Multiple neural correlates of detection in the human brain

Gordon L. Shulman*†, John M. Ollinger‡, Martin Linenweber‡, Steven E. Petersen*‡§, and Maurizio Corbetta*‡§

Departments of *Neurology and Neurological Surgery, ‡Radiology, and §Anatomy and Neurobiology, Washington University, St. Louis, MO 63110

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We used event-related functional MRI to examine the neural consequences of detecting the presence or absence of a stimulus. Subjects detected a brief interval of coherent motion embedded in dynamic noise that was presented throughout a test period. Several brain regions, including V1/V2, middle temporal complex (MT+), left intraparietal cortex, and the frontal eye field, were activated at the onset of the dynamic noise, irrespective of whether a coherent motion target was presented early or late in the test period, or not at all. These regions, many of which were motion sensitive, were likely involved in searching for and detecting the target. The blood oxygenation level-dependent signal in these regions was higher in trials in which a target was detected than in trials in which it was missed or not presented, indicating that these regions were modulated by detection. Moreover, the blood oxygenation leveldependent signal in these regions decayed quickly once a target was detected, even though the dynamic noise continued to be displayed, indicating that they were shut down after detection. Therefore, detection-related modulations occurred in the same regions that accumulate target information over time, in agreement with current psychological and neural models of detection. Many other regions, however, including areas in prefrontal cortex and anterior cingulate, were not involved in searching for a target. In these regions, activation began early in the test period when an early target was detected but began late in the test period when a late target was detected or when a response was correctly withheld in the absence of a motion target. The signal in these regions was therefore triggered by a discrete event during the test interval that was related to presence–absence detection.

When a person searches for an object over an extended time period, evidence for the presence of that object is collected over time. If this evidence exceeds some criterion value, a detection response is made (1). Many cognitive tasks have a similar structure, in which a search phase, during which a person monitors the environment for some event, is ended when sufficient information has accumulated to trigger a response.

In this paper we examine how the blood oxygenation level-dependent (BOLD) signal throughout the human brain is affected by the detection of a stimulus. For example, the amplitude of the signal may be increased if the stimulus is detected (2, 3). Moreover, detection of the stimulus may end search processes, decreasing the subsequent signal in relevant areas. Finally, the timing of the BOLD signal in different areas may reflect different functional roles. Single unit studies have shown that when a monkey discriminates between two directions of motion, the activity of parietal and prefrontal neurons during a stimulus presentation period predicts the response the monkey will make (4, 5). These cells appear to accumulate information over time and may participate in the transformation of the sensory input to a binary motor output. Continuous flow models of information processing indicate that under conditions emphasizing speeded responses accumulating evidence feeds into structures that organize motor responses (6). These ideas suggest that brain regions involved in detection should be active from the start of the search phase of a task until the target stimulus is detected. Conceivably, however, some brain regions respond after a discrete event during the test interval, such as the detection response, when further processes might be engaged. For example, behavioral studies indicate that target detection produces a prolonged interference with the detection of subsequent targets (7, 8).

In the present study, subjects saw an arrow cue that indicated the possible direction of subsequent coherent motion (Fig. 1). After the end of the cue period, dynamic noise (randomly replotted dots) was displayed for a 4.72-s test period. Coherent motion was briefly presented either 0.4–1.8 s (early-target trials) or 2.8–4.2 s (late-target trials) after the start of the test period or was not presented (no-target trials, not shown in Fig. 1). Subjects pressed a key if they detected the target motion and withheld a response if no motion was detected.

We separated trials into early-target hits (target presented, detection response) late-target hits, misses (target presented, no detection response), and no-target correct rejections (target not presented, no detection response). Areas involved in search and detection should be active from early in the test interval on all trial types. If neural activity in these regions is affected by target detection and the subsequent termination of search processes, the BOLD signal in early-target hit trials should show an initial modulation, relative to the other trial types, but should then fall off sharply. Other regions that are not engaged until presence–absence detection, however, should show a delayed response in late-target hit and no-target correct rejection trials, relative to early-target hit trials.

