31), and cuneus (primarily medial areas 19, 18, and 17) regions. The critical role of the retrosplenial cortex in memory retrieval is supported by evidence that lesions in this region can sometimes cause severe memory deficits (for example, ''retrosplenial amnesia'', see Valenstein et al., 1987). The role of the precuneus has been attributed to imagery (Fletcher et al., 1995a; Fletcher et al., 1995b; Fletcher, Shallice, Frith, Frackowiak, & Dolan, 1996) and to retrieval success (Kapur et al., 1995b). Consistent with the imagery hypothesis, Fletcher et al. (1996) found retrieval-related activations in the precuneus to be more pronounced for imageable than for nonimageable words (see Panel 8.7). However, Buckner et al. (1996) did not find the precuneus region to be more activated for object recall than for word recall (see Panel 8.7), and pointed out that imagery-related activations are more anterior (for example, $y=-50$) than the ones typically associated with episodic retrieval (for example, $y=-70$). In a recent cued-recall study, Krause et al. (1999) found that the precuneus was activated for both imageable and abstract words and for both visual and auditory study presentations, and concluded that this region is involved in episodic retrieval, irrespective of imagery content. Kapur et al. (1995b) proposed the retrieval success hypothesis because they found the precuneus cortex to be more active in a high-target than in low-target recognition condition (see Panel 8.3). The data in Table 8 provides support for this hypothesis: area 31 activations were much more common in Panel 8.3 than in any of the other panels.

Episodic memory retrieval is also associated with activations in lateral parietal, anterior cingulate, occipital, and cerebellar regions. Lateral parietal regions have been related to the processing of spatial information during episodic memory retrieval (for example, Moscovitch, S., Köhler, & Houle, 1995; Tulving et al., 1994b) and to the perceptual component of recognition (Cabeza et al., 1997b). Anterior cingulate activations (areas 32 and 24) have been attributed to response selection and initiation of action (Cabeza et al., 1997b; Shallice et al., 1994). An examination of Table 8 suggests that some anterior cingulate activations could be related to language processes, because they are more frequent for verbal than for nonverbal materials (compare Panels 8.1 and 8.2). As expected, occipital activations were more common during nonverbal retrieval, possibly reflecting not only more extensive processing of test stimuli but also memory-related imagery operations. Finally, cerebellar activations have been related to self-initiated retrieval operation (Bäckman et al., 1997; Cabeza et al., 1997b). The idea of initiation is consistent with the association of cerebellar activations with retrieval mode and effort (Panels 8.4 and 8.5), rather than with retrieval success (Panel 8.3).

Panel 8.6 consists of contrasts that investigated different aspects of context memory. Moscovitch et al. (1995) compared recognition of object identity (*what*) with recognition of object location (*where*), and found that

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Table 9: Priming		Frontal									Cingulate				Parietal			Temporal								Occip			Subcort		
Study	Contrast	10	9	46	11	47	45	44	6	8	4	32	24	23	31	7	40	39	38	ins	42	22	21	20	mt	37	19	18	17	bg	th	cb
9.1 Perceptual priming																																
Buckner 95a-1,	wd: (stem comp) unprimed-primed																										✪					
Bäckman 97	wd: (stem comp) unprimed-primed																										●					
Schacter 96a	wd: (stem comp) unprimed-primed																										✪					
Frith 95	pseudoword: new - new/rep																										■					
Schacter 95	possible obj: old - new																									○						
Blaxton 96a	wd: (frag comp) unprimed - primed											■																	○	●		❐
Buckner 98a	pict: novel - rep							○				■	■											✪		✪	✪	○				○
Poldrack 98	wd/nonwd: unprimed - primed															✪	○	●									○	✪			❐	✪
Elliott 98a	ideogram: novel - familiar																		○					●			✪				❐	
9.2 Conceptual priming																																
Raichle 94	*wd: pract - novel*	○										❐								✪												●
Blaxton 96a	wd: (sem ass) unprimed - primed					○						❐			❐				○		○	○		○						○		■
Demb95	wd: (abs/concr) unprimed-primed			○		○	○			○																						
Gabrieli96	wd: (abs/concr) unprimed-primed			○		○	○			○																						
Wagner97	wd: (living thing?) unprimed-primed	○		○		○	○																									
Wagner97	pict:(living thing?) unprimed-primed			○		○	○																									
Beauregard 98	wd:(sem cat dec) primed-unprimed																							○	●							

a fusiform region was more active for object identity than for location retrieval, whereas an inferior parietal region showed the opposite pattern (see also Kohler, Moscovitch, Winocur, Houle, & McIntosh, 1998; Owen, Milner, Petrides, & Evans, 1996c). This finding suggests that the ventral/dorsal distinction (Ungerleider & Mishkin, 1982) applies also to episodic retrieval. In the time domain, Cabeza et al. (1997c) contrasted recognition memory (*what*) with recency memory (*when*). Medial-temporal regions were more active during item memory than during temporal-order memory, whereas dorsal prefrontal and parietal regions were more active during temporal-order memory than during item memory (see also Eyler Zorrilla, Aguirre, Zarahn, Cannon, and D'Esposito, 1996). The dissociation between medial-temporal and prefrontal regions is consistent with classical neuropsychological findings (Corsi, cited by Milner, 1971). Parietal activations during temporal-order memory suggest the dorsal pathway may be associated not only with *where* but also with *when*.

