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Attention Response Functions: Characterizing Brain Areas Using fMRI Activation during Parametric Variations of Attentional Load

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Summary

We derived *attention response functions* for different cortical areas by plotting neural activity (measured by fMRI) as a function of attentional load in a visual tracking task. In many parietal and frontal cortical areas, activation increased with load over the entire range of loads tested, suggesting that these areas are directly involved in attentional processes. However, in other areas (FEF and parietal area 7), strong activation was observed even at the lowest attentional load (compared to a passive baseline using identical stimuli), but little or no additional activation was seen with increasing load. These latter areas appear to play a different role, perhaps supporting task-relevant functions that do not vary with load, such as the suppression of eye movements.

Introduction

In this paper, we identify the cortical regions involved in the attention demanding components of a visual tracking task. In a previous study, we found that this task (when compared to passive viewing of the same stimuli) produced bilateral activation in the parietal lobe, frontal lobe, and the MT complex (Culham et al., 1998). Although some of these activations were likely due to the attentional demands of the task, other activations may have instead reflected task support functions unrelated to attention demands (eye movement control, response contingencies, maintenance of task set, etc.). To determine the functional role of attentionally modulated cortical regions, here we examined *attention response functions* in numerous brain areas. That is, in addition to comparing an attention-demanding task to a nonattentional control task using traditional subtraction logic, we further examined how activation in different regions was affected by additional increases in attentional load. Such parametric designs, developed in cognitive psychology (Sternberg, 1969) to avoid the pitfalls of subtraction logic (Donders, 1969), have proven useful in neuroimaging to investigate the function of different brain regions (Cohen et al., 1997; Rees et al., 1997; Schlaug et al., 1996). Parametric designs may be especially important in understanding general purpose cognitive mechanisms like attention which are particularly susceptible to the choice of control task (typically passive viewing), the subject's strategy during the control task (e.g., vegetating versus attending to other things), and the subject's state of mind during the scan (e.g., drowsiness versus alertness).

A major goal of the present study was to use a parametric load manipulation to disentangle the functions of the cortical regions that have been shown to be activated by both attention and eye movements (Corbetta, 1998; Culham et al., 1998). While attention and eye movements are certainly tightly coupled, the nature of their relationship is highly debated (Klein, 1980; Klein and Pontefract, 1994; Shepherd et al., 1986). In the most extreme view, covert attention can only be accomplished by preparing a saccade to the attended location (Rizzolatti et al., 1994; Snyder et al., 1997). However, it seems unlikely that the eye movement system could be the sole mechanism underlying covert attention given differences in the capacity of the two systems: attention can be used to track multiple targets (Pylyshyn and Storm, 1988), whereas, the eyes can only foveate one target at a time. A more moderate view would suggest that covert attention is accompanied by a prepared (but not necessarily executed) saccade and that attention and eye movements share common but not identical neural substrates.

Here we use parametric load variations to take advantage of the different capacities of attention and eye movement systems. Specifically, we hypothesized that areas directly involved in attentional processing would show steadily increasing activation as attentional load increased; whereas, regions with activation due to eye movement factors would be activated by attention to one target but would show no further response gains as more targets were added. We were particularly interested in the activation function of the frontal eye fields (FEF), which are reliably activated by attentional tasks (Corbetta et al., 1998) but which have been postulated by some to serve purely oculomotor functions, remaining largely unaffected by cognitive factors (Paus, 1996).

To examine the effects of attentional load, we selected an "attentive tracking" task (Pylyshyn and Storm, 1988) in which subjects maintain their attention on individual targets of interest as they move through space. This paradigm is particularly well suited to parametric variations in attentional load because subjects can accurately track up to five targets without rapidly shifting or spreading a single attentional focus (Intriligator, 1997; Pylyshyn, 1994; Pylyshyn and Storm, 1988). We presented subjects with a display of nine randomly moving items and assigned a variable number of targets—between zero and five—to be tracked with attention (See http://defiant.ssc.uwo.ca/Jody_web/share/attentive_tracking_demo.htm for a web demonstration). Subjects report that the task seems increasingly difficult as more