Methods

Subjects. Twelve right-handed subjects gave informed consent in accordance with guidelines set by the Human Studies Committee of Washington University.

Stimuli. Fifty white dots, presented on a black background, were randomly positioned within a 3.25° circular aperture. Dynamic noise was produced by randomly replotting the dots on each 30-ms display frame. Coherent motion was produced by translating a fraction of the dots in each frame. The speed of coherent motion was 4.2°/s. A central fixation cross was present throughout the trial.

Procedure. An arrow cue indicated the direction in which subsequent coherent motion might occur. The arrow was presented for

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Abbreviations: BOLD, blood oxygenation level-dependent; FEF, frontal eye field; MR, magnetic resonance; MT+, middle temporal complex.

†To whom reprint requests should be addressed at: Department of Neurology, Washington University, Box 8111, 660 South Euclid, St. Louis, MO 63110. E-mail: gordon@npg.wustl.edu.

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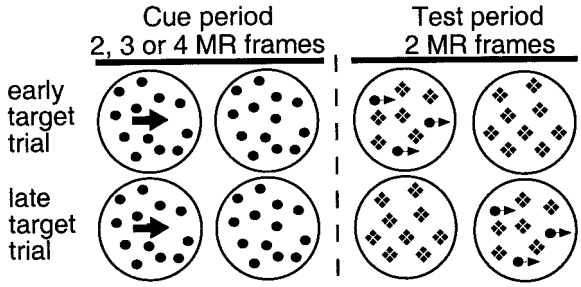

Fig. 1. Procedure in early- and late-target trials. The diamond symbols in the test period schematically indicate dynamic noise. The small arrows during the test period schematically indicate that some dots moved coherently.

Table 1. Number of areas that significantly rise above baseline on MR frames 3 and 4 as a function of trial type

Frame 3 > frame 2					Frame 4 > frame 3		
Early hit	Late hit	No-target	*N*		Late hit	No-target	*N*
Y	**Y**	**Y**	**11**				
Y	Y	N	2				
Y	N	Y	0				
Y	**N**	**N**	**23**	⇨	**Y**	**Y**	**21**
N	Y	Y	0		N	Y	0
N	Y	N	1		Y	N	2
N	N	Y	0		N	N	0
N	N	N	1				

1,600 ms and then removed for the duration of the cue period (Fig. 1). For 25% of the trials (cue trials), after a cue period of 4.72, 7.08, or 9.44 s [2–4 magnetic resonance (MR) frames, frame duration 2.36 s], the trial ended. For the other 75% of the trials (cue + test trials), after the cue period, dynamic noise was presented for a 4.72-s test period (two MR frames). In one-third of these cue + test trials, a coherent motion target (300-ms duration) was randomly presented between 0.4 and 1.8 s from the start of the test period (early-target trials); in one-third of these trials, the target was presented between 2.76 and 4.22 s from the start of the test period (late-target trials), and in one-third of these trials no target was presented (no-target trials). Target motion was always in the direction indicated by the arrow cue. Subjects pressed a key with their right hand as quickly as possible if they detected motion and withheld a response if no motion was detected. The percentage of dots undergoing coherent motion was determined for each subject in a behavioral presession so that roughly 80% of the targets were detected.

Imaging Methods. MRI scans were collected with a Siemens 1.5-Tesla Vision system, with the use of an asymmetric spin-echo echo-planar imaging (EPI) sequence sensitive to BOLD contrast (T2* evolution time = 50 ms, flip angle = 90°) (9). During each scan, 128 2.36-s frames containing 16 contiguous 8-mm axial slices (3.75 × 3.75 mm in plane) were acquired. Structural images were collected with a sagittal magnetization prepared rapid acquisition gradient echo (MP-RAGE) sequence. Functional data were realigned within and across scans to correct for head movement. Differences in the time of acquisition of each slice within a frame were compensated for by interpolation, so that slices were time-aligned to the beginning of each frame.