Two studies in the *Other* panel compared different types of retrieval tests. Cabeza et al. (1997b) compared recall and recognition. In contrast with expectations based on neuropsychological evidence, prefrontal regions were similarly activated in both tests. This finding may be related to the use of associative recognition—a form of recognition with a strong recollection component (Donaldson & Rugg, 1998; Yonelinas, 1997), or to the careful matching of task difficulty in the two tests. Fletcher et al. (1998b) compared free and cued recall, and found a dissociation in the right prefrontal cortex between dorsal cortex (areas 9 and 46), which was more active during free recall, and the ventrolateral cortex (area 47/frontal insula), which was more active during cued recall. This dissociation is consistent with Petrides' (1994, 1995) model (see Working Memory section), and suggests that some of the activations observed during episodic-memory retrieval tasks may reflect the working-memory components of these tasks. Finally, the *Other* section includes a study that investigated real life-autobiographical memories (Fink, Markowitsch, Reinkemeier, & et al., 1996). Consistent with evidence from focal retrograde amnesia (Levine et al., 1998; Markowitsch, 1995), autobiographic retrieval was associated with activations along a right fronto-temporal network.

In sum, episodic memory retrieval is associated with activations in prefrontal, medial-temporal, posterior midline, parietal, anterior cingulate, occipital, and cerebellar regions. Prefrontal activations tend to be right-lateralized (HERA pattern), and have been related to retrieval mode, retrieval effort, and retrieval success. The engagement of medial-temporal regions has been linked to retrieval success and recollection. Posterior midline activations seem also related to retrieval success. Parietal activations may reflect processing of spatial context, and anterior cingulate activations, selection/initiation processes. Cerebellar involvement has been attributed to retrieval self-initiated retrieval. Consistent with the ventral/dorsal pathway distinction, spatial retrieval engaged parietal regions and object retrieval, temporal regions. Parietal regions were also activated during temporal-order retrieval, suggesting a general role in context memory.

Priming

Results concerning priming processes are shown in Table 9, and divided into perceptual and conceptual priming. In several studies, perceptual priming has been explored by studying completion of word-stems. In the primed condition, it is possible to complete the stems with previously presented words whereas this is not possible in the unprimed condition. We noted in our previous review that visual perceptual priming is associated with decreased activity in occipital cortex (that is, unprimed> primed). The results by Blaxton et al. (1996a,b) on visual perceptual priming measured by

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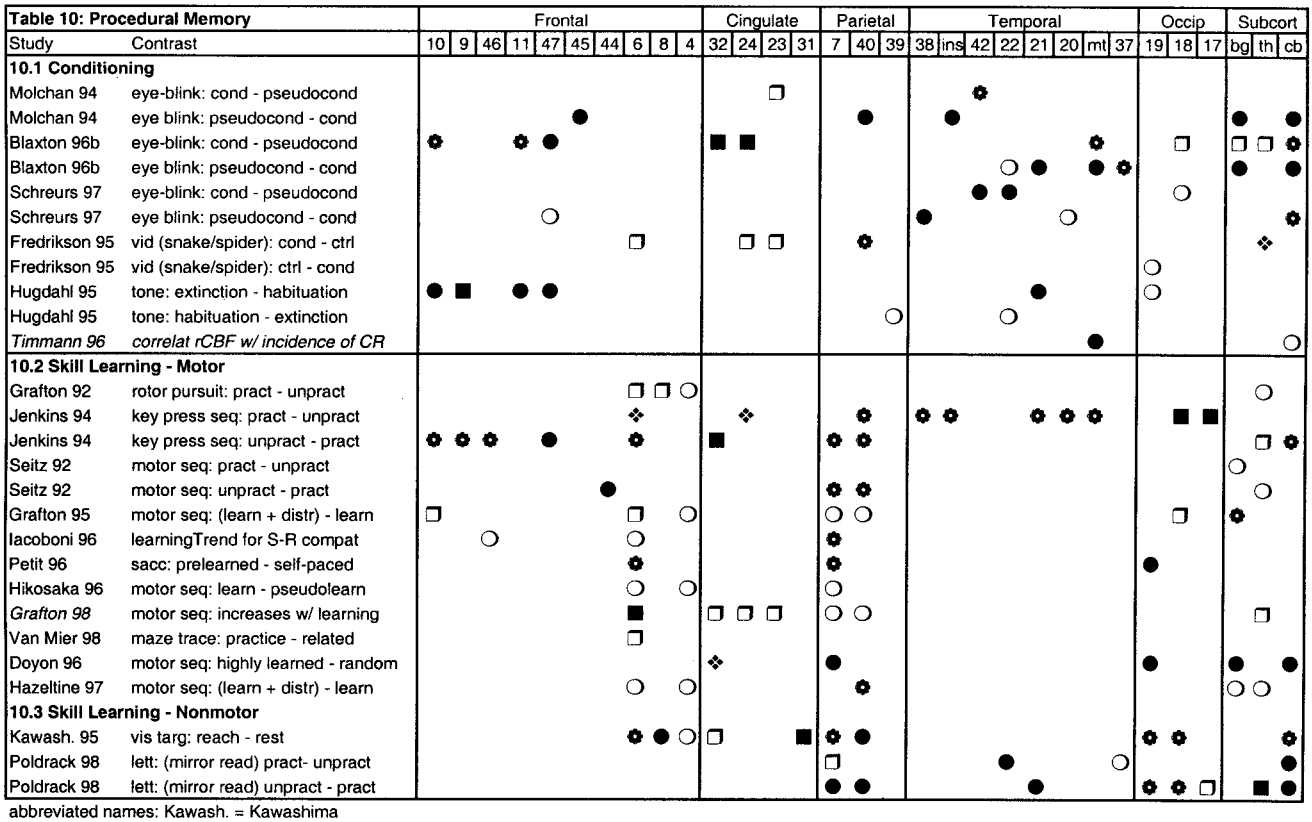
word fragments rather than word stems are consistent with this observation. Moreover, recent PET and fMRI studies on non-verbal visual perceptual priming have revealed priming-related reductions in regions in occipital and inferior temporal brain regions (Buckner et al., 1998a). Whereas most brain imaging studies of perceptual priming have involved short retention intervals, a study by Poldrack et al. (1998) indicated that priming effects can persist over days. The results of this study, which explored repetition priming (item-specific learning) within the context of an fMRI study of the neural basis of visual skill learning, suggested that the learning-related neural changes that accompany these forms of learning partly involve the same regions (for discussion of the relation between neural correlates of priming and skill learning, see Poldrack et al., 1998).