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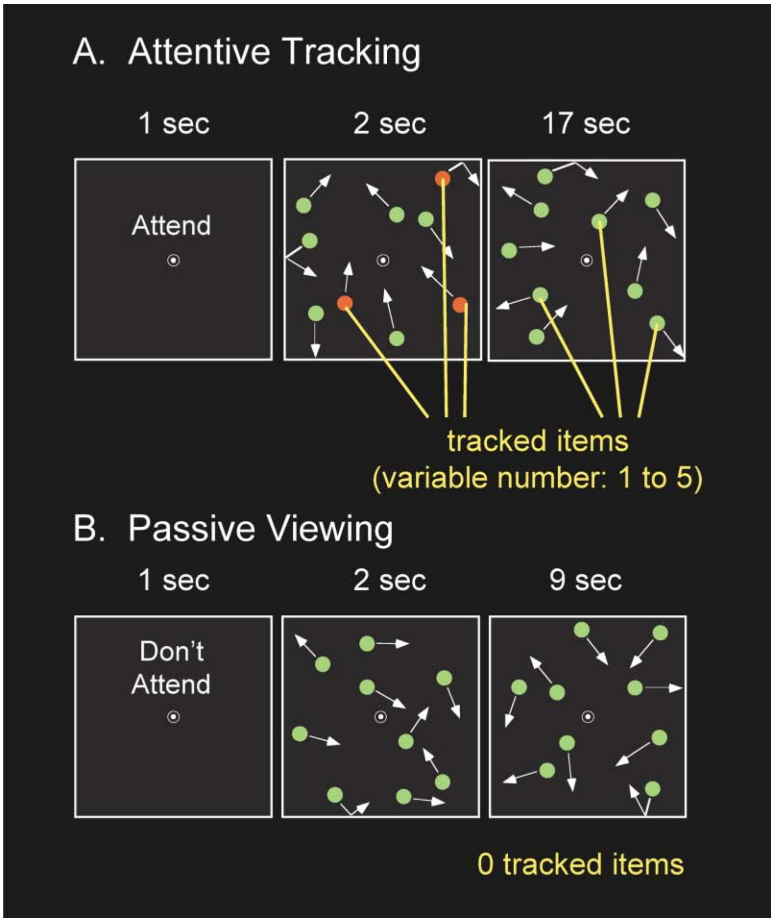

Figure 1. Experimental Stimuli and fMRI Paradigm

(A) The stimulus consisted of nine bouncing balls moving in random trajectories. In attentive tracking conditions, a variable number of balls (indicated here by yellow lines not present in the actual display) were cued in red for 2 sec. Subjects tracked the cued balls with attention (no eye movements) for the remainder of the epoch. (B) In passive viewing conditions, no balls changed color and subjects simply watched the display, fixating on the central bullseye, with no attentional effort.

items are added, with one item being trivial and five being very effortful. The increase in difficulty with added targets is confirmed by performance data showing declines with increasing load, as observed in prior studies (Pylyshyn and Storm, 1988; Yantis, 1992; Intriligator and Cavanagh, 2001) and in our subjects here (see Experimental Procedures). Furthermore, the task cannot be performed when attention is directed elsewhere (Treisman, 1993). Subjects were instructed to maintain central fixation on a bullseye target to equate eye movements in the passive viewing and all tracking conditions, as verified in a previous study in which eye movements were monitored in the magnet (Culham et al., 1998). The present results have been partially reported in abstract form (Culham et al., 1997).

Results

Functional MRI images were collected for eight subjects who performed an attentive tracking task over a range of difficulty levels while retinal stimulation was held constant. The display consisted of nine green "bouncing balls" in Brownian-like motion. Subjects mentally tracked a subset of the balls which had briefly been cued in red but then became indistinguishable from the untracked balls except for their history (Figure 1A). The number of tracked items varied from one to five in the attentive tracking conditions. A passive viewing or "attend zero balls" condition was also included in which no balls were cued and subjects made no tracking efforts (Figure 1B). Visual stimulation was constant across all conditions (except for the brief cueing period, excluded from the fMRI analyses) and only the task and its difficulty varied. In all conditions, subjects were instructed to use only their attention, not their eyes, to track the moving targets. Subjects were prescreened with an eye movement monitor to ensure that they could indeed perform the task accurately while maintaining fixation. Although performance was quite high in all conditions, there was a drop in accuracy with additional items, indicative of the increasing difficulty of the task as more items were to be tracked (See Experimental Procedures and Figure 4D).

Data were analyzed by addressing the relative contributions of two components: one component that identified task-related activation and one that identified further activation which increased with attentional load during the task. The logic for choosing these two components can be seen by considering hypothetical attention response functions, which plot neural activity over a range of attentional loads. A priori, we predicted that "task-only" regions that are not directly involved in attentional performance would show a task effect with no further increase in activation as task difficulty increases (Figure 2A); whereas, regions that are directly involved in attentional performance would show "load-dependent" activity that increases with attentional demands, being greater at high loads than low loads (Figure 2B). Of course, actual brain areas may show an "intermediate"