Data Analysis. The BOLD signal was analyzed with a linear regression model that used the cue and cue + test trials to estimate the time courses of the signals during the cue and test periods without making any assumption about the shape of the hemodynamic response (10). Signals during the test period were segregated according to the type of trial (early-target, late-target, no-target) and whether subjects made a detection response. Regions were defined from the main effect of MR frame (frames 1–10) in a voxel-level within-subject ANOVA on the time courses for the test period in target trials. The resulting *F*-statistic isolated regions that showed significant changes in the BOLD signal over time without making any shape assumption. Regions of interest were defined from regions that showed local maxima in this main effect image with *z* scores exceeding 5.23, corresponding to a whole-brain, voxel-wise Bonferroni multiple-comparison correction.

Definition of Early-Onset and Late-Onset Regions During the Test Period. Differences in the shapes of the time courses for different trial types (e.g., early- vs. late-target trials) were evaluated by testing for an interaction between trial type and MR frame. If a region showed a significant interaction, then *F* tests were conducted to compare trial types at individual MR frames.

Regions were classified as "early onset" (e.g., areas respond at the start of the test interval for all trial types) or "late onset" (e.g., the signal in late-target hit trials and no-target correct rejection trials is delayed relative to the signal in early-target hit trials), based on the MR frame at which the BOLD signal rose above baseline for different trial types. Formally, regions were classified as early onset, if for each of the three trial types (early- and late-target hit trials, and no-target correct rejection trials), the BOLD signal in MR frame 3 was significantly ($P < 0.05$) greater than the signal in frame 2 (see entries in bold in row 1 of Table 1). Frame 3 occurred at 4.72 s from the onset of the dynamic noise, roughly corresponding to the typical hemodynamic lag of the BOLD signal.

Regions were classified as late onset if the BOLD signal rose above baseline in frame 3 for early-target hit trials but did not rise above baseline until frame 4 for both late-target hit trials and no-target correct rejection trials. We expected the signal to increase in frame 4, rather than frame 3, during these latter trials because late targets were delayed by one frame. We did not expect to see clear differences between late-target and no-target trials, because the onset of the late target and the offset of the dynamic noise were separated only by 1/2 MR frame. These considerations led to the following formal late-onset criteria: (*i*) in early-target hit trials, the signal in frame 3 was significantly greater than the signal in frame 2; (*ii*) in late-target hit trials and no-target correct rejection trials, the signal in frame 3 was not significantly greater than the signal in frame 2; and (*iii*) in the latter two types of trials, the signal in frame 4 was significantly greater than the signal in frame 3 (see the entries in bold in row 4 of Table 1).

A region was defined as early or late onset only if multiple statistical tests were simultaneously satisfied. As the number of tests increases, the likelihood decreases that all tests will spuriously show a particular pattern. This procedure was therefore fairly conservative.

Results

Behavior. Subjects detected the motion target in 82.8% of the trials and made false alarms in 6.2% of the trials. There was no significant difference in the percentage of targets detected between early-target (81.9%) and late-target trials (83.7%) [$F(1,11) = 0.71$] or in the reaction time between early- (598 ms) and late-target (587 ms) hit trials [$F(1,11) = 1.2$].

Cue Period. BOLD signals during the cue period were identical to those reported by Shulman *et al.* (10) and will be discussed only briefly. The foveal arrow cue evoked transient signals in several occipital areas [e.g., lateral occipital, middle temporal complex (MT+) and more sustained signals in areas within the intrapa-