The study by Elliott and Dolan (1998a,b) measured perceptual priming by using a preference judgement task (which of two stimuli do you like better). This task was contrasted with an episodic memory test (which of two stimuli have you seen before). For both types of tasks, two conditions were included: one in which the stimuli (Japanese ideograms) had previously been presented, and one in which the stimuli were unfamiliar. Importantly, the initial presentation of stimuli was done in a subliminal fashion; the stimuli appeared for only 50 msec and the presentation was masked. This way of presenting the material prevented subjective identification of the stimuli. A comparison of blood flow responses associated with novel vs. familiar stimuli (across memory tasks) found that novel stimuli were associated with higher activity in several regions, including fusiform gyrus and cuneus. Thus, although the effect was observed across tasks (compare, Blaxton et al., 1996a,b), this study indicates that priming-related reductions in activity in visual areas occur even after subliminal presentation at study (see Beauregard, Chertkow, Bub, & Murtha, 1997 for a study of word priming, and Dehaene et al., 1998 for a study of motor priming following subliminal presentation).

Priming cannot only facilitate perceptual processes, but may also influence conceptual processes. Blaxton et al. (1996a,b) used a semantic association test, and found that the primed condition was associated with decreased activity in several regions, including left inferior prefrontal cortex (compare, Raichle et al., 1994). Similarly, several fMRI studies, which have included repeated semantic processing of the same items, have found reduced left prefrontal activation associated with the primed condition (Demb et al., 1995; Gabrieli et al., 1996; Wagner et al., 1997). The Demb et al. study showed that the left prefrontal reduction is not seen when words are non-semantically reprocessed, suggesting that the effect reflects a process-specific change (not a consequence of mere repeated exposure). The Wagner et al. study provided evidence that this process-specific effect can be obtained regardless of the perceptual format of the stimuli (pictures or words).



abbreviated names: Kawash. = Kawashima

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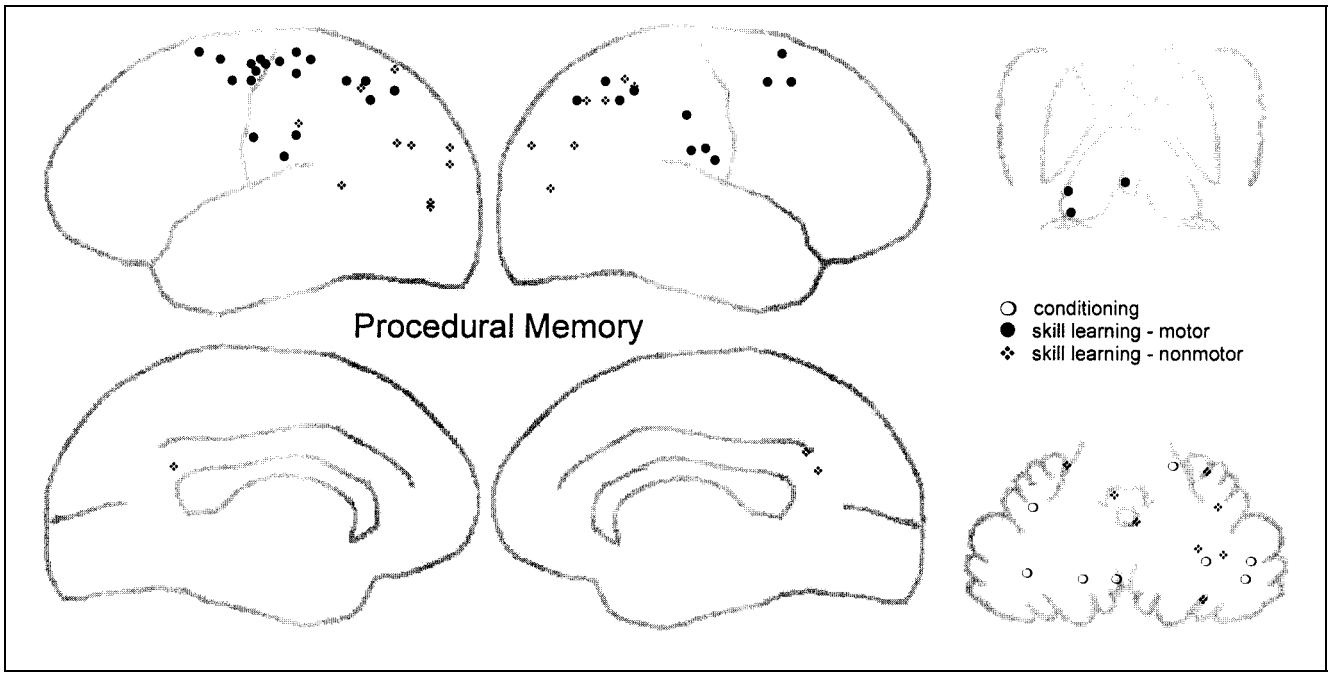

