Neuroanatomic Overlap of Working Memory and Spatial Attention Networks: A Functional MRI Comparison within Subjects

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Frontal and posterior parietal activations have been reported in numerous studies of working memory and visuospatial attention. To directly compare the brain regions engaged by these two cognitive functions, the same set of subjects consecutively participated in tasks of working memory and spatial attention while undergoing functional MRI (fMRI). The working memory task required the subject to maintain an on-line representation of foveally displayed letters against a background of distracters. The spatial attention task required the subject to shift visual attention covertly in response to a centrally presented directional cue. The spatial attention task had no working memory requirement, and the working memory task had no covert spatial attention requirement. Subjects' ability to maintain central fixation was confirmed outside the MRI scanner using infrared oculography. According to cognitive conjunction analysis, the set of activations common to both tasks included the intraparietal sulcus, ventral precentral sulcus, supplementary motor area, frontal eye fields, thalamus, cerebellum, left temporal neocortex, and right insula. Double-subtraction analyses yielded additional activations attributable to verbal working memory in premotor cortex, left inferior prefrontal cortex, right inferior parietal lobule, precuneus, and right cerebellum. Additional activations attributable to covert spatial attention included the occipitotemporal junction and extrastriate cortex. The use of two different tasks in the same set of subjects allowed us to provide an unequivocal demonstration that the neural networks subserving spatial attention and working memory intersect at several frontoparietal sites. These findings support the view that major cognitive domains are represented by partially overlapping large-scale neural networks. The presence of this overlap also suggests that spatial attention and working memory share common cognitive features related to the dynamic shifting of attentional resources. © 1999 Academic Press

Major cognitive domains are hypothesized to be selectively distributed across large-scale neural networks in the brain (Mesulam, 1981, 1990, 1998). One important question regarding the neural representation of cognition is whether individual network components are dedicated to discrete functions or are shared, thus leading to a partial overlap of networks. This question has been difficult to address since few studies give tasks in multiple domains to the same set of subjects. However, with the advent of modern functional neuroimaging tools, it is now possible to probe this question by directly comparing brain activation patterns within subjects across cognitive tasks. We followed this approach in the present study to examine the specificity of the modular organization of large-scale neural networks subserving working memory and spatial attention functions in the human brain.

Our investigation targeted working memory and spatial attention because prior neuroimaging studies have found similar frontal and parietal activations across groups of subjects engaged in each of these two distinct domains (see McCarthy, 1995; Cabeza and Nyberg, 1997; Smith and Jonides, 1997; Corbetta, 1998; d'Esposito *et al.,* 1998). However, the experimental paradigms developed to study working memory and spatial attention have typically conflated the two processes, which has led to difficulties in interpreting the convergence of their anatomical representation. For example, in a prototypical working memory experiment (Sternberg, 1966), several objects or letters are presented in a spatial configuration, and the subjects' task is to indicate whether a probe item given after a delay was a member of the original item set (object/verbal working memory) or in the same spatial location as a member of the original item set (spatial working memory). This type of working memory task inherently involves shifts of spatial attention as the subject encodes the object features and/or spatial locations of the memoranda. A prototypical spatial attention task involves the display of a brief priming cue that signals the subjects to direct their attention to a portion of the visual field in which a subsequent target appears with a given probability (Posner, 1980). Subjects take longer

to detect the target when it fails to appear in the cued direction, which is taken as evidence that attention was covertly shifted by the priming cue (the "invalidity effect"). This type of spatial attention task inherently involves iconic/working memory during the time interval that separates the cue from the target.

The goal of the present study was to directly compare the functional anatomy of working memory and spatial attention using experimental paradigms that minimize overlapping cognitive features. We conducted verbal working memory and covert spatial attention tasks on the same set of subjects in a counterbalanced order while they underwent echoplanar functional magnetic resonance imaging (fMRI). Both cognitive subtraction and cognitive conjunction analyses were applied to the data set to uncover activations that were distinct and common, respectively, to the two cognitive domains (Price and Friston, 1997). The working memory task was a variant of the 2-back letter paradigm described by Gevins and Cutillo (1993). This task contains a high working memory load, as it requires continuous on-line monitoring of the two most recently presented letters, but it does not require shifts of spatial attention, as the items consist of single letters presented foveally.

The spatial attention task was a variant of a paradigm described by Posner (1980) in which attentional shifts are triggered by centrally presented directional arrows. Our adaptation of the central expectancy task contains a high spatial attention load, as it requires subjects to covertly shift their attention laterally by 7.5°, but it contains no working memory load, since the arrow prime remains on the screen during the stimulus onset asynchrony (SOA) interval (Gitelman *et al.,* 1999). To rule out eye movement confounds, subjects' ability to maintain central fixation during both tasks was confirmed outside the MRI scanner using infrared oculography. This feature of the study is important because the frontoparietal brain regions engaged during working memory and spatial attention shifts overlap with those involved in the control of saccades (Anderson *et al.,* 1994; Pierrot-Deseiligny *et al.,* 1995; Courtney *et al.,* 1997; Corbetta, 1998; Gitelman *et al.,* 1998; Nobre *et al.,* 1998).