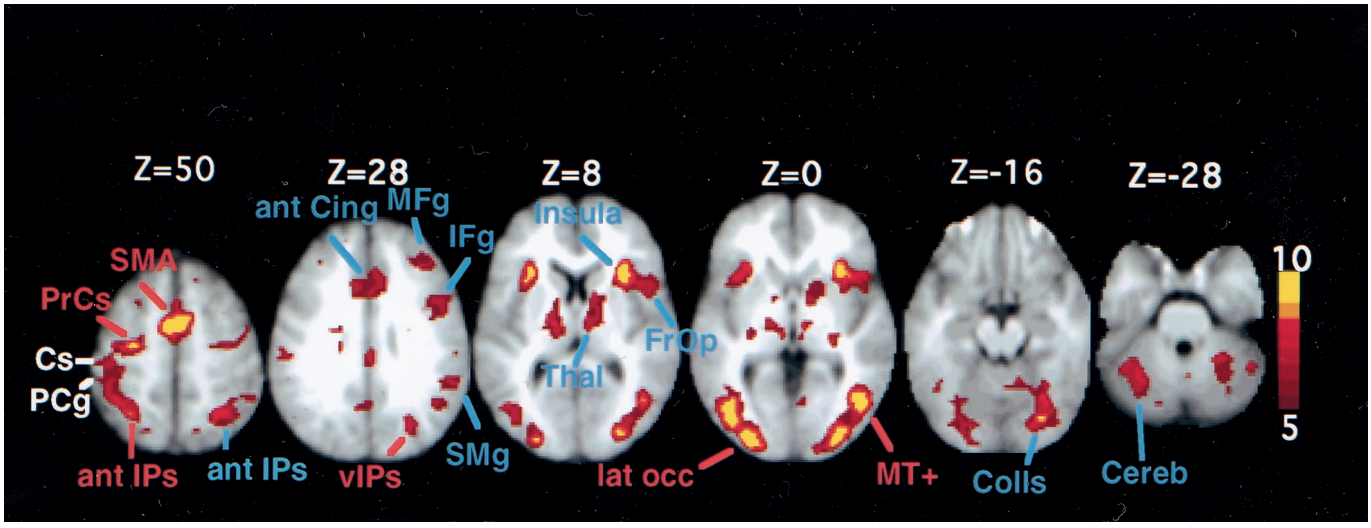

Fig. 2. Regions active during the test period. Regions labeled in white, red, and blue correspond to motor, early-onset, and late-onset regions, respectively. The color scale refers to the *z* value of the main effect of time in a within-subject voxel-wise ANOVA on the target period time courses. PrCs, precentral sulcus; Cs, central sulcus; PCg, postcentral gyrus; ant Ips, anterior intraparietal sulcus; ant Cing, anterior cingulate; SMg, supramarginal gyrus; Thal, thalamus; FrOp, frontal operculum; MFg, middle frontal gyrus; Ifg, inferior frontal gyrus; lat occ, lateral occipital; Colls, collateral sulcus; Cereb, cerebellum.

rietal sulcus. Frontal cortex activations were observed in the medial precentral sulcus and the supplementary motor area.

Accuracy of Time-to-Onset Estimation during the Test Period. We first showed that we can distinguish the time of onset of the BOLD signal produced by events, such as key presses, that occurred early or late in the test period. We examined the time course of the BOLD signal in regions significantly activated only by the right-hand key press (e.g., left central sulcus, left postcentral gyrus; see regions labeled in white in Fig. 2) in hit trials. Fig. 3 (top row) shows that key presses produced a BOLD signal that rose above baseline in frame 3 (each data point in the graph represents the signal in a single MR frame) of early-target hit trials and frame 4 of late-target hit trials. No significant signal was observed in no-target trials in which subjects correctly withheld a key press. The BOLD signals reflected the different times of onset of the key presses.

The time course of the BOLD signal in most nonmotor regions that were active during the test period showed two divergent patterns that reflected whether they were engaged during the search phase of the task (an early-onset pattern) or only became active at or after the time of presence–absence detection (a late-onset pattern). The left part of Table 1 shows the number of regions in which the BOLD signal rose significantly ($P < 0.05$) above baseline in frame 3 (i.e., the signal in frame 3 was significantly greater than the signal in frame 2) during the three trial types (early-target hit, late-target hit, no-target correct rejection). If the time at which the BOLD signal rose above baseline was unrelated to the trial type, then all regions would distribute equally among the eight different possibilities shown on the left side of Table 1. The observed distribution, however, clustered into two types, an early- and a late-onset pattern.