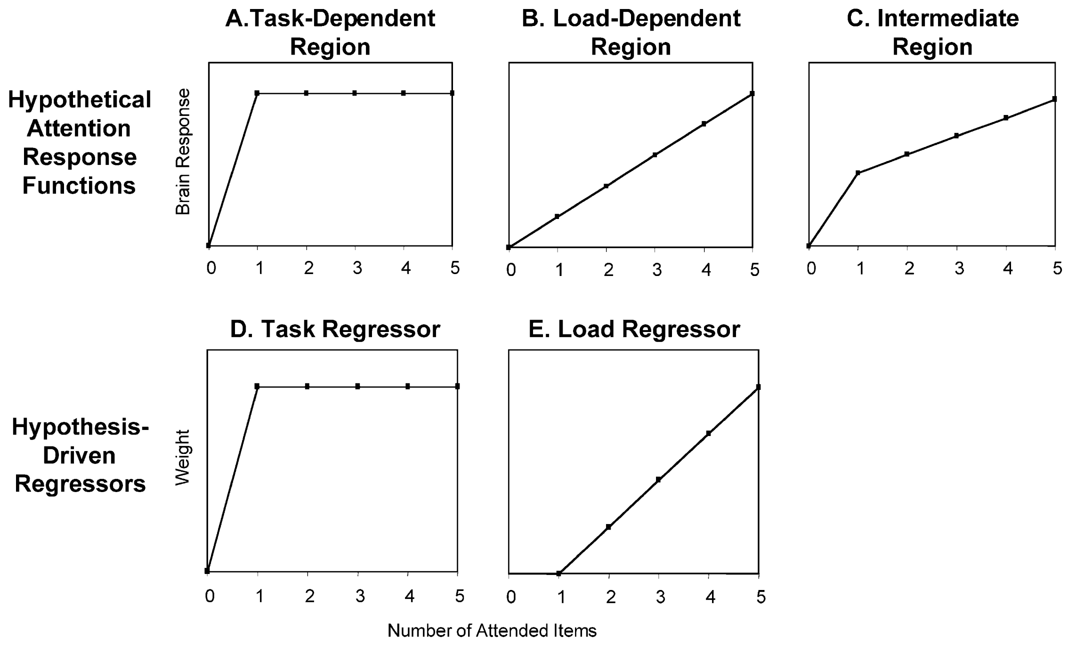

Figure 2. Hypothetical Data and Analysis Methods

Theoretical models suggest a variety of possible activation patterns: (A) brain regions that are only task dependent and would respond more strongly to the attention conditions than passive viewing, but with no additional gains in activity as attentional load increased; (B) regions that are load dependent and would show monotonic gains across the entire range of attentional load; and (C) regions that are both task and load dependent to varying degrees. We used two regressors: (D) the task component identified regions that had higher activation during all attentive tracking conditions (1–5 items) compared to passive viewing (0 items), regardless of any difficulty differences within the attentive tracking conditions; and (E) the load component identified regions that showed increased activation with increasing attentional load (1–5 items), regardless of the difference between the attentive tracking conditions and passive viewing. The two regressors were each modified for the specific sequence of conditions in the fMRI experiments and then convolved with the hemodynamic response function to more accurately model the fMRI response.

response, with an initial step in activation representing both basic task demands and attention demands for the easiest version of the task; subsequent steps in activation then represent only the increasing attention demands (Figure 2C). The goal of our analysis is to determine if either the first step (task effect) or the subsequent slope (load effect) is significant.

To accomplish this goal, we developed two contrasts directly motivated by the theoretical components we wish to evaluate. The *task* component compared all cases in which the subject performed an attentive tracking task (for one to five items), equally weighted, to the baseline in which the subject passively viewed the same stimuli (Figure 2D). The *load* component estimated the degree to which activation increased with task load for 1 to 5 items, excluding the passive viewing baseline (Figure 2E). As our results will show, the parametric load component is a better measure than the task component for a host of reasons. Nonetheless, it was important to include a non-task condition to demonstrate the different values of the two components, and passive viewing was the most appropriate choice for a baseline in these experiments. Had we used an alternative attentional task as a baseline (such as a foveal attention task; e.g., Somers et al., 1999), the strength of the task component would have depended completely on the difficulty of that task and the degree to which it tapped the same or different mechanisms (Wojciulik and Kanwisher, 1999). A passive viewing baseline can be criticized in that subjects' uncontrolled cognition could weaken the activation of task-sensitive areas (leading to Type II errors). However, it is highly unlikely that subjects were engaging in any systematic activity during passive viewing and the problem of Type II errors is only exacerbated by the use of an alternate attentional task.

Note that our approach differs from the more traditional use of standard polynomial regressors: linear, quadratic, cubic, etc. (e.g., Buchel et al., 1996). Applied to our task, the logic for this analysis is that task-only regions in which activity saturates with load will have significant higher order (especially quadratic) components. This approach is appealing; however, quadratic functions may not necessarily discriminate task-only functions from intermediate ones. Furthermore, combinations of linear and quadratic regressors may not match the hypothesized functions as well as one would like. Thus, we feel our contrasts are more appropriate for evaluating the hypotheses considered here while still providing the benefits of independent regressors.

Group-averaged data were analyzed in Talairach space (Talairach and Tournoux, 1988). Group analysis (rather than single subject analysis) was used to show response patterns across the brain without the necessity of selecting regions of interest (ROIs) which can be biased by the statistics used to select them and may inadvertently collapse across adjacent areas with differing attention response functions. Analyses conducted on single subjects were consistent with the group results and provided greater confidence regarding anatomical localization relative to sulci. However, given the number of subjects