MATERIALS AND METHODS

Subjects

Eleven right-handed adult volunteers (seven male, four female) provided informed consent and were paid to participate in the study. The mean age [±SD] of the subjects was 32.6 ± 7.3 years. The mean [±SD] score on the modified Edinburgh handedness scale (Ransil and Schacter, 1994) was +74.1 ± 31.3. None of the subjects had a history of psychiatric or neurological illness, and none were medicated at the time of testing. Eye movement data from three subjects were not obtained dur-

ing the working memory practice session, and reaction time data from one subject was incomplete during the spatial attention practice session. The experiment was approved by the Institutional Review Board at Northwestern University.

Verbal Working Memory: Task Design

The verbal working memory task was a blocked-design sequence containing two conditions, "2-back" (active) and "XG" (control), which alternated four times over the course of the behavioral run (Fig. 1a). Within each 60.9-s block, subjects first saw a header indicating the name of the block condition (e.g., "2-back"), followed by 19 single consonants presented foveally (subtending 1° of visual angle). The header duration was 1.4 s, and the letters were presented for 0.5 s, separated by a 2.5-s blank interstimulus interval. The stimuli were arranged so that subjects had to make four or five button-press responses within each block. During the active task, subjects responded if the letter they saw matched the one that was presented two letters back in the sequence (6-s retention interval). Each active block contained one 1-back or 3-back foil. During the control task, subjects made a response if they saw the letter "X" or "G" (0-back letter detection). Subjects were told to respond irrespective of whether the letters were in upper or lower case. Both the active and control conditions required that subjects hold two items in short-term memory, but in the active condition, the items were continuously updated. The number of motor responses, central fixation requirement, and visual display were matched across the active and control conditions. Two letter sequences were constructed and counterbalanced across subjects. The order of the starting block (active vs control) was also counterbalanced across subjects. A shorter version of the script was created to practice subjects while their eye movements were monitored in the cognitive psychophysics laboratory prior to the MRI session. The practice session was repeated if subjects did not achieve a minimum accuracy score of 75% correct.

Covert Spatial Attention: Task Design

The covert spatial attention task was a blocked-design sequence consisting of an active spatial shift condition and a go, no-go control condition, which alternated eight times over the course of the behavioral run (Fig. 1b). Each block lasted for 30.45 s. The total task duration was equivalent for the working memory and spatial attention tasks. The visual display for both conditions consisted of a central diamond ("◇") subtending 1° of visual angle, and two peripheral side boxes containing either an "x" or a "+" target stimulus (subtending 1.5° of visual angle at an eccentricity of 7.5°). In the active task, half of the central diamond was
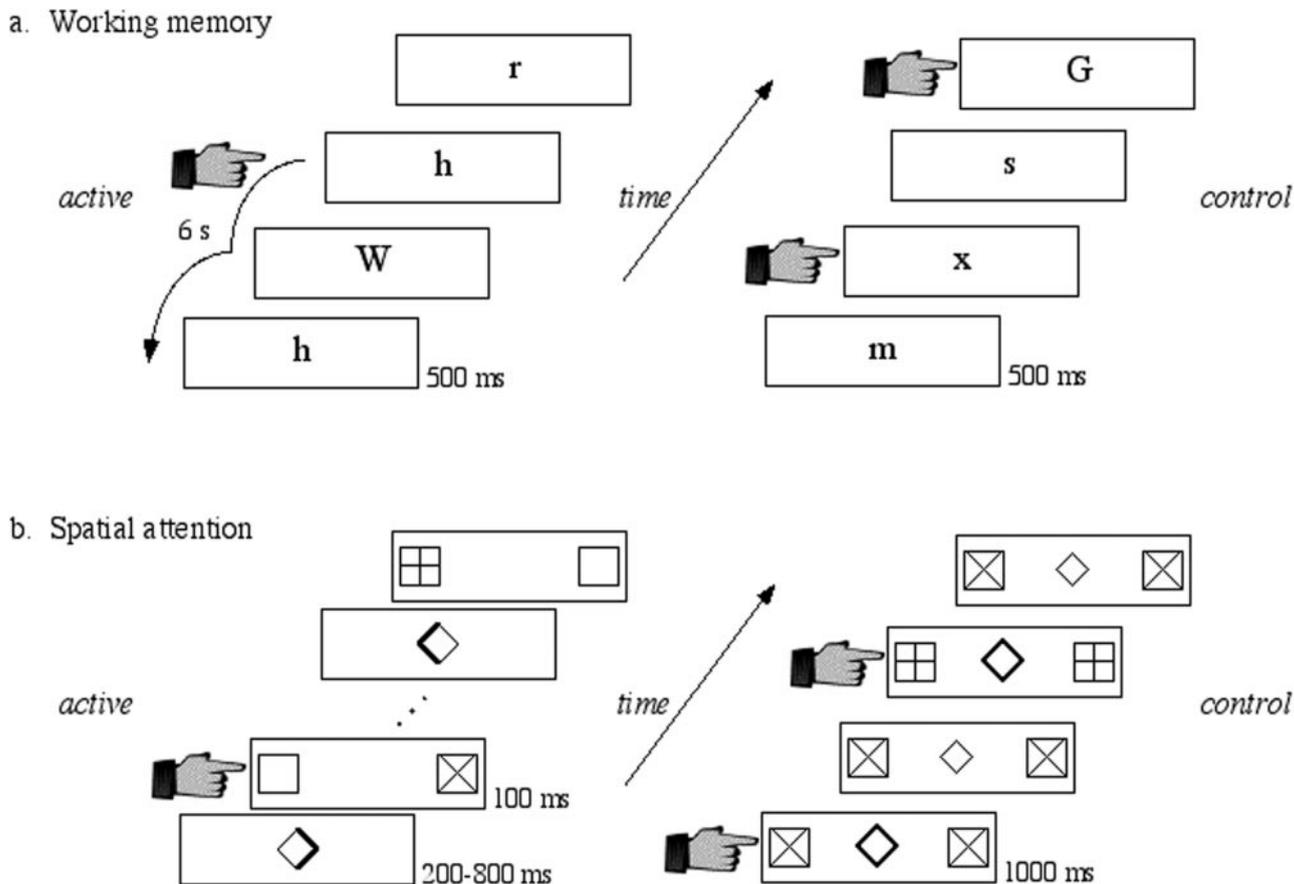
FIG. 1. Graphical representation of the (a) verbal working memory and (b) covert spatial attention tasks. Hand icons indicate the stimuli to which subjects responded.