Early-Onset Regions. Eleven regions in frontal, parietal, and occipital cortex (some labeled in red in Fig. 2) met the statistical criterion that defined early-onset regions (Table 1, row 1; see Table 2 for Talairach coordinates and peak *z* scores). Fig. 3 (second and third rows) shows the time course of the BOLD signal in four of these regions. These regions were activated early in the test period for all trial types and therefore were engaged during the search phase of the task. This characterization is supported by the fact that an early-onset pattern was observed in motion-sensitive regions (e.g., MT+), which responded to the onset of the dynamic noise at the start of the test period (11–13).

The shape of the time courses in Fig. 3 indicates that early-onset regions were modulated by signal detection. In early-target hit trials, the BOLD signal in frame 3 (see black arrow in Fig. 3) was significantly increased, relative to both late-target hit trials and no-target correct rejection trials. This modulation did not simply reflect the stimulus difference between these trial types. Fig. 4 shows that in early-target trials the BOLD signal was larger when the target was detected than when it was missed, even though the two types of trials involved the same sensory stimulus. This modulation involved both early (V1/V2) and intermediate (MT+) stages of the visual hierarchy. The signal in miss trials was similar to the signal in no-target trials, indicating that there was no detectable BOLD signal specific to the coherent motion. This lack of a specific detectable BOLD signal is not surprising, because weak coherent motion only occurred for 300 ms. Because there were almost five times as many hit trials as miss trials, contrasts involving the miss trials have less power, but the basic result was still obtained. The left side of Table 3 lists the early-onset regions, showing a significantly increased signal in frame 3 of early-target hit trials relative to the other trial types. Similar effects, although not reliable in all regions, were observed on frame 4 for late-target hit trials compared with no-target trials.

Further evidence that early-onset regions were affected by signal detection is seen in the significant decrease in signal during late frames (e.g., frame 5) in early-target hit trials, relative to both late-target hit trials and no-target correct rejection trials (see gray arrow in Fig. 3 and right side of Table 3). The BOLD signal decreased once a target was detected, even though dynamic noise was still displayed. This effect was evident in both motion-sensitive regions such as MT+ and motion-insensitive regions such as the medial precentral sulcus. Although a similar trend was observed in V1/V2, this effect was not as reliable (Table 3). Significant decreases also were observed relative to early-target miss trials (Table 3 and Fig. 4), indicating that late frame modulations were not caused by stimulus differences.

Late-Onset Regions. Twenty-one regions (see Table 1, row 4) in frontal, parietal, and occipital cortex and subcortical regions (some shown in blue in Fig. 2; see Table 2 for Talairach

