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Quantitative Analysis of Attention and Detection Signals During Visual Search

Gordon L. Shulman, Mark P. McAvoy, Melanie C. Cowan, Serguei V. Astafiev, Aaron P. Tansy, Giovanni d’Avossa, and Maurizio Corbetta

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Submitted 8 April 2003; accepted in final form 6 August 2003

Shulman, Gordon L., Mark P. McAvoy, Melanie C. Cowan, Serguei V. Astafiev, Aaron P. Tansy, Giovanni d’Avossa, and Maurizio Corbetta. Quantitative analysis of attention and detection signals during visual search. J Neurophysiol 90: 3384—3397, 2003. First published August 13, 2003; 10.1152/jn.00343.2003. Prior work has distinguished regions in the intraparietal sulcus (IPs) and frontal eye field (FEF) involved in the voluntary control of attention, from more ventral regions in the temporoparietal junction (TPJ) involved in target detection. The present results show that when subjects search for and detect a visual target stimulus among nontargets, these regions show sensory-, search-, and detection-related signals that both confirm and refine these functional distinctions. The different signals were isolated by an additive model that accounted for a large fraction of BOLD (blood oxygenation level—dependent) signal modulation over the brain. Both IPs and FEF were activated during search through nontargets, consistent with a role in maintaining attention-related signals during search. However, unlike FEF, IPs also showed stimulus-related activations, and may combine signals related to sensory and task-dependent components of salience. Although IPs-FEF showed search-related activations, the TPJ was deactivated during search. TPJ activations were confined to detection-related signals. These results provide a much stronger dissociation between the TPJ and IPs-FEF than previous work, while indicating functional differences between frontal and parietal regions that are often coactivated in studies of attention. Finally, continuous flow models of information processing predict that during search, signals from missed targets should be fed from sensory to associative regions rather than being gated by the decision criterion. Correspondingly, missed targets significantly activated parietal (e.g., right TPJ) and frontal (e.g., anterior insula, anterior cingulate) regions, although with a smaller magnitude than detected targets. Surprisingly, many cortical regions showed equivalent signals from detected targets and the completion of target-absent trials, reflecting a widespread signal unrelated to motor execution.

INTRODUCTION

Because any task unfolds over time, event-related methods have been developed to separate the blood oxygenation level-dependent (BOLD) signals from processes that occur at different points within a task (Fornisano et al. 2002). Studies have separated the signals from different phases of working memory tasks (Cohen et al. 1997; Courtney et al. 1997) or tasks in which a cue provides advance information about a subsequent target object (Kastner et al. 1999; Shulman et al. 1999). Although the different phases in these tasks occurred in distinct time periods, tasks often involve processes that overlap in time. Here we present a model that separates the BOLD signals related to searching for an object, detecting the object, and the sensory effects of the search display. This model-based decomposition is used to explore the neural correlates of visual search and target detection.

Recent studies have suggested that dorsal frontoparietal regions are involved in directing attention based on goals or expectations, whereas regions in the temporoparietal junction (TPJ) are involved in target detection, particularly if the target is unexpected and requires attention to be reoriented. Centrally presented, symbolic cues produce sustained activations in the intraparietal sulcus (IPs) and precentral regions, including the proposed human homolog of the frontal eye fields (FEF) (Corbetta et al. 2000; Kastner et al. 1999; Shulman et al. 1999). Central cues produce no activity in the TPJ (Corbetta et al. 2000), but the TPJ is activated by subsequent target stimuli, with larger signals for unexpected than for expected targets (Arrington et al. 2000; Corbetta et al. 2000; Linden et al. 1999; Macaluso et al. 2002; Marois et al. 2002; McCarthy et al. 1997). Although the monkey homolog of the TPJ is unclear, neurons in area 7a, on the gyral surface inferior to IPs, similarly show larger responses to stimuli at unattended than at attended locations (Robinson et al. 1995; Steinmetz and Constantinid 1995). We have suggested that the TPJ partly acts as a target-driven circuit breaker that interrupts ongoing processes (Corbetta and Shulman 2002), particularly if attention must be reoriented.

One goal of the current experiment was to measure the activity in dorsal frontoparietal regions and the TPJ during visual search for a target object embedded in a series of nontargets. Search for the target requires knowledge of target features, potential target locations, and the appropriate temporal interval. During search this information may be reflected in the activity of dorsal frontoparietal regions, as suggested by previous cueing experiments. Conversely, because the TPJ is mainly activated by task-relevant target stimuli, search through nontargets may produce only weak TPJ activations.

As search proceeds, the target object may be detected. A second goal of the experiment was to measure target-evoked signals during search. Target detection can be viewed as the evaluation of an evidence variable with respect to a decision criterion (Green and Swets 1966). Once the sensory evidence...
has exceeded the criterion, a response such as a key-press is executed. Here we compare the BOLD responses to targets during visual search that do (hit trials) or do not (missed-target trials) exceed the criterion. This comparison allows us to test hypotheses of how target-evoked signals are transmitted from sensory regions to associative regions involved in target-related functions, such as the preparation and execution of the motor response or the activation of a “circuit breaker” that interrupts search and reorients attention.

One hypothesis is that the activity level specified by the decision criterion acts as a gate for transmission of target-evoked signals to higher-order regions. Beck et al. (2001) reported that missed targets (changed faces in a change-detection task) activated extrastriate areas, but not dorsal frontal or parietal areas activated by detected targets, consistent with an early gating hypothesis. Alternatively, continuous flow models of information processing have suggested that sensory information feeds continuously into target-related processes, particularly those related to the motor response (Coles et al. 1985). Partial evidence about target identity during choice reaction time tasks biases the lateralized readiness potential (Gratton et al. 1988) toward the hemisphere contralateral to the responding hand. In single-unit studies of tasks that involve eye movement responses and encourage temporal integration of target information, cells in dorsolateral prefrontal cortex, LIP, and superior colliculus show a continuous growth of predictive activity (Gold and Shadlen 2000; Kim and Shadlen 1999; Shadlen and Newsome 2001), suggesting that evidence about target identity has fed continuously into regions preparing the response.

These hypotheses make the following predictions. If transmission of sensory information to higher-order regions involved in target-related processes is gated by a threshold, then missed targets should not activate these regions when target-related evidence is below the decision criterion. Alternatively, if sensory information flows continuously from sensory to higher-order regions, then missed and detected targets should activate the same regions. Single-unit studies have shown effects of missed targets on FEF activity (Thompson and Schall 1999). Although imaging studies have compared activations for missed and detected targets in early visual regions (Ress and Heeger 2003; Ress et al. 2000), there is less information about associative regions (Beck et al. 2001).