bolded to form an arrow that pointed to either the left or right hemifield. After a 200, 400, or 800-ms SOA, a target flashed in one of the side boxes for 100 ms. Overt eye movement strategies were minimized by the brief duration of the target. The arrow remained illuminated throughout the SOA to eliminate the iconic/working memory component to the task (Gitelman *et al.,* 1999). Subjects made a button-press response only if the target was an "x." Targets appeared on the cued side for 80% of the trials (validly cued trials) and on the uncued side for 20% of the trials (invalidly cued trials). Each block consisted of 15 2-s duration trials, half of which contained "x" targets. Subjects were instructed that the cue would signal the target side most of the time, and that they were to fixate in the center and discriminate the targets without making eye movements. Behaviorally, covert spatial shifts were measured as the difference in reaction time latencies to detect targets on validly cued vs invalidly cued trials (the "invalidity effect").

In the go, no-go control condition, the central diamond and both side boxes were displayed once every 2 s for a 1-s duration. The side boxes contained either "x" or

"+" stimuli bilaterally. On half of the trials, the central diamond was bolded. Subjects were instructed to respond only if the central diamond was bold, irrespective of the target stimuli that appeared in the side boxes. Thus, the control condition did not require covert shifts of attention for successful performance, but it was equated to the active condition in terms of the visual display, motor execution, central fixation requirement, and the conditional (no-go) aspect of responding. A version of the script was created to practice subjects while their eye movements were monitored in the cognitive psychophysics laboratory prior to the MRI session.

Eye Movement Recording

Eye movements were recorded using an infrared monitoring system (ISCAN, Burlington, MA) in the cognitive psychophysics laboratory during the practice training session. Stimuli were presented using Superlab software (Cedrus Corp., Phoenix, AZ) running on a Macintosh PowerPC computer (Apple, Cupertino, CA). Subjects viewed the stimuli at a distance of 40 cm from

a 21″ CRT. Eye movements were examined by displaying a map of eye position over time throughout the active and control stimulation periods using our in-house ILAB software (D.R.G.) running under the MATLAB environment (Mathworks Inc., Sherborn, MA). The number of pixels covered at horizontal eccentricities >2° away from fixation were counted to determine the proportion of time subjects engaged in overt lateral eye movements.

MRI Scanning

Imaging was conducted on a 1.5T Siemens Vision scanner (Erlangen, Germany) equipped with whole-body gradients and a quadrature head coil. Visual stimuli were backprojected into the scanner room using a Proxima active matrix LCD projector (San Diego, CA) and a custom-designed, nonmagnetic rear projection screen. The screen was placed approximately 170 cm from a nonmagnetic mirror located directly above the subjects' eyes. Subjects used a hand-held button to respond to the stimuli in the magnet. Subjects had their head immobilized with a vacuum pillow (Vac-Fix, Bionix, Toledo, OH) and restraint calipers built into the head coil. These devices help to minimize head movement to ≤1 mm in any direction during each functional run (Parrish *et al.,* 1998). A vitamin E capsule was taped to the subject's left temporal region to mark laterality for image processing.