Figure 11. Representative activation peaks (published coordinates) associated to processes of procedural memory.

Finally, it can be noted that the Buckner et al. (1998a,b,c) study, which was discussed in the section on perceptual priming, revealed reduced prefrontal activity, and the authors suggested that these reductions may be a neural correlate of conceptual priming. It is generally agreed that many memory tests rely upon a mixture of processes, and even the stem-completion task, which has been used in several studies of perceptual priming, has been associated with priming-related left prefrontal reductions (see Schacter & Buckner, 1998, p. 190). This may be taken as evidence that this task, too, taps both perceptual and conceptual processes. The data pattern associated with the last entry in Panel 2 of Table 9, the study by Beauregard, Gold, Evans, & Chertkow (1998) on primed semantic category decision, is clearly distinct from the other entries in this section. These authors reported results from a contrast of a primed condition with an unprimed condition, which differs from the typical way of assessing priming (looking for priming-related reductions in activity). Also, it should be noted that, although the test used in this study qualifies it for inclusion in the section on conceptual priming, the authors claimed that the priming effects obtained with this task are primarily perceptual (p. 1872).

Taken together, despite some exceptions (for example, Schacter et al., 1995), there is good agreement between the data pattern summarized in Table 9 and the suggestion by Schacter and Buckner of a neural correlate of priming: ''repeating items during performance of the same task, or even during performance of different tasks, can lead to decreases in the amount of activation present in specific brain areas'' (1998, p. 191). The exact neural mechanism that mediates this decrease in activation is unclear, but one possibility is that it reflects enhanced processing of the involved neurons or/and a specification of the involved neuronal population, resulting in a spatially less diffuse response (see Ungerleider, 1995).

Procedural Memory

Results concerning procedural memory processes are shown in Table 10 and Figure 11, and divided into three subcategories: conditioning, motor-skill learning, and nonmotor skill learning. Starting with conditioning, the studies on eye-blink conditioning point to a consistent role of cerebellum in this form of learning (decreased activity following conditioning). The studies by Molchan and colleagues (Molchan et al., 1994; Schreurs et al., 1997) included tone-airpuff pairings, and conditioning was also associated with increased activity in auditory cortex. A similar design was used in Blaxton et al. (1996a,b), although no auditory cortex activation was observed (for a discussion of possible reasons for discrepancies across studies, see Schreurs et al., 1997). It is worth pointing out that this often-termed ''simple'' form of learning seems to engage many brain regions. Involvement of an extensive network of brain regions in conditioning is further suggested by the studies on classical conditioning (for discussion, see Hugdahl, 1998).

Motor-skill learning is associated with activation of motor regions (for the involvement of somatosensory regions, see Honda et al., 1998). In the majority of studies, area 6 was involved, but learning-related

changes have also repeatedly been demonstrated in primary motor cortex (area 4). Further support for involvement of primary motor cortex comes from a study by Karni et al. (1995). They found that the size of the activated area in the primary motor cortex increased as a function of training. Parietal involvement has also been consistently observed, and several authors have suggested that fronto-parietal interactions may underlie task performance (for example, Iacoboni et al., 1996; Petit et al., 1996). Turning to the nonmotor subsection, inspection of the table suggests that a major difference between motor and nonmotor learning concerns activation of frontal motor areas. The only study of nonmotor learning in which activation of motor areas was observed is that by Kawashima et al. (1995). Although their task (visuomotor learning) was not intended to be a motor-skill learning task, it is possible that some component of motor learning was involved. Regarding consistent activation patterns within the class of nonmotor learning, different tasks were used, precluding the detection of consistent activation patterns. It is, nevertheless, noteworthy that cerebellar activation was observed across tasks, and Kawashima et al. (1995) concluded that their results supported the possibility that the cerebellum may have a role in a variety of cognitive functions. This possibility seems to be further supported by the present review. It is, furthermore, of interest to note the consistent involvement of parietal brain regions. This is in line with the pattern observed for motor-skill learning, and the overlap in activation patterns may reflect common processes underlying these two forms of procedural memory.

REVIEW BY REGION

When one reviews functional neuroimaging results across different domains, it becomes quite obvious that some brain regions are engaged in a wide variety of tasks across different cognitive domains. Activations in parietal area 7, for example, were consistently found in studies of attention, space perception, imagery, working memory, episodic memory, and procedural memory. The most parsimonious account of this kind of activation is that they reflect cognitive processes that are tapped by tasks in different domains. However, most functional neuroimaging studies have preferred to interpret activations within their own domain (however, see MacLeod, Buckner, Miezin, Petersen, & Raichle, 1998). Area 7 activations, for instance, were usually attributed to attentional processes in attention studies, to perceptual processes in perception studies, to working memory processes in working memory studies, and so on. These domain-specific interpretations are useful because they allow researchers in each area to refine hypotheses and to plan new experiments. For example, working memory researchers investigated whether left parietal activations were associated with phonological rehearsal or storage processes (Awh et al., 1996).