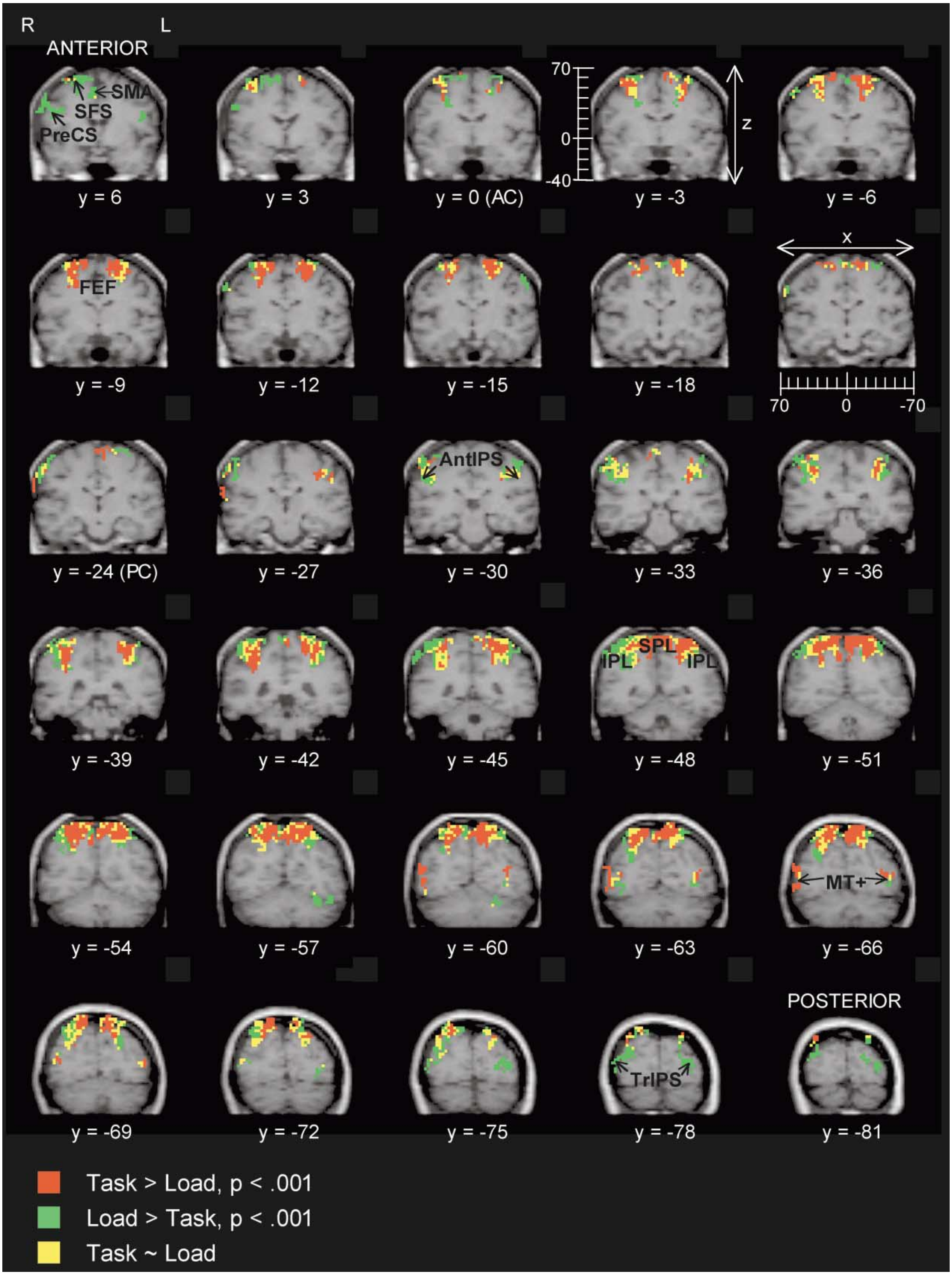

Figure 3. Relative Contributions of Task-Only and Load-Dependent Factors to group fMRI Activation

Average group data for eight subjects converted into Talairach space and superimposed on resampled coronal slices for one subject (not necessarily representative of group anatomy), depicted only for slices in which activation was observed. Multiple regression was used to extract the variance accounted for by the task and load components. Any voxel that was significantly correlated with either regressor (r >