T1-weighted anatomical scout images were initially prescribed for localization of the anterior commissure–posterior commissure (AC–PC) axis. Single-shot echo-planar functional MRI scans were acquired in 32 slices parallel to the AC–PC line (TR/TE = 4350/40 ms, flip angle = 90°, FOV = 220 mm, matrix = 64 × 64, slice thickness = 4 mm, in-plane resolution = 3.44 × 3.44 mm). Four dummy scans were taken at the beginning of each functional run to decrease the effect of nonsteady state longitudinal magnetization. T1-weighted anatomical images were acquired using a 3-D FLASH sequence (TR/TE = 15 ms/6 ms, flip angle = 20°, FOV = 220 mm, matrix = 256 × 256, slice thickness = 1 mm). Both the working memory and spatial attention tasks consisted of 112 scans, divided evenly between the active and control conditions.

Data Analysis

FMRI data were analyzed on a Hewlett-Packard (Cupertino, CA) UNIX workstation running under the MATLAB software environment using SPM96 (Wellcome Department of Cognitive Neurology, London, UK). Application Visualization System software (Advanced Visual Systems, Waltham, MA) was used for scalp editing, volume rendering, and graphical display. All functional images were realigned to the image taken proximate to the anatomical study using affine transformation routines built into SPM96 (Friston *et al.,* 1995a). The realigned scans were coregistered to the subject's anatomic dataset and then normalized to SPM96's template image, which conforms to the space defined by the ICBM/NIH P-20 project and closely approximates Talairach and Tournoux's stereotaxic atlas (Talairach and Tournoux, 1988). The functional data were smoothed with an isotropic Gaussian kernel (FWHM = 7 mm) prior to statistical analysis.

Statistical contrasts were set up using the general linear model implemented in SPM96 to calculate voxel-wise signal differences between the active and baseline conditions. Contrasts were evaluated at the individual subject and group-average levels. Single subtraction contrasts were first computed on the working memory and spatial attention tasks separately, relative to their respective baselines. To analyze the brain regions activated in common across tasks, a conjunction analysis was performed on the single subtraction maps according to the method described by Price and Friston (1997). The conjunction analysis reveals the brain regions that were equally active in both tasks relative to their own baselines, the statistical equivalent of a main effect of task condition in the absence of interaction effects (e.g., active versus baseline). To analyze the brain regions selectively engaged during verbal working memory (equivalent to a task × condition interaction), the spatial attention map was subtracted from the working memory map and masked by the main effect of working memory versus baseline (mask threshold $P < 0.05$). The masking procedure ensures that negative activations from the spatial attention map were discounted from the double-subtraction analysis. An analogous interaction and masking procedure was conducted to analyze the brain regions selectively engaged during the spatial attention task. SPM$|Z|$ maps were thresholded at a nominal $P < 0.001$ ($Z = 3.09$) and a cluster size = 3 and were superimposed onto the normalized anatomical brain space. Voxel values were considered statistically significant if they had a corrected voxel-wise or cluster-wise $P < 0.05$ with reference to the whole brain as implemented in SPM96 (Friston *et al.,* 1995a,b,c; Worsley and Friston, 1995). A template of the regions containing significant voxels in the group average was then compared against the individual SPM$|Z|$ maps at the same threshold to evaluate the consistency of the activation sites across subjects.

RESULTS

Behavioral Results

Practice session. The accuracy, reaction time, and eye movement data for the working memory and spatial attention tasks are summarized in Table 1. For the spatial attention task, the longer reaction times for the

TABLE 1
Mean (±S.E.M.) Behavioral Results

Session	Task	Condition	Reaction time (ms)	Accuracy	False alarms	Center gaze
Practice	Working memory	Active	352 ± 31	85 ± 6%	0.5 ± 0.2	95 ± 2.2%
		Control	334 ± 49	86 ± 5%	0.0 ± 0.0	99 ± 0.3%
	Spatial attention	Active	443 ± 18 Valid, 486 ± 25 Invalid	97 ± 1%	1.8 ± 0.3	97 ± 0.9%
		Control	556 ± 34	94 ± 5%	2.2 ± 1.7	96 ± 1.7%
fMRI	Working memory	Active	396 ± 20	97 ± 2%	0.9 ± 0.4	n/a
		Control	359 ± 36	99 ± 1%	0.2 ± 0.1	n/a
	Spatial attention	Active	463 ± 19 Valid, 532 ± 34 Invalid	94 ± 2%	1.2 ± 0.6	n/a
		Control	501 ± 23	94 ± 4%	0.4 ± 0.2	n/a

Note. Reaction times for the spatial attention task are broken down by validity.