**METHODS**

**Subjects and stimuli**

Twenty-two right-handed subjects gave informed consent in accordance with guidelines set by the Human Studies Committee of Washington University. Data were not analyzed from one subject because of difficulties in computing an accurate atlas transformation and from another subject because of poor behavioral performance. Each subject performed 2 search tasks, involving the detection of coherent motion in dynamic noise and the detection of a digit among letters during rapid serial visual presentation (RSVP) (Fig. 1A).

**MOTION-DETECTION TASK.** Fifty white dots, presented on a dark background, were randomly positioned within a 3.25-deg circular aperture. Dynamic noise was produced by randomly replotting the dots every 30 ms. Coherent motion was produced by translating a fraction of the dots each frame (speed = 4.2 deg/s).

**DIGIT-DETECTION TASK.** Four alphanumeric characters were positioned at the endpoints (eccentricity = 1.6 deg) of a virtual plus sign centered on fixation.

**Procedure**

**MOTION-DETECTION TASK.** Before each scan, the subject was instructed to detect coherent motion in one of 8 directions (defined by 45-deg increments). This direction was randomized over scans without replacement. On each trial, dynamic noise was presented for 7.08 s, corresponding to 3 magnetic resonance (MR) frames (in each 2.36-s MR frame, a whole-brain image was collected). On 75% of the trials, a coherent motion target of 300-ms duration was randomly presented between 580 and 1,780 ms from the onset of MR frames 1, 2, or 3 (Fig. 1B). Only one target was presented on a trial and the motion direction was always in the prespecified direction. No target was presented on the remaining 25% of the trials. The percentage of dots in coherent motion was determined for each subject in a preses- sion so that 70–80% of targets were detected.

**DIGIT-DETECTION TASK.** Before each scan, the subject was told to detect a specific digit (from the digits 2–9), which was randomized over scans without replacement. On each trial, 4 alphanumeric characters were simultaneously presented in successive 45-ms display frames over the trial’s 7.08-s duration. The interval between display frames was determined for each subject in a presession so that 70–80% of the targets were detected (group mean interval = 72 ms). On 75% of the trials, a target was presented in a single display frame at one of the four display locations, between 580 and 1,780 ms from the onset of MR frames 1, 2, or 3. No target digit was presented on the other 25% of the trials. All distractor characters were letters. Non- target digits were not presented.

In both tasks, subjects pressed a button with their right hand as quickly as possible on target detection and otherwise withheld a response. Subjects maintained fixation throughout the scan on a small central cross. The interdisplay frame interval (for the digit task) or the motion coherence (for the motion task) was occasionally adjusted between scans to maintain performance at a desired level. A scanning session included 16 scans, segmented into 4 groups of 4 scans. Each group involved a single task (digit, motion) that changed across successive groups. Task order was counterbalanced between subjects.

**Imaging methods**

MRI scans were collected on a Siemens 1.5-tesla vision system, using an asymmetric spin-echo EPI sequence sensitive to BOLD contrast (T2*) (TR = 2,360 ms, T2* evolution time = 50 ms, flip angle = 90 deg). A total of 128 2.36-s MR frames were acquired on each scan, where each frame included 16 contiguous 8-mm axial slices (3.75 × 3.75 mm in-plane). Structural images were collected with a sagittal MP-RAGE T1-weighted sequence (TR = 9.7 ms, echo time TE = 4 ms, flip angle = 12 deg, inversion time TI = 300 ms) and a T2-weighted spin-echo sequence (TR = 3,800 ms, TE = 90 ms, flip angle = 90 deg).

**Data analysis**

**PREPROCESSING OF BOLD SIGNALS.** Data were realigned within and across scans to correct for head movement. A whole brain normalization, applied to each scan, corrected for changes in signal intensity across scans. Differences in the acquisition time of each slice in an MR frame were compensated by sinc interpolation so that all slices were aligned to the start of the frame.

**REGRESSION MODELS OF THE BOLD SIGNAL.** The BOLD signal in each subject was analyzed with 2 regression models. The first model made no assumptions about the shape of the hemodynamic response function (HRF) or underlying neural activity and estimated a separate time course for each of the 8 trial types in a task: hit trials (1st, 2nd, and 3rd frame targets that were detected), miss trials (1st, 2nd, and 3rd frame targets that were missed), correct-rejection trials, and false alarm trials. This model has been extensively described and validated.
(Ollinger et al. 2001a,b; Shulman et al. 1999) and yields an accurate time course for each trial type.

These time courses mix the effects of different neural processes, given that the signal in a region may be affected by the stimulus display, by searching for a target, by detecting a target, or by some combination of these processes. One strategy for relating the BOLD signal to a particular process such as search is to specify what a “search-related” time course should look like and then examine all the time courses in the brain for this pattern. However, this strategy assumes that the effects on the time course of other processes such as the stimulus display or target detection have also been accounted for.

Therefore a second regression model was computed that specified the effects of stimulus, search, and detection processes on the observed BOLD time course. The point of this model was to identify the voxels activated by each process (e.g., indicate which voxels were search-related). The assumed temporal profiles of the 3 processes for early target hit trials and correct-rejection trials are shown in Fig. 1C (left and middle panels). 1) A stimulus process lasted for the duration of the display (7.08 s). 2) A search process began at the onset of the display, and ended either when a target was detected (hit trials) or, if no response was made, when the display terminated (correct-rejection trials). Because, on average, targets were presented in the middle of an MR frame, search duration was assumed to be 0.5, 1.5, and 2.5 MR frames for early, middle, and late target hit trials. 3) Separate detection processes were included for hit and correct-rejection trials. The correct-rejection process was included because in previous work we observed signals related to the functional end of a trial (Shulman et al. 2001, 2002b). The hit process was included because hit trials also involved the target stimulus and execution of a motor response. The hit process began when a target was detected (which on average occurred at 0.5, 1.5, and 2.5 frames on early, middle, and late target hit trials). The correct-rejection process began at stimulus offset. Hit and correct-rejection detection processes were assumed to be transient and were modeled as delta functions. Therefore on every correct-rejection and hit trial, stimulus, search, and detection processes were active, but correct-rejection and hit trials involved different detection parameters, resulting in a 4-parameter model.