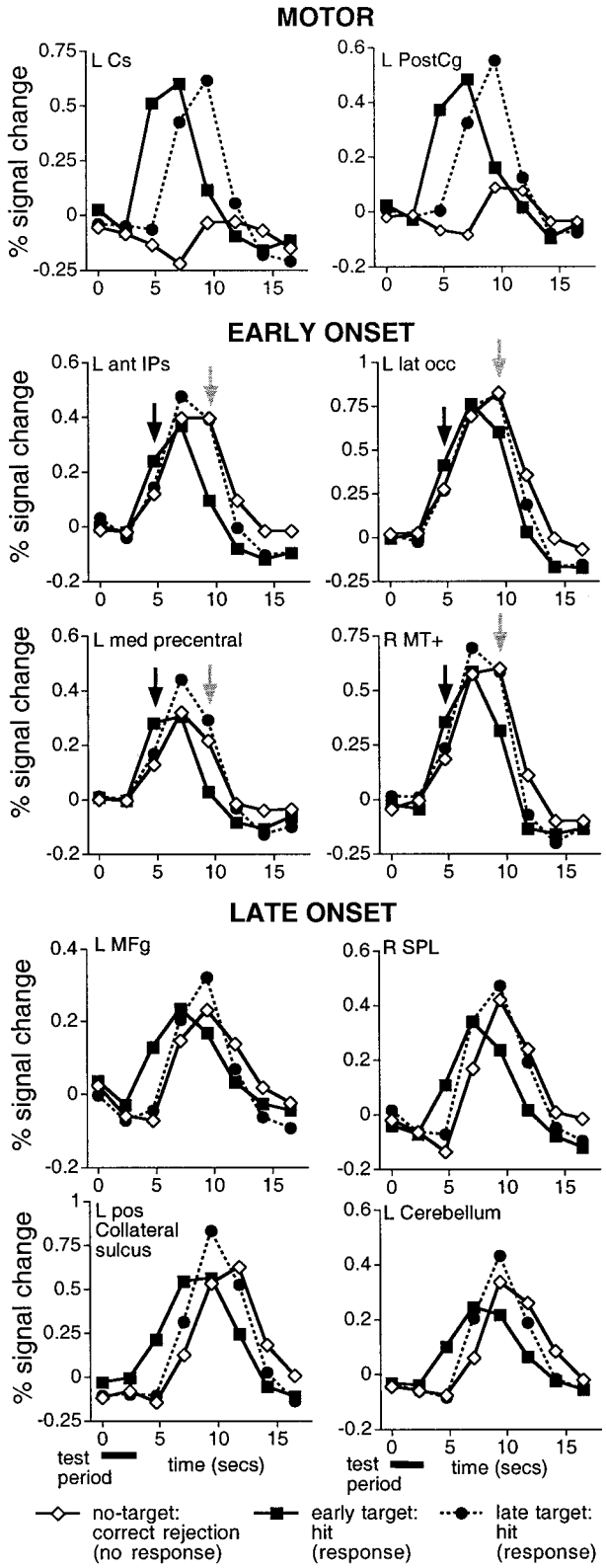

Fig. 3. Group mean time course of the BOLD signal for motor, early-onset, and late-onset regions. The black arrows point to frame 3, which showed a significantly higher signal in early-target hit trials than in late-target hit or no-target correct rejection trials. The gray arrows point to frame 5, which showed a significantly smaller signal in early-target hit trials than in late-target hit or no-target correct rejection trials. Cs, central sulcus; PostCg, postcentral gyrus; ant IPs, anterior intraparietal sulcus; lat occ, lateral occipital; med, medial; MFg, middle frontal gyrus; SPL, superior parietal lobule; pos, posterior.

coordinates and *z* scores) met the statistical criterion that defined late-onset regions. Fig. 3 (rows 4 and 5) shows that in early-target hit trials, the BOLD signal rose above baseline in frame 3, as for early-onset regions. In late-target hit trials or in no-target correct rejection trials, however, the BOLD signal did not rise above baseline until frame 4, one frame later. The robust signal in no-target trials contrasts strongly with the absence of a reliable signal in these trials in motor regions.

We have confined our description of the timing of the signal to early vs. late in the test interval, because the time courses for the motor regions showed that we can reliably distinguish events separated by one MR frame. However, the results indicate that events separated by less than one MR frame can sometimes be distinguished. The BOLD signal in late-target hit trials, for example, generally decayed earlier than the signal in no-target trials, consistent with the hypothesis that the search was terminated when the late target was detected, rather than at the end of the dynamic noise interval, roughly 1/2 MR frame later (a result similar to the fall-off of the BOLD signal in early-target hit trials; see Fig. 3, early-onset regions). Significant differences between late-target hit trials and no-target trials were observed in frame 7 in 9/11 early-onset regions and 12/21 late-onset regions.

Discussion

The current results demonstrate a strong effect of presence–absence detection on the shape and timing of the BOLD signal. A relatively small set of early-onset areas was active from the start of the test period and therefore was engaged while subjects searched the dynamic noise for a target. These early-onset areas were modulated by the detection of the target. The BOLD signal in early-target hit trials initially was enhanced, relative to the other trial types, but then showed a sharp fall-off after detection. A second, larger set of late-onset areas became active only at or after the point of presence–absence detection. These regions were not involved in the search for the target.