invalidly versus validly cued trials were statistically significant ($t(9) = 5.18$, $P < 0.001$), indicating that subjects covertly shifted their attention during the task. The oculographic analysis showed that subjects maintained fixation 97% of the time, on average, during both tasks. Given that our subjects are highly trained, this result suggests that the MRI activation patterns are not related to eye movements. Examples of the eye movement patterns from a representative subject are illustrated in Fig. 2.

fMRI session. The accuracy and reaction time data for both tasks are summarized in Table 1. For the spatial attention task, the longer reaction times for the invalidly versus validly cued trials were statistically significant ($t(10) = 4.06$, $P < 0.002$), indicating that subjects covertly shifted their attention during the task. Separate 2 × 2 repeated measures ANOVAs on the reaction times and adjusted accuracy scores (hits minus false alarms) did not yield any significant task × condition interactions ($P > 0.05$). Therefore, differential fMRI activation patterns across tasks are not likely due to relative differences in the level of difficulty. Subjects performed both tasks near ceiling levels of accuracy (Table 1).

fMRI Results

Dorsal and medial views of the brain regions engaged in the working memory and spatial attention tasks relative to their respective baselines are illustrated in Fig. 3a. The activation patterns are then broken down into those that were common across the two tasks (conjunction analysis, Fig. 3b) and those that were selective for each task (subtraction analysis, Figs. 3c and 3d).

Conjunction analysis: Brain regions engaged equally in verbal working memory and spatial attention shifts. The set of brain activations engaged equally in verbal working memory and spatial attention shifts is listed in Table 2 and illustrated in Fig. 3b. These included activations in the intraparietal sulcus (BA 7/40), ventral precentral sulcus (BA 6), supplementary motor area (BA 6), frontal eye fields (BA 6), thalamus, cerebellum (bilateral cerebellar cortex and vermis), left temporal neocortex (middle temporal gyrus BA 37/21 and temporal pole BA 38), and right insula. Although the supplementary motor area activation extended into the dorsocaudal anterior cingulate gyrus (BA 32) in both tasks (see Fig. 3a), this portion of the activation did not
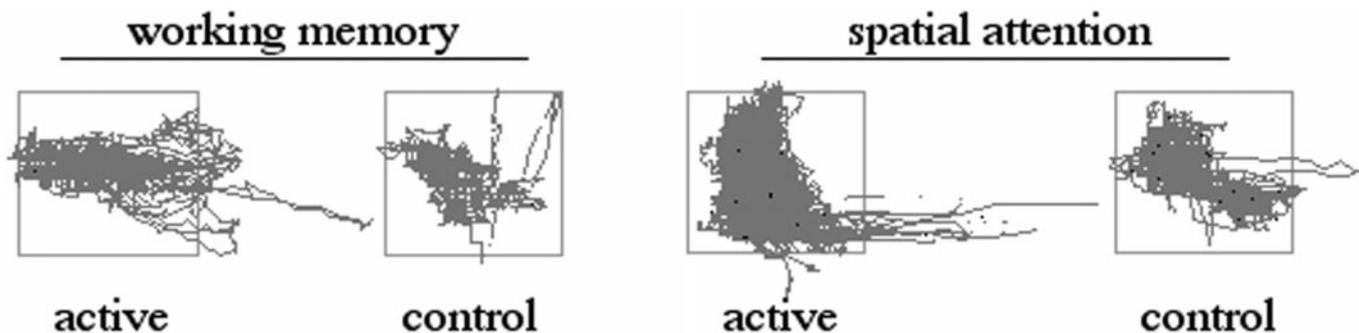