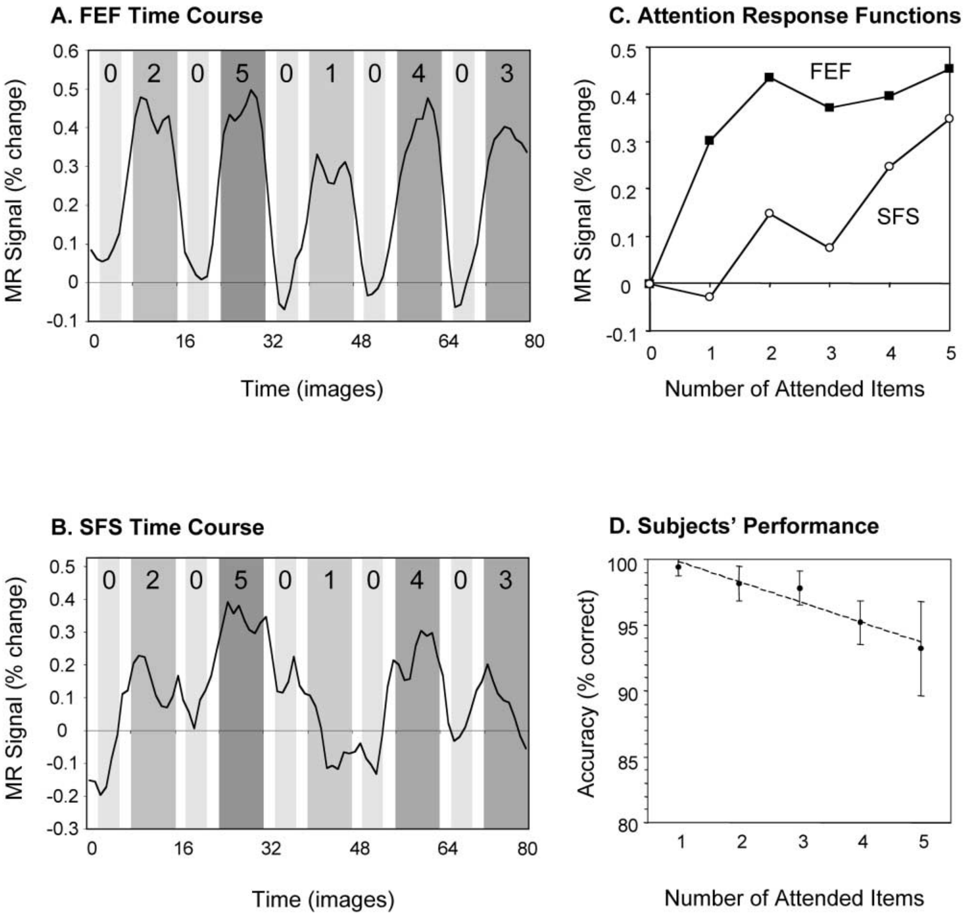

Figure 4. Sample Time Courses and Attention Response Functions from Two Areas along with Subjects' Performance Data

(A) Group time course extracted from voxels in the frontal eye fields (taken from slices with y = 26–28, Figure 3). (B) Group time course extracted from more regions in the superior frontal sulcus anterior to the frontal eye fields (taken from slices with y = 20–22, Figure 3). (C) Attention response functions in FEF and SFS. (D) Subjects' performance data, showing that although subjects could perform highly accurate tracking (>90% correct) even for the most difficult condition of tracking 5 balls, performance declined with increasing load, consistent with the subjective increase in difficulty. The straight line indicates the best linear fit (r = −.968).

and areas, only group data are shown here. Regressors for the task and load components were adapted to the averaged time course and convolved with the hemodynamic response function.

To depict the data, we selected all voxels in which either the task or load component was significant and then evaluated whether the relative contributions of the two components differed significantly. As shown in Figure 3, task-only areas, in which the task component was significantly greater than the load component, were rendered in red and included the frontal eye fields (FEF), superior parietal lobule (SPL) and adjacent precuneus on the medial side, and most of the MT+ complex (although a few voxels were load dependent). Load-dependent regions, in which the load component was significantly greater than the task component, were rendered in green and included the superior frontal sulcus (SFS), precentral sulcus (PreCS), supplementary motor area (SMA), anterior intraparietal sulcus (AntIPS) at its junction with the postcentral sulcus, the more posterior intraparietal sulcus (IPS) and inferior parietal lobule (IPL), and a region at the junction of the transverse occipital sulcus and the IPS (TrIPS). Mixed voxels, in which task and load components did not differ significantly, were rendered in yellow and occurred in transition zones, possibly due to the blurring introduced by Talairach averaging. Area MT+ and TrIPS overlapped with activated regions identified using a motion localizer run (motion—stationary gratings) in the same session.

For comparison with the typical analysis using polyno-

.36, $p < .001$ uncorrected) was color coded by the relative contributions from the two regressors. Voxels in which the task regressor contributed significantly more than the load regressor ($p < .001$ uncorrected) are red, voxels in which the load regressor contributed significantly more than the task regressor ($p < .001$ uncorrected) are green, and voxels with no significant difference between the two regressors are yellow. Talairach coordinates are specified by the coronal slice number (y = anterior-posterior), a scale for the vertical axis (z = superior-inferior, shown in the y = −3 slice), and a scale for the lateral axis (x = right-left, shown in the y = −21 slice). The left side of the image corresponds to the right side of the brain (radiologic convention).

mial regressors (linear, quadratic, etc.), we also generated a map showing regions with a significant quadratic component. A map of the linear component produced significant voxels for virtually all the same regions found by the two-component model. This is not surprising given that both task and load regressors include a linear component (albeit estimated over different parts of the data). Regions with a significant task but not load component also had a significant quadratic component (FEF, SPL, MT+). However, the quadratic component was only significant at much lower probability values ($p < .05$ versus $p < .001$), likely due to the fact that it provided only a suboptimal approximation of the expected attention response function. Furthermore, at these lower probability values, other regions appeared which were not observed in any other comparisons. We also extracted time courses and attention response functions for regions of significance. These functions verified the expected pattern of results, as shown in Figure 4 for the FEF (a task-only area) and the SFS (a load-dependent area).