At the same time, it would be useful to systematically compare functional neuroimaging data in different cognitive domains and to develop general theories that account for the involvement of brain regions in a variety of cognitive tasks. Although these goals are beyond the scope of this review, the sections below briefly discuss the role of different regions in cognitive processes. These discussions are based on Table 11, which summarizes typical activation patterns in Tables 1 to 10.

Prefrontal Regions

The prefrontal cortex was found to be involved in almost all high-level cognitive tasks. Prefrontal activations were particularly prominent during working memory and memory retrieval (episodic and semantic), and less prevalent during perception and perceptual priming tasks. This pattern is consistent with the idea that the prefrontal cortex is involved in working memory processes, such as monitoring, organization, and planing (for example, Goldman-Rakic, 1996; Petrides, 1994; Stuss, Eskes, & Foster, 1994). However, it would be simplistic to associate the prefrontal cortex solely to working memory. For example, some of the same prefrontal regions engaged by working tasks are also recruited by simple-detection tasks that do not involve a maintenance component (for a review, see D'Esposito, in press). In other words, although working memory is undoubtedly one of the main functions of prefrontal cortex, this region is not devoted solely to working memory operations.

Regarding lateralization, prefrontal activations during language, semantic memory retrieval, and episodic memory encoding were usually left-lateralized, those during sustained attention and episodic retrieval were mostly right-lateralized, and those during working memory were typically bilateral. Two ideas can partially account for this lateralization pattern. Since semantic retrieval tasks typically involved either verbal or verbalizable stimuli, the notion that linguistic stimuli engage primarily the left hemisphere, whereas nonlinguistic (that is, pictorial, visuospatial) engage primarily the right accounts not only for language activations, but also for semantic retrieval activations. However, this notion cannot readily explain why verbal materials are associated with left-lateralized activations in the case of semantic retrieval, but with right-lateralized activations in the case of episodic retrieval. This pattern is accommodated by the HERA model (Nyberg et al., 1996a; Nyberg et al., 1998; Tulving et al., 1994a), which proposes that semantic retrieval and episodic encoding activations are left-lateralized, whereas episodic retrieval activations are right-lateralized. Yet, episodic encoding activations sometimes follow the verbal/pictorial pattern, rather than the HERA pattern (for

Table 11: Typical Activations	Frontal										Cingulate				Parietal			Temporal								Occip			Subcort		
Process	10	9	46	11	47	45	44	6	8	4	32	24	23	31	7	40	39	38	ins	42	22	21	20	mt	37	19	18	17	bg	th	cb
1. Attention																															
1.1 Sustained	●														◎																
1.2 Selective																										◎	◎				
1.3 S/R Compatibility											❖					◎															
1.4 Orientation								◎							◎	◎											◎				◎
1.5 Division of attention								○																							
2. Perception																															
2.1 Object																						○		◎	◎	◎	◎	◎			
2.2 Face																								◎	◎	◎	◎				
2.3 Space/Motion								◎							◎	◎										◎					
2.4 Smelling			◎																												◎
3. Imagery																															
3.1 Object																									◎			●			
3.2 Space/Motion								◎							◎	○										◎					
4. Language																															
4.1 Spoken wd Rn - spoken resp																		○				○									◎
4.2 Spoken wd Rn - no spoken resp						○													○	◎	◎										
4.1 Written wd Rn - spoken resp																			○	○	○										◎
4.1 Written wd Rn - no spoken resp					○	○		❖													○					○	○				
5. Working Memory																															
5.1 Verbal/Numeric		◎	◎				○	◎							◎	○															◎
5.2 Object		◎	◎			◎	○				❖					◎									◎						
5.3 Spatial		◎	◎					◎							◎	◎										◎	◎				
5.4 Problem solving	◎	◎	◎		○	◎		◎	◎		❖				◎	◎	◎									◎	◎				◎
6. Semantic Memory Retrieval																															
6.1 Categorization						○																○									
6.2 Generation						◎	○				❖																				
7. Episodic Memory Encoding																															
7.1 Verbal		○	○			○																		○							
7.2 Object		○	○			○	◎	◎			❖													◎	◎	●	◎	❖			
7.3 Spatial															◎	○								◎	○	◎					●
8. Episodic Memory Retrieval																															
8.1 Verbal	◎	●	●			◎					❖				❖																
8.2 Nonverbal	◎	●					●																	●		◎	◎				
8.3 Retrieval success	●													❖	○																
8.4 Retrieval effort					○							❐				◎															◎
8.5 Retrieval mode	●	◎	●				○				❖																				
8.6 Context memory (> item)								◎							◎	●															
9. Priming (deactivations)																															
9.1 Perceptual																										◎					
9.2 Conceptual			○		○	○																									
10. Procedural Memory																															
10.1 Conditioning																															◎
10.2 Skill Learning - Motor (> unpracticed)								○		○					◎	◎													◎		
10.3 Skill Learning - Nonmotor															◎	●											◎	◎			●

Proportion of contrasts in subsection: ● = 40-50%; ● = 51-70%; ● = 71-100%. Activations were displayed as lateralized if there were at least twice as many activations in one hemisphere than in the other (bilateral activations counted for both hemispheres).

example, Kelley et al., 1998). Thus, a full account of the data may require an integration of the verbal/pictorial view and the HERA view.