FIG. 2. Eye movement patterns from a representative subject. Boxes demarcate a ±2° window around central fixation.
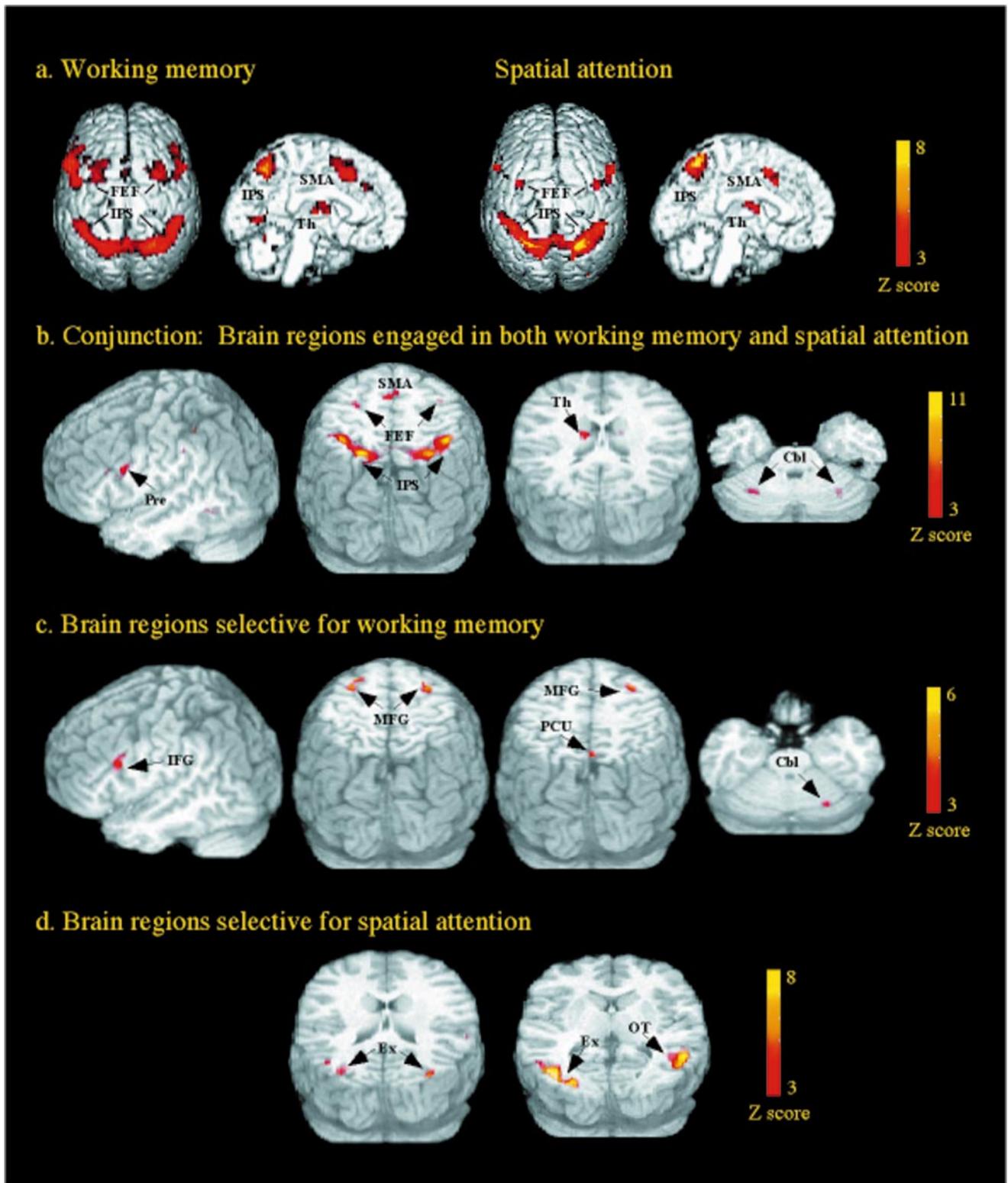
FIG. 3. Functional MRI results. (a) Dorsal and medial views of the activation patterns in the working memory and spatial attention tasks. (b) Conjunction analysis: brain regions equally engaged in verbal working memory and covert spatial attention. (c) Subtraction analysis: brain regions selectively engaged in verbal working memory. (d) Subtraction analysis: brain regions selectively engaged in covert spatial attention. Abbreviations: Cbl, cerebellum; Ex, extrastriate cortex; FEF, frontal eye field; IFG, inferior frontal gyrus; IPS, intraparietal sulcus; MFG, middle frontal gyrus; OT, occipitotemporal junction; Pre, precentral sulcus; PCU, precuneus; SMA, supplementary motor area; Th, thalamus.

TABLE 2

Brain Regions Engaged during Both Verbal Working Memory and Covert Spatial Attention Tasks

Task	Brain region	BA	Side	Subject prevalence	Z value	Stereotactic coordinates		
						x	y	z
Conjunction	Intraparietal sulcus	7/40	right	11/11 (100%)	11.16	24	−60	60
					9.61	45	−45	51
			left	11/11 (100%)	9.84	−21	−60	48
					6.37	−42	−48	45
	Precentral sulcus	6	right	9/11 (82%)	8.61	54	12	30
			left	10/11 (91%)	7.32	−54	15	27
					6.81	−42	3	33
	Supplementary motor area	6	midline	11/11 (100%)	7.54	0	12	45
	Frontal eye fields	6	left	10/11 (91%)	7.27	−27	−3	45
			right	9/11 (82%)	5.92	36	6	48
					5.79	51	3	42
	Thalamus		left	5/11 (45%)	7.16	−12	−9	15
					6.16	−9	−3	9
			right	4/11 (36%)	5.88	15	−3	15
	Cerebellum		left	10/11 (91%)	6.37	−30	−66	−39
					4.87	−39	−57	−39
			right	11/11 (100%)	6.03	48	−57	−33
					5.79	36	−66	−36
					5.05	36	−75	−36
			vermis	7/11 (64%)	5.09	3	−51	−24
	Middle temporal gyrus	21/37	left	6/11 (55%)	5.47	−48	−63	−6
					5.41	−45	−54	−12
					4.96	−60	−42	6
					4.84	−54	−57	−6
	Insula		right	6/11 (55%)	5.09	42	21	−6
	Temporal pole	38	left	4/11 (36%)	5.02	−54	15	−6

survive the threshold imposed on the conjunction analysis. The extensive degree of overlap is noteworthy, given that the tasks were designed to tap into two distinct cognitive domains.