Discussion

We have shown that the expected network of visual, parietal, and frontal regions is activated by an attention-demanding visual task. However, we are now able to point to two types of processes underlying this activation and the regions supporting each: (1) task-specific functions unaffected by increasing demands on attention, and (2) of most interest, attention-specific functions. FEF and the superior parietal lobule were particularly notable as areas mediating task-specific functions. In these regions, activation was enhanced by the requirement to attend and to perform the task but showed little dependence on whether the attentional demands were low or high. In contrast, in the IPS for example, the activation increased with load, providing evidence for attention-based processes that are increasingly engaged as the number of targets to be tracked increases.

Regions with Task-Only Attention Response Functions (FEF, SPL)

Task-only regions show a significant gain in activation between active and passive conditions, but with no additional gain as more items are added, suggesting that they are not driven by attention per se, but rather by basic support functions of the task. One likely task support component that could account for such functions is the planning of a saccade which must then be suppressed. There are two possible hypotheses for how eye movement planning could generate task-only functions.

In the first hypothesis, observers may be continuously planning only a single saccade to the optimal location during attentive tracking. For example, in the case of a single tracked ball, the ball itself would be the optimal saccade target. In the case of multiple balls, one might expect a saccade to be planned either to the most salient or confusable of the tracked balls or to the centroid of the group. In this case, one and only one saccade would be in preparation at any one time during the attentive tracking conditions, regardless of the number of tracked items; whereas, there would be little reason to prepare any saccades in the passive viewing condition. FEF activation could arise not only from the covert preparation of the saccade, but also the act of suppressing it to maintain fixation in all conditions. Indeed, there is converging evidence from numerous paradigms to suggest that the FEF are crucial to the suppression of eye movements. Physiologically, a subpopulation of neurons in the FEF are active during fixation but suppressed during saccades (Bizzi, 1968; Bruce and Goldberg, 1985; Segraves and Goldberg, 1987). Consequently, stimulation of the FEF in monkeys (Burman and Bruce, 1997) and in humans (Priori et al., 1993) can inhibit or delay saccades. Moreover, neurological patients with frontal lobe lesions that include the FEF have difficulty suppressing saccades (Guitton et al., 1985). In neuroimaging, one PET study (Petit et al., 1995) observed greater FEF activation during fixation on an imaginary point compared to gazing straight ahead in darkness, two conditions which had equivalent visual stimulation and a comparable number of small eye movements. Furthermore, fixation-related activation may be exaggerated under conditions that make it more difficult to maintain fixation, such as imagining saccades (Lang et al., 1994) or peripheral attention.

In the second hypothesis, the FEF could be involved in covert (i.e., attention) in addition to overt eye movements, as has been suggested (Goldberg and Bushnell, 1981), but they could be quite limited in the number of targets which can be selected. Surprisingly little research has been done to investigate the number of saccades that can be planned at one time, though some evidence suggests that two saccades can be simultaneously in preparation (Hallett and Lightstone, 1976; McPeek et al., 2000). Given that our data for the FEF show increases in signal up to two tracked items, it may be that FEF can encode up to two items; however, the absence of any increases for loads beyond two items suggests either that the capacity of FEF does not exceed this value or that this is not the mechanism by which attentive tracking is accomplished.

Neurons in the superior parietal lobule (including the precuneus on the medial side of the parietal lobe), corresponding to Brodmann's area 7a, may also be related to eye movement support functions or to limited capacity attentional mechanisms. Specifically, in monkeys, neurons in area 7a appear to code the direction of gaze during fixation (Andersen and Gnadt, 1989; Sakata et al., 1980). Although physiological studies of the medial parietal lobe are sparse, data from two groups (Caminiti et al., 1996; Olson et al., 1993, 1996) suggest that neurons in precuneate regions (medial area 7 and the adjacent posterior cingulate cortex) are involved in coding information about target location with respect to current eye position. Thus, comparable human areas may also be involved in forming a gaze-dependent spatial representation. Alternatively, area 7a may play a role in visual attention but with a low capacity limit below that taxed by this task.

Regardless of the specific explanation for task-only functions, our main point is that such regions are unlikely to be directly involved in multiple object tracking. We have thus demonstrated that parametric studies can be very useful in defining capacity limits, although it remains for future research to determine the basis of such limits.

Regions with Load-Dependent Attention Response Functions (IPS, SFS, PreCS, TrIPS)

In contrast to the task-only attention response functions, numerous regions showed a clear load-related increase. This suggests these areas play a direct role in task performance, due either to the added control of attentional mechanisms or the increased visual information selected by attention. By definition, attention and the selection of information are usually considered synonymous (Broadbent, 1958). While it may be possible to dissociate the source of attentional control from the sites at which it acts (Corbetta et al., 1991), these issues are not central here.