A fifth, “missed-target” parameter was added to model trials in which a target was presented but missed. Figure 1C (right panel) shows the assumed waveforms for an early-target miss trial, in which a target occurred early but was missed. Missed-target trials were modeled by assuming that search proceeded over the entire trial and that a transient response occurred at the time the missed target was presented and at the end of the trial (as on correct-rejection trials).

Hemodynamic responses for each process were generated by convolving an idealized representation of the neural waveform for each
process (i.e., Fig. 1C) with a gamma function (Boynton et al. 1996). Although the neural waveforms are only approximations to the actual time course of neural activity associated with each process, discrepancies are minimized by the sluggish nature of the hemodynamic response. The BOLD responses associated with the different processes (e.g., stimulus or search) were assumed to combine as a weighted sum. The regression procedure computed the weights for each process that best fit the data at that voxel. For example, the stimulus process might require a large weight in some regions (e.g., V1) but not in others (e.g., anterior cingulate).

**STATISTICAL ANALYSIS AND MODEL-FITTING.** The processes active at a voxel (e.g., search) were determined by testing the significance of the estimated model parameters (e.g., the estimated weight from the regression procedure). For each subject, each parameter map was put into atlas space (Talairach and Tournoux 1988), smoothed by a filter with a full width at half-maximum of 4 mm, and tested with a voxel-level t-test to determine whether the parameter differed from zero. All analyses treated subjects as a random effect and were corrected over the brain for multiple comparisons (Forman et al. 1995). A model parameter may be statistically significant at a voxel even though the fit of the model to the time course is poor. However, model parameters for poorly modeled voxels are difficult to interpret. Therefore the process model was fit directly to the group time courses from the frame-by-frame model at each voxel and an adjusted $r^2$ map was computed ($r^2$ values were adjusted downward for the number of model parameters). Statistical maps of model parameters were masked using a cutoff-adjusted $r^2$ value of 0.6, which was arbitrary but excluded poorly modeled voxels.

**MAGNITUDE NORMALIZATION OF MODEL PARAMETERS.** Model parameters were normalized to show the relative magnitudes of each process. The regression coefficient $a$ for each parameter was divided by a BOLD response magnitude

$$N_{\text{th,process}} = \left( \sum_{j=1}^{\# \text{regressors}} p(j|\text{th})a_{\text{th}}^j \right)^{1/2},$$

where $p(j|\text{th})$ is the proportion of trials in which the $j$th process is present that contains the $j$th parameter. For example, the denominator for the search and stimulus processes was

$$N_{\text{search}} = N_{\text{stim}} = \sqrt{a_{\text{search}}^2 + 0.75a_{\text{stim}}^2 + 0.25a_{\text{c}}^2}.$$  

**RESULTS**

**Behavior**

Table 1 shows the hit rates and reaction times for each task as a function of the MR frame at which a target was presented. Both tasks were difficult, with an overall hit rate <80%, but performance was higher on the digit task. The hit rate increased with the target frame, probably reflecting changes in target uncertainty as the trial progressed, and this effect was larger for the motion task. The reaction time data showed similar effects. These suggestions were confirmed statistically. Both hit rate and reaction time showed significant effects of Task [hit rate: $F(1,19) = 25.9, P < 0.001$; reaction time: $F(1,13) = 75.8, P < 0.001$], and Target Frame [hit rate: $F(2,38) = 13.7, P < 0.001$; reaction time: $F(2,26) = 6.04, P < 0.01$], and an interaction of Task by Target Frame [hit rate: $F(2,38) = 4.03, P < 0.05$; reaction time: $F(2,26) = 8.81, P < 0.005$]. False alarm rates (2.7% for motion, 4.0% for digit) did not differ between tasks [F(1,19) = 1.92, P > 0.1].

The temporal profiles in the process model (Fig. 1C) did not reflect the change in temporal uncertainty over the search period. For example, the search profile was flat rather than increasing. Although these profiles gave good fits to the BOLD time course (see following text), the BOLD signals in some regions may have been affected by changes in temporal uncertainty (Ghose and Maunsell 2002).

**Imaging**

Results averaged across the digit and motion tasks are mainly presented, although stimulus-, search-, or detection-related signals that varied significantly across tasks were found in some regions.

**Search-related signals in IPs and FEF**

Cueing experiments indicate that dorsal frontoparietal regions may be the source of top-down signals for the voluntary selection of stimuli (Corbetta et al. 2000; Hopfinger et al. 2000; Kastner et al. 1999; Shulman et al. 2002a). Because similar signals should be present during visual search for a known target (Wolfe 1994), we expected dorsal frontoparietal regions to show maintained activity during search. Figure 2 shows regions in which searching through nontargets produced significant responses. The graphs show group-averaged time courses from the frame-by-frame model for the 4 correct trial types (solid lines). The fit of the process model to the time courses from the frame-by-frame model is also shown (dotted lines) in 2 regions. Although the point of the model was to identify regions affected by specific processes, not to generate time courses, the close fits support the adequacy of the model assumptions (see $r^2$ values in tables).

Consistent with expectations, search-related activations (warm-colored voxels) were observed in dorsal parietal and frontal regions, including bilateral IPs and the ventral extension of IPs (vIPs) into the left occipital lobe, and precentral regions such as FEF and ventral precentral (vPc) cortex (Table 2). Search-related activations were also observed in supplementary motor area (SMA), and to a lesser degree in right MT+, bilateral insula, and regions in pre-SMA and right anterior cingulate. Similar search-related regions have been observed in a change-detection task (Huettel et al. 2001).

**Stimulus-related signals in IPs, but not FEF**

The results also indicated an interesting difference between the signals in IPs and FEF. Figure 3 shows lateral views of regions in which search-related, stimulus-related, or both types of signals were significant (top row, activations; bottom row, deactivations). Whereas both IPs and FEF showed search-related activity, only IPs also showed significant stimulus-related activity (see Table 2 for normalized magnitudes of the stimulus-related signal in search-related regions). Joint stimulus- and search-related activations were also observed in MT+.
The difference between IPs and FEF was qualitatively evident from their time courses (Fig. 2). In both regions, the BOLD signal for all trial types rose above baseline on MR frame 3. This increase was greater on early-target hit trials (green function) than on the other trial types, reflecting a detection-related signal from the early target (detection-related signals for middle and late targets occurred at later MR frames). After detection, the BOLD signal fell off, reflecting the termination of search. However, this fall-off was less steep for IPs than for FEF, reflecting the ongoing effect of the stimulus display on the signal in IPs. Figure 4A compares the time course on early target hit trials in IPs and FEF, showing the more sustained IPs response.