Subtraction analysis: Brain regions selectively engaged in verbal working memory. The set of brain regions that were relatively more engaged by the verbal working memory task is listed in Table 3 and illustrated in Fig. 3c. These included the premotor cortex bilaterally (just rostrodorsal to the frontal eye fields BA 6), dorsal tip of the left inferior frontal gyrus (Broca's area BA 44), precuneus, right inferior parietal lobule BA 40, and right cerebellar cortex.

Subtraction analysis: Brain regions selectively engaged in spatial attention shifts. The set of brain regions that were relatively more engaged by the spatial attention task is listed in Table 3 and illustrated in Fig. 3d. These included bilateral activation in the occipitotemporal junction and extrastriate cortex BA 18/19.

DISCUSSION

Attempts to integrate findings from the functional imaging literature on working memory and spatial attention have relied on meta-analytic techniques to uncover similarities in the activation patterns across tasks and subject groups (McCarthy, 1995; Cabeza and Nyberg, 1997; Smith and Jonides, 1997; Corbetta, 1998; d'Esposito *et al.,* 1998). However, meta-analytic techniques suffer from several limitations when applied to imaging results, including nonequivalent baseline contrasts (Demonét *et al.,* 1996), intrasubject variability in behavioral performance and blood oxygenation-level detection, and hardware-specific differences in signal acquisition across research centers. More recent experimental designs that emphasize parametric variations within subjects are typically restricted to subcomponents of a single cognitive domain (e.g., Cohen *et al.,* 1997). In contrast, the present study directly compared activation patterns across cognitive domains within the same set of subjects. Our experiments were also designed explicitly to isolate working memory and spatial attention functions by minimizing their potential interactions. The results from our study reveal a coextensive but anatomically distributed set of brain regions that participate in cognitive operations subserving both working memory and visuospatial attention. These functions intersect at several frontoparietal sites, including the ventral precentral sulcus, supplementary motor area, frontal eye fields, and intraparietal sulcus.

Brain Regions Selectively Engaged during Verbal Working Memory and Covert Spatial Attention Tasks

Task	Brain region	BA	Side	Subject prevalence	Z value	Stereotactic coordinates		
						x	y	z
Working memory	Middle frontal gyrus	6	Right	8/11 (73%)	5.76	33	15	48
					5.32	30	6	54
			Left	7/11 (64%)	5.37	−27	9	54
					4.97	−21	18	54
	Inferior frontal gyrus	44	Left	7/11 (64%)	4.96	−39	15	27
	Precuneus	7	Midline	4/11 (36%)	4.93	3	−63	45
	Inferior parietal lobule	40	Right	8/11 (73%)	4.16	45	−60	33
	Cerebellar cortex		Right	6/11 (55%)	4.02	39	−60	−45
Spatial attention	Occipitotemporal junction		Left	10/11 (91%)	7.58	−48	−72	3
			Right	8/11 (73%)	7.29	57	−54	3
					6.72	54	−66	3
	Extrastriate cortex	18/19	Left	7/11 (64%)	7.35	−30	−87	0
					7.34	−42	−78	3
					4.80	−24	−63	−3
			Right	6/11 (55%)	6.28	33	−84	12
					5.08	42	−81	0

Additional sites of conjoint activation included portions of the thalamus, cerebellum, left temporal neocortex, and right insula. Therefore, it appears that two distinct tasks, one based on verbal working memory and the other on covert spatial attention, display overlapping areas of activation which are particularly conspicuous in dorsal parietal and dorsal frontal cortices.

Such a macroscopic level of neuroanatomic overlap is compatible with three alternative hypotheses. First, the overlap may reflect interdigitating neuronal populations with distinct functions whose borders cannot be resolved at 1.5 T. Given our acquisition parameters and smoothing kernel, the effective smoothness of the maps (FWHM) as calculated within SPM96 was 9.2 × 8.9 × 8.5 mm, which is at least one order of magnitude larger than the resolution of individual cortical columns (Mountcastle, 1997). Second, the overlap may reflect multitasking functions of neurons within the same anatomical region. Third, the overlap may reflect the operation of a subordinate neural computation common to both cognitive domains.

We propose that the neuroanatomic overlap observed in the present study relates to the shifting of an attentional focus, irrespective of whether the shifts occur over space, time, or cognitive domains. The working memory task required subjects to continuously shift their attentional focus from an external to an internal frame of reference in order to compare the identity of letters in working memory buffers to those presented externally. By contrast, the covert cuing task required subjects to shift their attentional focus from one point in space to another in order to discriminate the features of the impending target. Covert shifts of attention activate this common set of brain regions regardless of whether the shifts are endogenously or exogenously driven (Kim *et al.,* 1999). Furthermore, Coull and Nobre (1998) found that shifting attention across space or time elicited activation along a coextensive frontoparietal network similar to that observed in the present study. Finally, recent studies have shown that switching between external and internal visual frames of reference recruits neural processing along the dorsal processing stream (Lumer *et al.,* 1998; Marois *et al.,* 1998).