Load-dependent functions were observed in parietal and frontal cortex. One extensive focus of activation fell within the intraparietal sulcus, particularly the anterior end (which merges into postcentral sulcus, Ono et al., 1990) and the lateral aspects spreading into the inferior parietal lobule. These foci have been implicated in numerous past studies of attention and eye movements (Corbetta, 1998). The load-dependent response functions suggest that the IPS is directly involved in the cognitive components of the tracking task, particularly spatial attention and working memory. The SFS also showed a load-dependent response, in contrast to the more posterior FEF which did not. This is consistent with data suggesting a role for the SFS in working memory (Courtney et al., 1998). An additional area of the PreCS, inferior to the FEF (which lies at the junction of the precentral and superior frontal sulci; Paus, 1996), also showed a load-dependent function. This area is activated by visual working memory (Courtney et al., 1997), memory load (Cohen et al., 1997), and cognitive set switching (Konishi et al., 1998), suggesting a general role in cognitively demanding tasks. In the case of both the SFS/FEF and IPS/SPL, we see instances of two adjacent areas, which could both be activated by an all-or-none attention task, but which show different response properties across separate ranges of attentional load.

Although the response to attentive tracking is rather weak in motion area MT+ which was only weakly load dependent, more robust activity was seen in a second motion-selective zone in a region we have called "TrIPS." Retinotopic mapping studies have identified two visual areas in that vicinity, area V3A (Tootell et al., 1997) and V7 (Tootell et al., 1998). V3A shows a high degree of motion selectivity (Tootell et al., 1997) and indeed, our load-dependent activation overlapped with activation produced by a moving stimulus examined in a separate run. V7 is a more recently identified area that has not yet been well characterized. Although no retinotopic mapping was performed here, our previous study included comparisons of attentive tracking activation with retinotopic maps and noted activity in V7 (Culham et al., 1998). Both V3A and V7 show strong enhancements in local retinotopic regions when attention is directed to the corresponding area of the visual field (Tootell et al., 1998) and activation in the TrIPS area has been identified across a wide range of attentional tasks (Wojciulik and Kanwisher, 1999). Given the motion selectivity, rich representation of visual space, and high attentional selectivity of these areas, it makes sense that they may be recruited in the attentional tracking of moving targets in a load-dependent manner.

General Conclusions

In sum, we developed a parametric design that generated attention response functions from fMRI activations. These functions characterize the attention demanding functions of a task into two types: task functions, which support overall performance (such as eye movement suppression) but do not reflect the level of load, and load functions, which are directly involved in handling increased load. Our analysis of these task and load components showed that they can reveal regions of cortex that play different roles in task performance. In some cases, they suggested functional differences between adjacent regions of cortex which might not be observed with simple subtraction paradigms.

Experimental Procedures

Cognitive Task

Nine balls (1.5° diameter) moved randomly and independently within a dark gray square (20 × 20°) on a black background (see Figure 1). Balls bounced off the edge of the square and repelled one another, never colliding with or occluding one another. A bull's-eye appeared in the center of the display and repelled the balls to avoid drawing fixation away from the center. Subjects maintained fixation on this point throughout all epochs whether tracking one or several balls or just passively viewing.

The experimental paradigm consisted of attentive tracking epochs separated by passive viewing epochs during 5.5 min scans. Each epoch began with a brief (1 s) text label, "Attend" or "Don't Attend," respectively, followed by the presentation of the bouncing balls. In attentive tracking epochs, a subset of one to five balls turned red for 2 sec before reverting to green. Subjects continued to track the cued balls for the remaining 17 s even though the appearance of the tracked target balls was identical to the untracked distractor balls. During passive viewing epochs lasting 11 s, no balls were cued and subjects were instructed to passively watch the whole display without paying attention to any balls in particular.

To facilitate averaging within and between subjects while counterbalancing for order effects, two carefully selected orders were given to four subjects each: 0-2-0-5-0-1-0-4-0-3 and the reverse, 0-3-0-4-0-1-0-5-0-2, where 0 indicates passive viewing. Each order was repeated twice within a scan and five to eight scans were acquired per subject and averaged.

Subjects

The experiment was conducted on eight young (under 32), healthy, right-handed subjects with no optical, visual, or neurological deficits. Subjects were prescreened during a 45 min pretest session prior to the MRI session. This pretest included screening for fMRI suitability, an explanation of the task, practice trials given until the subject felt comfortable with the task (typically only 2–3 min), calibration of an eye movement monitor, and fifty test trials during which subjects' accuracy was measured along with their ability to maintain fixation during the task. In each test trial, a subset of balls turned red for 2 sec, then reverted to green while subjects continued tracking them for a 5 sec interval, after which a single ball turned white and the subject indicated whether the white ball was a tracked target or an untracked distractor. All subjects could perform the pilot task reasonably accurately ($\geq$90% correct where chance is 50%), even in the most difficult condition of tracking five balls. Raw behavioral data for three of eight subjects was lost during a lab transition and was re-collected after the scanning session with more trials (100–200) than had initially been obtained. Although group performance was good in all conditions, it declined nearly linearly from 99% correct for 1 item to 93% correct for five items, consistent with the increasing difficulty of the task, as shown in Figure 4D ($r = -.968$, $p < .005$, one-tailed). According to subjects' subjective reports, most errors occur when a tracked ball approaches an adjacent distractor and the subject becomes uncertain which ball is which. To keep the load constant throughout a given attentive tracking condition in the magnet, subjects were instructed to keep tracking the assigned number of balls throughout the epoch even when they were uncertain whether they were still tracking the original items. Even with this option to select replacements for lost targets, the task remains extremely challenging when tracking four or five targets (see the online demo at http://defiant.ssc.uwo.ca/Jody_web/share/attentive_tracking_demo.htm). One of the subjects (author J.C.) was highly experienced with the task; however, her pattern of task-dependent and load-dependent fMRI regions was consistent with the other naïve subjects.