Dissociation of IPs-FEF and the TPJ during search

Because the TPJ is mainly activated by target stimuli, weak responses were expected during search through nontargets. Figure 2 (cool-colored voxels) shows that search actually deactivated the TPJ (which includes the supramarginal gyrus (SMg) and superior temporal sulcus (STs)), in strong contrast to the search-related activations in IPs and FEF (see also Table 3). Search-related deactivations were also observed in right lateral prefrontal cortex, anterior medial occipital cortex (see also Shmuel et al. 2002; Tootell et al. 1998), and precuneus/posterior cingulate.

Prior work has shown that regions in right TPJ and lateral

### TABLE 2.  
Regions with a significant positive search parameter, normalized magnitudes of model parameters, and adjusted $r^2$ values, obtained by fitting the 4-parameter model to the group time courses for each region.

<table>
<thead>
<tr>
<th>Region</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>z-Score</th>
<th>Stim</th>
<th>Search</th>
<th>Det Hit</th>
<th>Det CR</th>
<th>$r^2$ (adj)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Occipital-parietal</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R MT+</td>
<td>45</td>
<td>-65</td>
<td>2</td>
<td>3.6</td>
<td>0.87</td>
<td>0.23</td>
<td>0.40</td>
<td>0.51</td>
<td>0.96</td>
</tr>
<tr>
<td>L SPL</td>
<td>-19</td>
<td>-63</td>
<td>44</td>
<td>3.6</td>
<td>0.08</td>
<td>0.44</td>
<td>0.90</td>
<td>0.88</td>
<td>0.93</td>
</tr>
<tr>
<td>L IPs</td>
<td>-27</td>
<td>-55</td>
<td>48</td>
<td>3.3</td>
<td>0.43</td>
<td>0.70</td>
<td>0.61</td>
<td>0.44</td>
<td>0.93</td>
</tr>
<tr>
<td>R IPs</td>
<td>27</td>
<td>-53</td>
<td>50</td>
<td>4.2</td>
<td>0.52</td>
<td>0.55</td>
<td>0.66</td>
<td>0.66</td>
<td>0.93</td>
</tr>
<tr>
<td>L vIPs</td>
<td>-25</td>
<td>-73</td>
<td>26</td>
<td>3.9</td>
<td>0.43</td>
<td>0.56</td>
<td>0.72</td>
<td>0.69</td>
<td>0.92</td>
</tr>
<tr>
<td>Frontal</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L FEF</td>
<td>-27</td>
<td>-15</td>
<td>50</td>
<td>4.1</td>
<td>-0.29</td>
<td>0.86</td>
<td>0.47</td>
<td>0.11</td>
<td>0.75</td>
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<tr>
<td>R FEF</td>
<td>25</td>
<td>-13</td>
<td>52</td>
<td>5.9</td>
<td>0.04</td>
<td>0.90</td>
<td>0.47</td>
<td>0.30</td>
<td>0.87</td>
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<tr>
<td>L dPrCs</td>
<td>-41</td>
<td>-9</td>
<td>46</td>
<td>4.0</td>
<td>-0.08</td>
<td>0.86</td>
<td>0.54</td>
<td>0.31</td>
<td>0.85</td>
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<tr>
<td>R dPrCs</td>
<td>-45</td>
<td>-5</td>
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<tr>
<td>L SMA</td>
<td>-7</td>
<td>-1</td>
<td>54</td>
<td>4.5</td>
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<td>-1</td>
<td>54</td>
<td>4.3</td>
<td>-0.22</td>
<td>0.83</td>
<td>0.55</td>
<td>0.32</td>
<td>0.82</td>
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<tr>
<td>R pro-SMA</td>
<td>7</td>
<td>5</td>
<td>42</td>
<td>4.2</td>
<td>-0.30</td>
<td>0.56</td>
<td>0.80</td>
<td>0.66</td>
<td>0.91</td>
</tr>
<tr>
<td>R ant cingulate</td>
<td>9</td>
<td>17</td>
<td>36</td>
<td>3.7</td>
<td>-0.12</td>
<td>0.36</td>
<td>0.93</td>
<td>0.89</td>
<td>0.90</td>
</tr>
<tr>
<td>L ant insula</td>
<td>-29</td>
<td>17</td>
<td>4</td>
<td>5.1</td>
<td>-0.29</td>
<td>0.52</td>
<td>0.83</td>
<td>0.57</td>
<td>0.88</td>
</tr>
<tr>
<td>R ant insula</td>
<td>31</td>
<td>17</td>
<td>8</td>
<td>4.5</td>
<td>-0.16</td>
<td>0.54</td>
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<td>0.70</td>
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</tbody>
</table>
prefrontal cortex show greater signal increments for unexpected (i.e., invalidly cued) than expected (i.e., validly cued) targets (Corbetta et al. 2000). Figure 4B indicates that these regions (from Corbetta et al. 2000) extensively overlap regions that show search-related deactivations. The overlap was most evident in SMg and STs, but was also observed in lateral prefrontal cortex. Finally, Fig. 3 (bottom row) shows that search-related deactivations in the TPJ were distinguished from stimulus-related deactivations in more posterior regions in superior occipital cortex and angular gyrus (Huettel et al. 2001) (Table 3), and in auditory regions.

Widespread detection-related signals

The process model identified regions activated by missed and detected targets, allowing an evaluation of continuous flow models of information processing. This section describes the signals for detected targets, whereas the next section considers those for missed targets. Target detection and/or detection of the end of the trial produced widespread but transient increases in activity that were superimposed on stimulus- and search-related signals. Figure 5A shows that on both hit and correct-rejection trials, significant detection-related signals were observed in many, although not all, cortical regions (e.g., the "hole" in posterior IPL/superior occipital cortex). Similar effects were observed in the right hemisphere. No voxel showed a significant negative correct-rejection parameter, whereas only small regions in left dorsal prefrontal cortex and ventral anterior cingulate showed a significant negative hit parameter (green voxels).

Because a motor response was not made on correct-rejection trials, this widespread signal was unrelated to motor execution. It probably reflected to some extent processes related to target detection. Although correct-rejection trials did not involve an explicit target, the offset of the display likely functioned as a "target," given that it was a task-relevant stimulus that indicated the trial was over. Right TPJ, for example, showed equivalent detection-related signals on hit and correct-rejection trials.