As for distinctions between different prefrontal areas, a theory that accounts for part of the data is Petrides' model of frontal function (Owen, 1997; Petrides, 1994; Petrides, 1995). According to this model, ventrolateral regions (areas 45 and 47) are involved in "selecting, comparing, or deciding on information held in short-term and long-term memory", whereas mid-dorsal regions (areas 9 and 46) are involved "when several pieces of information in working memory need to be monitored and manipulated" (Petrides, 1995 p. 89). Consistent with this model, area 45/47 activations were found even in simple language tasks, while activations in areas 9/46 were associated with working memory and episodic encoding and retrieval. However, areas 9/46 were also activated during sustained attention tasks, which do not involve the simultaneous consideration of several pieces of information.

Differences across tasks can also be found in frontopolar (area 10), opercular (area 44), and dorsal (areas 6 and 8) prefrontal regions. As indicated by Table 11, frontopolar activations were typical for episodic memory

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retrieval and problem-solving tasks. In the case of episodic retrieval, they were found for both retrieval success and retrieval mode, suggesting they are probably not related to performance level or task difficulty. Memory researchers have suggested that area 10 is involved in maintaining the mental set of episodic retrieval (for example, Nyberg et al., 1995; Düzel et al., 1999), but this idea does not account for its involvement in problem-solving tasks. Not surprisingly, activations in left area 44, which corresponds to Broca's area, were commonly found for reading, verbal working memory and semantic generation. The role of right area 44 is unknown, but it was engaged by nonverbal episodic retrieval tasks. Area 6 seems to play a role in spatial processing (orientation of attention, space/motion perception and imagery), working memory, and motor-skill learning. Midline area 6 activations correspond to SMA and were common for silent reading tasks. Area 8 was involved in problem-solving tasks, possibly reflecting eye movements.

Cingulate Regions

Cingulate regions can be roughly classified as anterior (for example, areas 32 and 24), central (areas 23 and 31), and posterior (posterior area 31, retrosplenial). Central cingulate activations are rare and will not be discussed here. Posterior cingulate activations were consistently found during successful episodic memory retrieval, and were discussed in that section together with other posterior midline activations (medial parietal, cuneus, precuneus). Anterior cingulate activations occurred primarily in area 32 and were consistently found for S-R compatibility (Stroop), working memory, semantic generation, and episodic memory tasks.

There are three main views of the anterior cingulate function: initiation, inhibitory, and motor. According to the initiation view, the anterior cingulate cortex is involved in "attention to action", that is, in attentional processes required to initiate behavior (for example, Posner, Petersen, Fox, & Raichle, 1988). This idea is consistent with evidence that damage to this region sometimes produces *akinetic mutism*, that is, an almost complete lack of spontaneous motor or verbal behavior (for example, Nemeth, Hegedus, & Molnar, 1988). This idea is consistent with the involvement of this region in demanding cognitive tasks, such as working memory and episodic retrieval.

The inhibitory view postulates that the anterior cingulate is involved in suppressing inappropriate responses (for example, George et al., 1994; for the related response competition view, see Carter et al., 1998). This idea accounts very well not only for its involvement in the Stroop task, in which prepotent responses must be inhibited, but also in working memory, in which interference from previous trials must be controlled. Obviously, initiation and inhibition views are not incompatible: the anterior cingulate cortex could both initiate appropriate responses and suppress inappropriate ones (Paus, Petrides, Evans, & Meyer, 1993). Moreover, these views share the idea that the anterior cingulate cortex plays an "active" role in cognition by controlling the operations of other regions, including the prefrontal cortex.

In contrast, the motor view conceptualizes the anterior cingulate as a more "passive" structure: it basically receives cognitive/motor "commands" from various regions (for example, prefrontal cortex), and "funnels" them to the appropriate motor system (Paus et al., 1993). This view assumes that different anterior cingulate regions are engaged, depending on whether responses are ocular, manual, or verbal. For example, due to its close connections to the auditory cortex, area 32 is assumed to play a role in vocalization and speech (Paus et al., 1993). This idea accounts well for activations during tasks involving verbal materials, such as Stroop, semantic generation, and verbal episodic retrieval tasks. In contrast, this notion would not readily accommodate activations during spatial-working memory and problem-solving tasks. Given the heterogeneous structure and complex connectivity of the anterior cingulate (for a review see, Devinsky, Morrell, & Vogt, 1995), it is possible that different functions, including initiation, inhibition, and motor, are engaged, depending on the particular sub-region involved and its interactions with the rest of the brain.

Parietal Regions

Parietal regions were consistently activated during tasks involving attention, spatial perception and imagery, working memory, spatial episodic encoding, episodic retrieval, and skill learning. Medial parietal activations were frequently found during episodic memory retrieval, as discussed in that section. This section is concerned with lateral parietal activations. In general, these activations have been related either to spatial perception/attention or to verbal working memory storage. According to the first interpretation, parietal regions are part of a dorsal occipito-parietal pathway involved in spatial perception (Ungerleider & Mishkin, 1982), and/or part of a "posterior attention system" involved in disengaging spatial attention (Posner & Petersen, 1990). These spatial views account very well for parietal activations during spatial tasks of perception, imagery, and episodic encoding, as well as for those during skill-learning tasks, which, typically, involve an important spatial component. In contrast, the spatial interpretation has difficulties accommodating parietal activations during nonspatial processes, such as naming colors in the Stroop task, holding letters in working memory, and retrieving words from long-term memory.