Early-Onset Regions. The BOLD signal in early-onset regions began early in the test period and at roughly the same time for all trial types. This pattern indicates that these regions initially became active when the dynamic noise was searched for a motion target. This interpretation is supported by the fact that motion-sensitive regions such as V1/V2, MT+, and the lateral occipital region, which respond to the dynamic noise (10), all showed an early-onset pattern.

Activations in these regions did not simply reflect passive sensory stimulation by the dynamic noise. Although this seems clear for the frontal regions, supplementary motor area, and the medial precentral sulcus, which do not respond to the passive presentation of radially moving stimuli (10), it is shown more generally by the fact that virtually all early-onset regions showed two detection-related modulations. The BOLD signal was significantly enhanced in early frames and significantly decreased in late frames when an early target was detected, relative to when it was missed, detected late, or not presented.

The most likely explanation for the signal decrease in late frames is that once the target was detected, the search was terminated, decreasing the BOLD signal. This effect was even evident in motion-sensitive regions such as MT+, which showed a reduced response while the dynamic noise continued to be displayed. Previous imaging studies also have shown attentional modulations in MT+ (12, 14), and the present data indicate that the BOLD signal in MT+ tracked momentary changes in the attentional demands of the task.

The enhancement for detected targets may reflect an endogenous modulation, such as the match between the subject's expectation for a particular direction of motion, formed during the cue period, and the actual direction that was detected (15).

Table 2. Talairach coordinates and *z* scores for peak voxel in early-onset and late-onset regions

Early onset	*x*	*y*	*z*	*z* score	Late onset	*x*	*y*	*z*	*z* score	Late onset	*x*	*y*	*z*	*z* score
SMA	5	3	48	11.2	ant cingulate	7	17	34	8.9	R supramarginal gyrus	51	−41	30	7.7
L medial precentral	−27	−11	48	9.8	R lateral precentral	45	−3	34	8.5	L pos collateral sulcus	−17	−81	−18	7.7
R medial precentral	35	−11	50	7.1	L MFg	−33	35	34	8	R pos collateral sulcus	27	−79	−18	9.6
L ant IPs	−31	−55	46	9.2	R MFg	33	43	20	7.3	L ant collateral sulcus	−27	−71	−10	6.9
R ventral IPs	29	−73	24	8	R dorsal IFg	49	11	24	7.6	R ant collateral sulcus	29	−65	−14	9.1
L lateral occipital	−29	−89	−2	11.6	L ant insula	−29	19	8	9.8	L ant fusiform	−41	−59	−10	8
R lateral occipital	31	−89	−4	10.9	R ant insula	29	21	6	10.7	L thalamus	−15	−15	6	8
L MT+	−43	−71	2	10	R frontal operculum	51	5	16	9	R thalamus	7	−17	12	7.8
R MT+	43	−65	0	10.8	R ant IPs	29	−53	48	8.7	L cerebellum	−31	−53	−32	8.8
L V1/V2	−21	−91	−10	10.4	R postcentral gyrus	47	−45	42	6.6	R cerebellum	23	−51	−26	7.8
R V1/V2	19	−95	−8	10.3	R SPL	15	−69	40	7.7					

ant, anterior; pos, posterior; IPs, intraparietal sulcus; MFg, middle frontal gyrus; IFg, inferior frontal gyrus; SPL, superior parietal lobule.

Alternatively, the target modulation may reflect trial-by-trial variability in the neural signal. Trials in which the neural signal happened to be large would trigger a detection response (16).

Thompson *et al.* (3) have reported greater cell activity in monkey frontal eye field (FEF) in trials involving hits than misses and greater activity in trials involving false alarms than correct rejections. This pattern is orthogonal to that reported by Ress *et al.* (2), in which BOLD signals in V1 during threshold detection were larger after correct responses (hits and correct rejections) than incorrect responses (false alarms and misses). In our study, a signal enhancement was observed in hit trials, but not in correct rejection trials, a pattern more similar to that reported by Thompson *et al.* (3) for monkey FEF. The current modulation, however, was observed at multiple levels in the visual system, including V1/V2, MT+, intraparietal cortex, and the medial precentral sulcus, which is thought to be a homolog of the FEF (17). Previous work from this laboratory shows that the intraparietal cortex and FEF are involved in directing visual attention to a relevant stimulus and in maintaining a visual expectation on-line during a memory delay (10, 18). Whereas activity in MT+ and other occipital regions probably reflected the analysis of relevant visual features and the accumulation of information about the presence of motion, intraparietal cortex and FEF were likely involved in directing attention or using the directional information provided by the arrow cue to guide the search for a target.