To gain insight into the relation between detection-related signals and sensory signals, the detection-related signals for the digit and motion tasks were compared within regions in which the sensory responses for the 2 tasks were significantly differ-
ent. The warm colors in the statistical map in Fig. 5B indicate voxels in which the stimulus-evoked response was significantly larger in the digit than in motion tasks. Fusiform cortex was well activated, reflecting the presence of shapes in the digit task but mainly spatiotemporal noise in the motion task (Grill-Spector et al. 1998; Malach et al. 1995). The left panel in Fig. 5C plots the magnitude of the stimulus parameter in the digit task against the magnitude of the stimulus parameter in the motion task in regions showing task-specific stimulus effects. The middle and right panels in Fig. 5C plot the magnitudes of the hit and correct-rejection detection parameters in these same regions. These plots show that differences in sensory-evoked responses did not positively correlate with differences in detection-related responses. (This is qualitatively different from the time courses in Fig. 5B. The arrows point to MR frame 3, on which the signal increase during early-target trials, relative to the other trial types, is similar for both tasks.) A t-test comparison of the detection-related signals on correct-rejection trials for the digit and motion tasks in these regions yielded no significant differences, whereas the detection-related signal on hit trials was actually smaller in the digit than motion tasks in 2 regions.

Finally, we note that more restricted detection-related signals were observed in addition to the diffuse signal. For example, the detection-related signal on hit trials was significantly larger for the motion than for the digit tasks in right MT+ (x, y, z, = 43, −65, 4; z-score = 3.9) and right ventral precentral cortex (x, y, z = 47, 3, 28; z-score = 3.7), which may be involved in polymodal processing of motion (Bremner et al. 2001). Similarly, some regions showed larger detection-related signals on hit than correct-rejection trials (see following text), reflecting the motor response on hit trials.

**Activation of associative regions by missed targets**

Continuous flow models of information processing predict that signals from missed targets should be observed in associative regions rather than being gated by the decision criterion. This prediction is confirmed in Fig. 6, which shows the regions significantly activated by missed targets (red and orange voxels), as determined from the missed-target parameter of the process model. Significant missed-target signals were observed in associative regions that did not show stimulus-related activations, including frontal regions in pre-SMA, anterior cingulate, anterior insula, precenral/IFg and MFG, and parietal regions in L IPS, L postcentral sulcus, and R SMG. Missed target activations were also observed in regions that showed stimulus-related signals, such as L MT+, L lateral occipital cortex, and R vIPs (Table 4). These latter activations might have reflected sensory responses, to the extent that these regions gave stronger sensory responses to targets (e.g., coherent motion) than to non-targets (e.g., dynamic noise), and/or the interaction of sensory signals with top-down signals that specified target identity or task judgment. All significant missed-target signals were activations rather than deactivations. A voxel-level t-test indicated that the missed-target signal was significantly smaller than the hit signal in almost all well-modeled regions showing a detection-related signal.

**Insight into the functional correlates of the missed-target activations**

Insight into the functional correlates of the missed-target activations was gained by comparing the map of missed-target activations to the difference map of voxels showing a significantly larger hit than correct-rejection (CR) parameter. This hit−CR map emphasized signals related to motor execution, which occurred only on hit trials, while subtracting out the widespread detection-related signal. Therefore the overlap be-

### Table 3. Regions discussed in the text with significant negative stimulus or search parameters, normalized parameter magnitudes, and adjusted $r^2$ values from the 4-parameter model

<table>
<thead>
<tr>
<th>Region</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>z-Score</th>
<th>Stim</th>
<th>Search</th>
<th>Det Hit</th>
<th>Det CR</th>
<th>$r^2$ (adj)</th>
</tr>
</thead>
<tbody>
<tr>
<td>L SMg</td>
<td>−55</td>
<td>−41</td>
<td>48</td>
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<td>−0.87</td>
<td>0.45</td>
<td>0.35</td>
<td>0.61</td>
</tr>
<tr>
<td></td>
<td>−47</td>
<td>−45</td>
<td>36</td>
<td>4.4</td>
<td>0.10</td>
<td>−0.75</td>
<td>0.63</td>
<td>0.69</td>
<td>0.62</td>
</tr>
<tr>
<td>R Sf</td>
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<td>−53</td>
<td>22</td>
<td>3.9</td>
<td>−0.31</td>
<td>−0.81</td>
<td>0.35</td>
<td>0.69</td>
<td>0.73</td>
</tr>
<tr>
<td></td>
<td>45</td>
<td>−49</td>
<td>42</td>
<td>4.8</td>
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<td>−0.75</td>
<td>0.58</td>
<td>0.71</td>
<td>0.66</td>
</tr>
<tr>
<td></td>
<td>53</td>
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<td>40</td>
<td>4.8</td>
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<td>−0.72</td>
<td>0.69</td>
<td>0.69</td>
<td>0.78</td>
</tr>
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<td>R STs</td>
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<td>12</td>
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<td>−0.65</td>
<td>0.66</td>
<td>0.81</td>
<td>0.75</td>
</tr>
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<td>R IFg</td>
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<td>−0.72</td>
<td>0.58</td>
<td>0.78</td>
<td>0.65</td>
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<tr>
<td></td>
<td>51</td>
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<td>−0.77</td>
<td>0.65</td>
<td>0.62</td>
<td>0.68</td>
</tr>
<tr>
<td>L IPL/ SO</td>
<td>−53</td>
<td>−67</td>
<td>22</td>
<td>6.1</td>
<td>−0.98</td>
<td>−0.07</td>
<td>−0.07</td>
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<td>0.88</td>
</tr>
<tr>
<td></td>
<td>−41</td>
<td>−77</td>
<td>28</td>
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<td>−0.01</td>
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<td>0.91</td>
</tr>
<tr>
<td></td>
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<td>−79</td>
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<td>−0.10</td>
<td>−0.02</td>
<td>0.02</td>
<td>0.92</td>
</tr>
<tr>
<td>R IPL/ SO</td>
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<td>0.00</td>
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<td>0.90</td>
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<td>5.1</td>
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<td>0.62</td>
<td>0.86</td>
</tr>
<tr>
<td></td>
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<td>0.39</td>
<td>0.82</td>
</tr>
<tr>
<td>R ant STg/STs</td>
<td>−35</td>
<td>−31</td>
<td>12</td>
<td>4.8</td>
<td>−0.68</td>
<td>−0.04</td>
<td>0.72</td>
<td>0.74</td>
<td>0.63</td>
</tr>
<tr>
<td>L Aud Ctx</td>
<td>−37</td>
<td>−33</td>
<td>14</td>
<td>4.4</td>
<td>−0.71</td>
<td>−0.19</td>
<td>0.61</td>
<td>0.80</td>
<td>0.65</td>
</tr>
</tbody>
</table>
between the hit–CR map and the missed-target map indicated whether missed targets activated response-related regions.