In order to ensure that activation was not due to unwanted eye movements, all subjects were also tested with an eye movement monitor (Ober2, Permobil) prior to the scanning session over approximately 4 min while they performed the attentive tracking accuracy test described above. All subjects were able to track the balls with negligible pursuit or saccadic deviations. We chose not to record eye movements in the MRI scanner because the residual metallic parts present in our Ober2 system interfered with functional images, particularly in anterior areas (Sunaert et al., 1999) such as FEF that we wanted to include here. In a previous study using a surface coil to record posterior cortex, we measured eye movements during attentive tracking throughout the scanning session for three subjects (Culham et al., 1998). Two of the subjects who participated in the present experiment (J.C. and E.W.) had their eye movements monitored throughout multiple scans in the previous paper (Culham et al., 1998) and in two other peripheral attention experiments (Wojciulik and Kanwisher, 1999; Wojciulik et al., 1998). In all cases, both subjects demonstrated highly reliable fixation. We further investigated the pattern of eye movements in Subject J.C. outside of the magnet and found only a small variability in eye position (SD in eye position $<=1°$) which was not correlated with attentional load. Our two subjects with reliable fixation (J.C. and E.W.) here showed the same pattern of activations as the six other subjects, including FEF/SFS and SPL/IPL dissociations. Thus the pattern of results we observed cannot be accounted for by subjects' ability to maintain fixation accurately. Even assuming that some subjects did stray from the fixation instructions and make eye movements, a scenario we believe unlikely, this could not explain the difference in attentional response functions seen here as the eyes can only follow one target at a time, no matter how many are to be tracked. Given that the FEF show increasing activation as saccade frequency increases (Paus et al., 1995), our load-independent FEF response functions provide tangential evidence that no such differences occurred.

MRI Acquisition

Functional images were collected using a 1.5 Tesla General Electric Signa scanner with echo-planar imaging (Advanced NMR) at the Massachusetts General Hospital (MGH) Nuclear Magnetic Resonance (NMR) Center in Charlestown, MA. A headcoil was used for coverage of the whole head. Twelve near-axial slices (tilted by approximately 15° from the AC-PC line) covered occipital, parietal, and superior frontal cortex, with incomplete coverage of inferior frontal cortex, temporal cortex, and cerebellum.

Functional MRI acquisitions used asymmetric spin echo pulse sequences (time of repetition, $TR = 2$ s) to minimize the contribution of large blood vessels. Voxel sizes were 3.125 mm × 3.125 mm (inplane) × 7–8 mm (slice thickness).

Subjects lay on their backs within the bore of the magnet and viewed the stimuli comfortably via a mirror that reflected images displayed on a rear-projection screen (Da-lite Corp.) placed perpendicular to the subject's body at neck level. Stimuli were generated with custom software (Vision Shell™, MicroML) on a Macintosh IIvx computer and presented with a Sony 2000 color LCD projector. To minimize head movement, a bite bar was used with four experienced fMRI subjects, while four naive subjects were stabilized with tightly packed foam padding surrounding the head.

Data Analysis

Analyses were performed initially in custom software designed at MGH (XDS, Tim Davis) and then imported into Brain Voyager (Brain Innovation, Maastricht, Netherlands) for display purposes. Image sequences were examined for head motion (artifactual activation at brain edges or motion seen in a cinematic loop) and when it was observed, either a motion correction algorithm (automatic image registration, AIR, Woods et al., 1998) was applied or if the motion was greater than 1 mm, those data were discarded. Data were smoothed using a Hanning filter over a 3 × 3 voxel area for an approximate functional resolution of 6 mm. Each subject's data were condensed into a single 80 image time course (to allow averaging between subjects in the two orders when data from one order were repacked for compatibility) and converted to Talairach space (Talairach and Tournoux, 1988), averaged and analyzed using the custom software system Tal_EZ (Bush et al., 1996). Due to the extensive temporal and spatial averaging, the statistical significance levels shown for group analyses (Figure 3) were reduced. Talairached group data were imported into Brain Voyager (functional-to-anatomical alignment difficulties prohibited importation of the raw data) and a multiple regression was performed using the general linear model with the task and load components. The two components were independent and the resulting statistical maps did not depend on the order in which they appeared in the model. An independent scan comparing moving and stationary rings was used to localize MT+ (near the ascending limb of the inferior temporal sulcus) and TrIPS (at the junction of the IPS and transverse occipital sulcus).

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