According to the working memory interpretation, parietal regions are involved in the storage of verbal information in working memory (Awh et al., 1996; for a review, see D'Esposito, in press; Jonides et al., 1998a; Paulesu et al., 1993). This idea is consistent with evidence that left posterior parietal lesions can impair verbal short-term memory (Saffran & Martin, 1975; Warrington, Logue, & Pratt, 1971). In general, the verbal storage interpretation can account very well for left parietal activations during verbal tasks, but cannot readily accommodate those during tasks involving nonverbalizable materials. A full account of the role of parietal regions may require the integration of both the perception/attention and working memory interpretations.

Temporal Regions

The temporal lobes can be subdivided into four broad regions: lateral (insula, 42, 22, 21, and 20), medial (areas 28, 34–36, and hippocampal regions), posterior (area 37), and polar (area 38). Posterior activations in area 37 are considered in the next section, together with occipital activations. Temporal pole activations in area 38 were very scarce, and, hence, they were never consistent enough to be included in Table 11. The reason for the dearth of area 38 activations is probably just technical. Due to its extreme ventral location (for example, $Z=-30$), this region is often beyond the brain volume covered by the scans. Moreover, due to susceptibility artifacts, fMRI data for this region is characterized by a very low signal-to-noise ratio. The shortage of functional neuroimaging data on area 38 is unfortunate because this area is likely to have a very important role in cognition, for example, by linking frontal-lobe and temporal-lobe regions (Markowitsch, 1995).

As indicated by Table 11, lateral temporal activations were consistently found for language and semantic memory retrieval and were mostly left-lateralized. Spoken word-recognition tasks usually yielded bilateral activations, possibly reflecting the auditory component of these tasks. The involvement of left superior and middle temporal gyrus (areas 22 and 21) in language operations is consistent with research on aphasic patients (for a review, see Benson, 1988). Since area 21 was also consistently activated during semantic retrieval tasks—not only for verbal but also for nonverbal materials—it is possible that this area reflects semantic, rather than linguistic, operations. This idea is supported by the involvement of this region in object perception.

Medial-temporal lobe activations were repeatedly found for episodic memory encoding and nonverbal episodic memory retrieval. The involvement of medial-temporal regions in episodic memory is consistent with lesion data (Scoville & Milner, 1957; for a review see Squire & Zola-Morgan, 1991). Two recent metaanalyses investigated the location of encoding- and retrieval-related activations within medial-temporal regions. Lepage, Habib, & Tulving (1998) focused on PET data and concluded that encoding-related activations are more common in anterior hippocampal regions, whereas retrieval-related activations are more prevalent in posterior hippocampal regions, a pattern described as the hippocampal encoding/retrieval (HIPER) model. Schacter and Wagner (1999) included additional PET studies, as well as fMRI data, and concluded that in fMRI studies encoding-related activations are typically found in posterior medial-temporal regions, whereas in PET studies they are found in both anterior and posterior medial-temporal regions, but are more common in anterior regions. Anterior medial-temporal activations could have been missed by fMRI studies due to susceptibility artifacts, but Schacter and Wagner argue that these artifacts tend to affect temporal pole regions, but not hippocampal regions. In contrast, they suggest that the inconsistency between PET and fMRI data could reflect differences in behavioral paradigms. For example, conditions involving relational processing tended to yield more anterior medial-temporal activations than those that do not (Schacter & Wagner, 1999). In sum, it is still unclear whether episodic memory activations in medial-temporal regions are organized according to an encoding/retrieval gradient or according to a dimension that cuts across encoding and retrieval, such as relational vs. non-relational processing. Relational processing has been proposed as the main role of the hippocampus, but other functions, such as novelty (for example, Tulving et al., 1996) and spatial/navigation (for example, O'Keefe & Nadel, 1978; Maguire et al., 1998a), have been suggested as well (for a discussion of hippocampus theories, see Cohen et al., 1999).

Occipito-Temporal Regions

The engagement of temporo-occipital regions (areas 37, 19, 18, and 17) in cognitive tasks seems to be of two kinds: activations associated with perceiving and manipulating visuospatial information, and deactivations associated with perceptual priming. Visual processing along the ventral pathway is assumed to be organized hierarchically, with early image analyses engaging areas close to the primary visual cortex and higher-order object recognition processes involving more anterior areas (for a review, see Ungerleider, 1995). Consistent with this idea, activations in areas 18 and 19 occurred for most visuospatial tasks, whereas activations in area 37 were associated with object processing. For example, area 37 activation was found when subjects perceived objects and faces, maintained images of objects in working memory, and intentionally encoded objects. Perception-related occipital activations are enhanced by visual attention (for example, Corbetta et al., 1990) and, hence, they can be expected during visual-attentional tasks, as

well as during demanding visual-skill learning tasks (for example, mirror reading).