Regions with significantly larger hit than correct-rejection parameters are shown in Fig. 6 in yellow and orange (the orange voxels show the overlap of the hit–CR map with the missed-target map). Most regions in the hit–CR map were in the left hemisphere, contralateral to the responding hand. Some of these regions also showed missed-target signals (e.g., L postcentral sulcus), reflecting the activation of response-related processes by missed targets. Bilateral activations in the hit–CR map were observed in the anterior insula and ventral precentral cortex (vPrC). Bilateral insula and L vPrC also showed significant search-related activity (Fig. 2, Table 4), indicating that they were involved in processes over and above motor execution, such as holding a response in readiness to be initiated by target-evoked signals. These regions were also activated by missed targets. Interestingly, missed-target activations were weak in the left central sulcus (Cs in Fig. 6). A 1-cm-diameter sphere was centered at the left central sulcus coordinate that showed the most significant z-score in the hit–CR map (x, y, z = −39, −29, 52; z-score = 5.4). An uncorrected t-test on this region of interest yielded only a marginal effect of missed targets (z-score = 1.84, P < 0.1). Therefore although missed targets activated regions involved in response-related processes, they at best weakly activated regions involved in the latter stages of motor execution.

The time courses for the missed-target trials (Fig. 6, dotted lines) show that missed targets evoked a transient signal at the time of target presentation but that search continued, culminating in a “correct-rejection” signal at the end of a trial. This sequence conforms to the assumptions of the process model. In the anterior insula, for example, the signal on both early-target miss and hit (solid green line) trials diverged from the signal on correct-rejection trials (solid red line) on MR frame 3, with the missed-target signal smaller than the hit signal. At later MR frames, the signal on early-target hit trials fell off sharply,
whereas the signal on early-target miss trials converged on the signal for correct-rejection trials.

Although the statistical map of missed-target activations in Fig. 6 was computed from the process model, an analysis directly on the time courses on missed-target trials yielded a similar conclusion. A 2-factor ANOVA was computed on the 3 missed-target time courses with the MR frame at which the missed target was presented as one factor and Time as the other factor (with levels 1–10, reflecting the 10 time points in each time course). A significant interaction of the 2 factors indicates voxels in which the time course for a missed target depended on the frame at which the missed target was presented. The most significant regions from the process model, such as the anterior insula, ventral PrC, and pre-SMA, were well activated in the ANOVA map (not shown), whereas overlapping regions were activated in lateral occipital and parietal cortex.

**DISCUSSION**

Dorsal frontoparietal regions are involved in directing attention to a location or direction of motion based on behavioral goals or expectations (Corbetta et al. 1993; Gitelman et al. 1996; Hopfinger et al. 2000; Kastner et al. 1999; Nobre et al. 1997; Shulman et al. 2002a; Vandenbergh et al. 1996; Yantis et al. 2002). The present results indicate that IPs and FEF also show maintained activity during search for a target (Fig. 2). In addition, they suggest a functional difference between the 2 regions. IPs regions combine search- and stimulus-related signals, whereas FEF shows only search-related signals (Figs. 3 and 4A). Because these two regions are often coactivated in studies of attention, functional differences are of particular interest.

We previously contrasted the functions of IPs-FEF and the TPJ (Corbetta and Shulman 2002). When a cue provides advance information about a target that is subsequently detected, IPs-FEF, but not the TPJ, responds during the cue period (Corbetta et al. 2000). IPs-FEF also responds to the subsequent target, but now the TPJ responds as well, particularly if the target is unexpected (Arrington et al. 2000; Corbetta et al. 2000; Macaluso et al. 2002). The present results demonstrated a much stronger dissociation between the TPJ and IPs-FEF.

**TABLE 4.** Regions discussed in the text with a significant miss parameter, normalized magnitudes of model parameters, and adjusted r² values from the 5-parameter model

<table>
<thead>
<tr>
<th>Region</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>z-Score</th>
<th>Stim</th>
<th>Search</th>
<th>Hit</th>
<th>CR</th>
<th>Miss</th>
<th>r² (adj)</th>
</tr>
</thead>
<tbody>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SMA</td>
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<td>2</td>
<td>2</td>
<td>3.6</td>
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<td>0.06</td>
<td>0.91</td>
<td>0.83</td>
<td>0.32</td>
<td>0.08</td>
</tr>
<tr>
<td>preSMA</td>
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<td>1</td>
<td>1</td>
<td>3.0</td>
<td>0.23</td>
<td>0.33</td>
<td>0.94</td>
<td>0.77</td>
<td>0.55</td>
<td>0.84</td>
</tr>
<tr>
<td>ant cing</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>3.0</td>
<td>0.19</td>
<td>0.10</td>
<td>0.98</td>
<td>0.93</td>
<td>0.44</td>
<td>0.68</td>
</tr>
<tr>
<td>R MFg</td>
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<td>29</td>
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<td>0.85</td>
<td>0.31</td>
<td>0.64</td>
</tr>
<tr>
<td>L vPrC/IFg</td>
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<td>30</td>
<td>5.0</td>
<td>0.08</td>
<td>0.10</td>
<td>0.99</td>
<td>0.89</td>
<td>0.60</td>
<td>0.70</td>
</tr>
<tr>
<td>R vPrC/IFg</td>
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<td>17</td>
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<td>5.0</td>
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<td>0.83</td>
<td>0.46</td>
<td>0.56</td>
<td>0.84</td>
</tr>
<tr>
<td>R ant insula</td>
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<td>23</td>
<td>6</td>
<td>5.1</td>
<td>0.16</td>
<td>0.44</td>
<td>0.91</td>
<td>0.72</td>
<td>0.53</td>
<td>0.76</td>
</tr>
<tr>
<td>R ant insula</td>
<td>33</td>
<td>23</td>
<td>6</td>
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<td>0.91</td>
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<td>0.76</td>
</tr>
<tr>
<td>Parietal/occipital</td>
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<td>0.63</td>
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<tr>
<td>R IPs</td>
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<td>0.86</td>
<td>0.82</td>
<td>0.33</td>
<td>0.85</td>
</tr>
<tr>
<td>R SMg</td>
<td>27</td>
<td>29</td>
<td>26</td>
<td>4.0</td>
<td>0.31</td>
<td>0.54</td>
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<td>0.77</td>
<td>0.37</td>
<td>0.71</td>
</tr>
<tr>
<td>L ling</td>
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<td>7</td>
<td>7</td>
<td>4.0</td>
<td>0.08</td>
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<td>0.75</td>
</tr>
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<tr>
<td>L lat occ</td>
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<td>0.92</td>
<td>0.89</td>
<td>0.42</td>
<td>0.84</td>
</tr>
</tbody>
</table>
The role of dorsal frontoparietal regions during search