Although the cingulate gyrus is hypothesized to play an important role in spatial attention and working memory, we did not observe activation in this region, except for the portion of the anterior cingulate located immediately rostroventral to the supplementary motor area (Fig. 3a; see also Gitelman *et al.,* 1999). Failure to engage other regions of the cingulate gyrus may relate in part to the high level of baseline control employed in the subtraction analysis of the present study. For example, we previously reported activation of the anterior and posterior cingulate during a similar covert attention task when compared against a low-level passive viewing baseline (Kim *et al.,* 1999). During *n*-back working memory tasks, cingulate activation is also sensitive to variations in levels of baseline control, with more activation observed at lower levels of control (Smith *et al.,* 1996; Carlson *et al.,* 1998). Higher-level baseline tasks are likely to engage additional executive functions mediated by the cingulate gyrus that are shared with cognitive processes related to working memory and spatial attention.

Brain Regions Engaged in Verbal Working Memory

The double-subtraction analysis yielded additional activations specialized for verbal working memory in the premotor cortex, precuneus, left inferior prefrontal cortex, right inferior parietal lobule, and right cerebellum. These results are consistent with previous verbal working memory studies (reviewed in Smith and Jonides, 1997; Jonides *et al.,* 1998). However, our results suggest that the portion of the parietal lobe that is selectively engaged by verbal working memory is more anatomically restricted than previously reported using positron emission tomography (Jonides *et al.,* 1998). Interestingly, we have also found activation along the intraparietal sulcus and precuneus during an auditory sentence comprehension task that involved more extensive linguistic working memory (Thompson *et al.,* 1998). During this task, the intraparietal sulcus activation was relatively left-sided and confined to a more medial sector adjacent to the precuneus.

The activation in the premotor cortex during the working memory task is immediately rostrodorsal to the frontal eye fields in a region Courtney *et al.* (1998) described as being specialized for spatial working memory. Our finding of relatively greater activation in this region during verbal (nonspatial) working memory than during covert spatial attention qualifies the interpretation regarding the neural processing supported by this brain region. Specifically, this region does not appear to code covert attentional shifts, or else we would have found relatively greater activation in this region during our spatial attention task.

Brain Regions Engaged in Covert Spatial Attention

Activations specialized for covert spatial attention included the occipitotemporal junction and extrastriate cortex. These results are consistent with neuroimaging studies of covert shifts/selective attention (Corbetta *et al.,* 1993; Corbetta, 1998; Kastner *et al.,* 1998; Gitelman *et al.,* 1999; Kim *et al.,* 1999), and neuropsychological studies documenting contralesional neglect following damage to the occipitotemporal junction (Rafal and Robertson, 1995; Hasselbach and Butter, 1997). One alternative explanation of the activation seen in the frontal eye fields and intraparietal sulcus during the spatial attention task is that subjects were attempting to inhibit eye movements during the covert shift condition. However, the activation in these regions was equivalent to that seen in the verbal working memory task, where none of the stimuli appeared at lateral eccentricities. We have previously reported that activation in the frontal eye fields and intraparietal sulcus was greater during covert and overt attentional shifts than during saccadic eye movements (Gitelman *et al.,* 1998; Nobre *et al.,* 1998). Our results support a growing body of evidence that these brain regions are involved in attentional processes beyond the mere control of saccades.

Conclusions

The foregoing analysis illustrates that the neural networks subserving working memory and spatial attention intersect in sites located along the dorsal processing stream, although they are not completely overlapping. The level of intersection suggests that the same neural populations within the frontal and posterior parietal cortices may be recruited into different neural networks based on the demands of the task. The degree of overlap observed using these methods cautions against generalizations regarding the modularity of specific brain regions activated by any single cognitive task. A given brain region may be recruited for different purposes under different task-relevant conditions, or it may be activated by more than one task because of a more global computation (such as attentional switching) that is common to all. The relationship of specific neuronal populations to different functional networks is relatively unexplored in primates, but other vertebrate and invertebrate preparations have demonstrated network switching via neurohormonal regulation. In the lamprey, for example, switches in the affiliations of neurons for motoric actions related to swimming, burrowing, and crawling depend on serotonin activation of calcium-activated potassium currents within the same neuronal pool (Ayers *et al.,* 1983; see discussion in Mesulam, 1998). Whether task-dependent neuromodulation of network affiliations occurs in the human brain remains an open possibility. This type of intersection in the large-scale networks controlling discrete cognitive domains may represent a more flexible mental organization that affords the organism a wider range of sensorimotor interactions with stimuli in the environment.

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