Priming-related occipital *de*activations are assumed to reflect a facilitation in neural computations when the same information is processed again (for a review, see Schacter & Buckner, 1998). According to this view, the involvement of occipital regions in perception and priming would reflect the same mechanism; priming-related deactivations could be described as weaker perception-related activations. In sum, most activations in occipito-temporal regions are accommodated by a visual processing view: they occur during the processing of visual information coming from eyes (perception) or from memory (imagery), and weaken when the same information is repeatedly processed (priming).

Subcortical Regions

We reviewed activations in basal ganglia, the thalamus, and the cerebellum. Although basal ganglia activations were common during motor-skill learning, only the cerebellum was consistently activated in several different processes and, hence, we focus on this last region. Evolutionary, anatomical, neuropsychological, and functional neuroimaging evidence indicates that the cerebellum plays an important role in cognition (for a review, see Leiner, Leiner, & Dow, 1995), but the nature of this role is controversial. The cognitive role of the cerebellum has been related as motor preparation (Thach, Goodkin, & Keating, 1992), sensory acquisition (Bower, 1997), timing (Ivry, 1997), and attention/anticipation (Akshoomoff, Courchesne, & Towsend, 1997). Each of these views can easily account for some cerebellar activations in Table 11, but not for all of them. For example, the motor-preparation view accounts well for activations during tasks involving motor responses, such as word production and conditioning, while the sensory-acquisition view can easily accommodate activations during perceptual tasks, such as smelling. The timing view provides a good account for activations during tasks involving relations between successive events, such as conditioning and skill learning, while the attention/anticipation view explains well activations during attention and problem solving. As in the case of the other structures, it is a challenge for future research to unify these different views or to anatomically dissociate these different functions.

CONCLUDING REMARKS

In this review, we have looked for consistent activation patterns from functional brain imaging studies of different cognitive functions (attention, perception, imagery, language, and memory). Within each examined domain, consistent activation patterns were observed across studies. These activation patterns were based on data that were significant at the level of single studies, according to statistical tests that take into account individual variability (typical for analyses of PET data), or were observed for a majority of individual subjects (typical for analyses of fMRI data). Hence, the consistent between-study activation patterns can be expected to hold true at an individual subject level as well. Admittedly, in keeping with the goal of the review, we have emphasized consistencies, rather than focussing on discrepancies from the general patterns. Surely, variability exists at the individual level, as well as at the group level, and, no doubt, much can be learned from focussing on variability, rather than consistency (for a related discussion, see Schreurs et al., in press). At the same time, for theoretical as well as methodological reasons, it is important to know that results generalize beyond the individual study level. By showing that specific brain regions are consistently activated by specific cognitive challenges, the outcome of the present review points to a fairly high degree of generalizability.

A second important outcome of the review, given that it cuts across cognitive domains, is that it allowed an analysis of the occurrence of specific regional activations across these different domains. Indeed, in the Review by Region section, it was shown that some brain regions are activated by several different cognitive demands. Such an outcome may shed light on the functional role of brain regions. It is quite likely that different tasks, classified as belonging to different cognitive domains, share processing components and, hence, activate overlapping regions. Careful task analysis may support the conclusion that the common activation reflects the involvement of lower-order computations. Conversely, it is also conceivable that such an analysis suggests broadening of the functional conceptualization of an area.

In the context of regional activations observed across cognitive domains, it must also be noted that activation of one and the same region in two distinct domains need not imply that the region has the same functional role in both cases. Rather, it has been argued that the functional role of a brain region depends, at least in part, on its *neural context* (McIntosh, in press). Neural context refers to the pattern of interactions among brain regions. If a specific region is commonly activated by distinct cognitive challenges, it is still possible that the inter-regional interactions among this region and other regions differ depending on type of cognitive challenge. The notion of neural context suggests that the regions' functional role is determined by these connectivity patterns. More generally, this perspective suggests that brain regions are not committed to specific functions, but may play a role in a variety of cognitive and other operations. The data presented in here help to identify network components for various cognitive operations.

In sum, there are three different approaches to interpreting functional neuroimaging data: local, global, and network. The *local approach* involves relating the role of each brain region to a process within the cognitive

domain of interest (for example, memory). The Review by Process section contributed to this approach by identifying consistently engaged regions for each cognitive domain. The *global approach* involves associating the role of each brain region to a general process, which is tapped by various tasks in different domains. The Review by Region section contributed to this approach by identifying regions consistently activated across domains. Finally, the *network approach* involves interpreting the role of each region in relation to other regions engaged by the same task, that is, within the context of a network. Although network analyses were not reported, the present review contributed to this perspective by identifying some of the key components of the networks underlying different cognitive processes. These three approaches are equally important and should complement each other. Although the local approach has been the dominant so far, we believe that the future of functional neuroimaging requires the harmonic development of all three approaches.

Acknowledgments

We thank Robert Bradka for assistance, as well as Randy Buckner, Russell Poldrack, Endel Tulving, and Anthony Wagner for comments.

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Note

1. Klingberg and Roland (1998) reported right prefrontal activation during encoding of abstract figures and sounds. While this observation is in keeping with other findings of right prefrontal activation during encoding of nonverbal material, it must be noted that the task they defined as an encoding task involved a mixture of encoding and retrieval processes. Also, the stimuli that was presented in their encoding task was not novel, but had been exposed to the subjects at least one time prior to scanning. For these reasons, it is unclear whether the observed right prefrontal activation was related to encoding or retrieval processes.

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