A stimulus may be salient because of its sensory characteristics (Yantis and Hillstrom 1994; Yantis and Jonides 1990) or because its features are task-relevant (Folk et al. 1992, 2002). This latter, task-dependent component of salience reflects the modulation of sensory information by top-down signals that specify behaviorally relevant stimuli (Wolfe 1994).

Search-related activations in the IPs and FEF may have reflected 2 types of signals involved in the task-dependent component of salience. 1) They may have reflected signals that specified target identity (e.g., the digit “5”) or restricted search to task-relevant spatial locations or temporal intervals (Coull and Nobre 1998; Ghose and Maunsell 2002). Consistent with this idea, dorsal frontoparietal regions that showed search-related signals partially overlap regions involved in attending to spatial locations or features such as motion direction (Corbetta et al. 2000; Shulman et al. 2002a). 2) They may have reflected the interaction of the first type of signal with sensory signals from nontargets (Schall and Hanes 1993; Thompson et al. 2001). This interaction determines the task-dependent salience of the nontargets. Finally, search-related signals in IPs and/or FEF may have maintained a linkage between the target categorization and the right-hand button press (Iacoboni et al. 1996; Rushworth et al. 2001).

Stimulus-related activations in IPs may have reflected the sensory component of salience, resulting from the dynamic luminance discontinuities that defined the boundaries of the motion display or the character locations of the RSVP display (Gottlieb et al. 1998). Therefore IPs may have been affected by both sensory and task-dependent components of salience. Alternately, the sustained activity in IPs but not FEF may have reflected a difference in the gain of the modulation of sensory signals by top-down signals, rather than a functional difference. Within extrastriate cortex, overlap of the search and stimulus maps was confined to MT+ (Fig. 3). Because macaque MT and MST connect with VIP and LIP (Maunsell and Van Essen 1983; Ungerleider and Desimone 1986), the similar patterns of activity in MT+ and IPs may have reflected these projections.

The role of the TPJ during search

The simultaneous presence of search-related activations in IPs-FEF and deactivations in the TPJ strongly dissociates these 2 sets of regions. The interpretation of deactivations is controversial. There are concerns, for example, that deactivations may reflect vascular phenomena, such as “local stealing,” rather than neural activity (Haxby et al. 1994). However, the spatial distribution of deactivations in many tasks is not consistent with local stealing. A set of deactivations occur in the same cortical regions across a wide variety of cognitive tasks (Mazoyer et al. 2001; Shulman et al. 1997), indicating that very different distributions of activations can produce the same distribution of deactivations. Similarly, deactivated regions are often not adjacent to activated regions. Recent studies have provided evidence that BOLD deactivations reflect reductions in overall neural activity (both excitation and inhibition) (Gold and Lauritzen 2002; Shmuel et al. 2002). Shmuel et al. showed that BOLD deactivations in medial occipital cortex during a visual task were associated with decreases in blood flow and oxygen consumption. Gold and Lauritzen showed that artificially decreasing the input to the cerebellum from frontal cortex in rats reduced both the spiking activity of Purkinje cells and blood flow (although to a smaller extent). Therefore although the interpretation of deactivations is currently unsettled (for one perspective, see Raichle et al. 2001), we view search-related deactivations in the TPJ as reflecting a reduction in overall neural activity during search.

The empirical dissociation between IPs-FEF and the TPJ does not depend on a specific theory of why the TPJ is deactivated during search. However, we offer one possible account within the previously outlined framework, in which the TPJ acts as a “circuit breaker” that interrupts ongoing processes when a target is detected. When subjects are not in a focused task state (e.g., during the intertrial interval), they may be prepared to respond to a wide variety of stimuli, such as a ringing telephone, the light from a door opening onto a darkened room, and so forth. However, when subjects are in a focused task state, such as when searching for a known target, it is important that these task-irrelevant stimuli not trigger the “circuit breaker.” We suggest that a filter determines the range of stimuli that should or should not be input to the TPJ. When searching for a known target, the range of allowable stimuli is small. This filtering ensures that during search, the circuit breaker is triggered by the search target (e.g., the digit “5”), not by the door opening or by a distracter stimulus (e.g., a letter in the digit task). The resulting reduction in the processing of ambient stimuli in the TPJ during search, relative to the unfocused task state of the intertrial interval, decreases the overall neural activity (Drevets et al. 1995). The suggestion is not that the TPJ is shut off during search, but that it processes a more limited set of stimuli. Because the TPJ contains millions of cells, a deactivation may reflect decreased activity in many cells, maintained activity in some cells, and increased activity in a small set of cells.

When stimuli meet the current definition of a target (i.e., a stimulus that requires a response or action, covert or overt), they pass the filter and increase TPJ activity, particularly if they require attention to be reoriented. Right TPJ regions that show a sustained deactivation during search also show a transient activation that is larger for unexpected than for expected
targets (Fig. 4B) (Corbetta et al. 2000). Similarly, the TPJ is activated by distracter stimuli in nontarget locations if they contain features that match the target object (Sèrenes et al. 2001). These distracter stimuli pass the filter because they share target features. Dorsal frontoparietal regions may be involved in setting up the filter.

Continuous flow of target signals from sensory to associative regions during search

The relatively broad range of regions in frontal and temporoparietal cortex activated by missed targets (Fig. 6) was particularly interesting, given that it seems unlikely that all of these activations reflected only the evaluation of an “evidence variable” with respect to a decision criterion. Rather, sensory information fed continuously into associative regions involved in different target-related functions.

Some of these functions were related to the preparation and execution of a motor response to a target. Missed-target signals were observed in frontoparietal regions, such as SMA/pre-SMA, anterior insula, and ventral precentral cortex/IFg, which may correspond to ventral premotor cortex in the monkey. Cells in premotor cortex show delay-related activity as the monkey prepares a response to a visual target, as well as activity when the target appears and the movement is executed (Weinrich and Wise 1982). In the present work, L ventral precentral cortex and the anterior insula showed search-related signals, perhaps reflecting the holding of a response in readiness, as well as stronger signals for detected targets (hits) than correct rejections, reflecting the motor response to the visual target. These regions may hold a response in readiness to be initiated by target-evoked signals that are fed continuously from sensory areas, resulting in activations from missed targets. Only weak, nonsignificant signals to missed targets were observed in the primary motor region most reliably activated by the motor response, indicating that missed targets did not activate cortical regions involved in the final stages of motor execution.

However, missed targets did not only activate response-related processes. Missed-target activations in the parietal lobe were distributed from anterior IPs to the TPJ, and showed a strong right hemisphere bias, despite the fact that the button press was performed with the right hand. Right TPJ also showed equivalent detection-related signals for hits and correct rejections, which did not involve a response. Finally, right TPJ was deactivated during search, further contrasting it with the frontal regions noted above. The missed-target activations in the TPJ may conflict with our characterization of this region as a circuit breaker, in that missed targets were not detected and did not terminate search, yet still activated the TPJ. One possibility is that these activations, which were weaker than the activations for detected targets, reflected input signals and processing within the TPJ rather than output signals. Target-related signals were passed by the filter to the “circuit breaker” and were processed, even when below criterion, but did not produce an output that terminated search.

In summary, missed-target activations in parietal and frontal regions likely reflected multiple processes rather than the evaluation of only an evidence variable with respect to a decision criterion. Other functions engaged by missed targets might have included categorization or decision processes not tied to specific motor responses, registering of targets in working memory (perhaps DLPFC; Jiang et al. 2000), and monitoring and/or resolution of conflict caused by partially activated responses. This latter function may have involved regions in the anterior cingulate (Botvinick et al. 2001) that were activated by missed targets but were anterior to cingulate motor areas (Picard and Strick 1996).

Whether a target was detected or missed partly depended on the subject’s decision criterion, which can vary from lax to strict (Green and Swets 1966). The present results do not indicate whether the amplitude of missed-target activations depended on this criterion level or was inversely related to the subject’s confidence on a trial that a target was not presented.

Widespread consequences of detection

Although a restricted set of regions showed greater detection-related signals on hit than on correct-rejection trials (Fig. 6), widespread detection-related signals of comparable magnitudes were observed on both types of trials (Fig. 5A). The widespread nature of the signal indicated that it modulated regions with very different functions. For example, whereas detection-related signals were observed in regions involved in visual attention, such as IPs and FEF, they were also observed in auditory cortex. Moreover, regions within visual cortex that showed different stimulus-related signals for the two tasks showed similar detection-related signals (Fig. 5, B and C).

We consider two interpretations of this widespread signal. First, it may have resulted from detecting target presence or absence. Target detection interferes with the detection of subsequent targets (Broadbent and Broadbent 1987; Duncan 1980; Raymond et al. 1992), perhaps reflecting effects of a diffuse signal generated by detection. This account assumes that absence detection involved detecting the offset of the search display. A related possibility is that the widespread signal was related to processes recruited at the functional end of the trial. Because only one target was presented on a trial rather than multiple targets, the task ended after target detection on hit trials and stimulus offset on correct-rejection trials. Previously, we observed widespread signals after the termination of an extended state of readiness (Shulman et al. 2002b). Completing a trial might produce a global change in arousal. More speculatively, a diffuse task-termination signal might reset activity in cortical regions, including regions that were activated or deactivated by the task.

We have noted that target-evoked signals below the decision criterion fed into higher-order regions involved in target-related functions. However, missed targets did not significantly activate many regions that showed the widespread detection-related signal. This result raises the possibility that some detection-related processes reflected in this signal were gated by task completion. Alternately, this result may have simply reflected statistical thresholding.

Separating processes in time

The BOLD signals from overlapping neural processes were separated by experimentally manipulating their temporal profile (latency and duration) and modeling the contribution of each process to the BOLD time course. We tested the model by showing that it could satisfactorily account for the observed time courses, using goodness-of-fit measures. This procedure
may be useful for testing models of cognitive function in neuroimaging experiments. However, the labels “stimulus,” “search,” and “detection” in the model were simply descriptors for processes that conformed to one of 3 temporal waveforms. For example, the “search” process also involved maintaining a response in readiness, probably accounting for the search-related activations in SMA (Alexander and Crutcher 1990) and perhaps those in ventral precentral cortex and anterior insula.

In conclusion, the current study separated the BOLD signals for stimulus-, search-, and detection-related processes as subjects searched for and responded to a visual target. Figure 7 summarizes these signals for a lateral view of the right hemisphere. The search display produced stimulus-related activations (e.g., occipital cortex, IPs) and deactivations (e.g., auditory cortex) that were maintained for the duration of the display, and search-related activations (e.g., FEF, IPs) and deactivations (e.g., TPJ) that were maintained for the duration of search. Search-related activations in IPs-FEF may have reflected top-down signals that controlled how the search was conducted. Within these search-related areas, stimulus-related signals were observed in IPs but not FEF, perhaps reflecting a differential sensitivity to sensory salience. Search-related deactivations in the TPJ and lateral prefrontal cortex may have reflected the effects of a filter that restricted the processing of nontargets in these regions.

As search proceeded missed targets activated right TPJ, as well as frontal regions involved in response-related processes, reflecting the continuous flow of target-related signals to associative regions involved in a variety of functions. Some frontal regions that responded to missed targets also showed both search-related activations and larger detection-related signals for hits than for correct rejections (e.g., anterior insula), and may have held responses in readiness to be initiated by target-evoked signals. Finally, target detection on hit trials produced signals in many cortical regions of equivalent magnitude to the signals at the completion of correct-rejection trials, reflecting a widespread cortical signal that was not related to motor execution.

We thank J. Ollinger, T. Conturo, E. Akbudak, A. Snyder, and F. Miezin for software and hardware development.

**DISCLOSURES**

This work was supported by National Eye Institute Grant EY-12148.

**REFERENCES**


Coul J and Nohre AC. Where and when to pay attention: the neural systems for directing attention to spatial locations and to time intervals as revealed by both PET and fMRI. *J Neurosci* 18: 7426–7435, 1998.