The involvement of FEF during the search for a target is also consistent with previous single-unit (19, 20) and neuroimaging studies. Several imaging studies, for example, have shown that this region, while active during eye movements, also is activated by attentional processes when the eyes remain still (21–23).

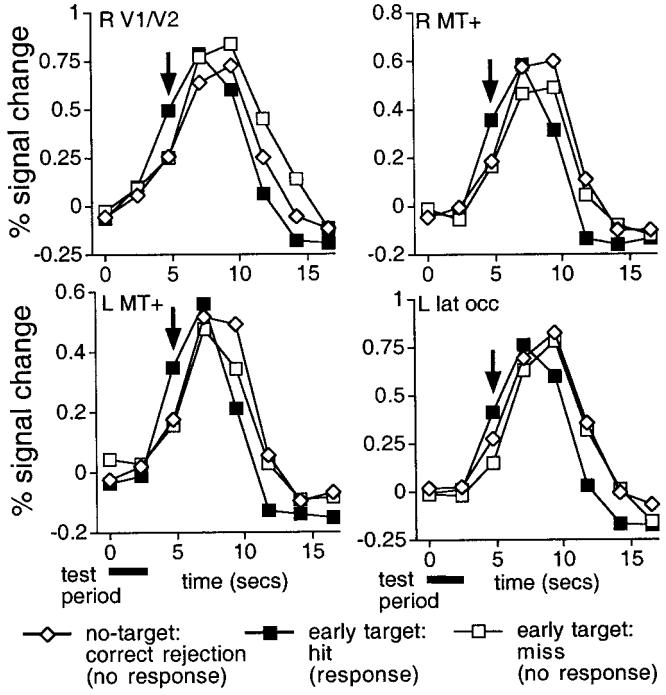

Fig. 4. Group mean time course of the BOLD signal in four early-onset regions during early target hit and miss trials and no-target correct rejection trials. The black arrows point to frame 3, which showed a significantly higher signal in early-target hit trials than in early-target miss or no-target correct rejection trials.

Late-Onset Regions. The BOLD signal in late-onset regions rose above baseline early in the test period in early-target hit trials, but late in the test period in both late-target hit trials and no-target correct rejection trials. This pattern of results indicates that these regions were not active during the search for a target.

It is very unlikely that these regions involved a purely motor function. First, late-onset signals did not reflect motor execution because they were activated by roughly the same magnitude both in trials in which a response was made and in trials in which a response was withheld. Second, late-onset signals could not reflect motor preparation. Motor preparation had to start at the beginning of the test period, because subjects did not know when

Table 3. Significant differences between different trial types at early and late MR frames in early onset regions

	MR frame 3 Early hit greater than			MR frame 5 Early hit less than		
	Late hit	No-target	Early miss	Late hit	No-target	Early miss
SMA	***	***		***	***	***
L med PrC	*	***		***	***	*
R med PrC		*		***	***	*
L ant IPs	*	***		***	***	***
R vIPs		*	*	***	***	*
L lat occ	*	***	*	***	***	*
R lat occ	*	*	***	***	***	*
L MT+	**	***	*	***	***	
R MT+	*	***	*	***	***	*
L V1/V2	*	*	**			*
R V1/V2	*	**	*	*		

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.005$.

PrC, Precentral; IPs, intraparietal sulcus; med, medial; v, ventral; ant, anterior; lat, lateral; occ, occipital.

a target might be presented. Subjects, in fact, made half of their responses early in the test interval and half of their responses late in the test interval. Regions involved in motor preparation therefore should show an early-onset pattern, which may explain the observed time courses in supplementary motor area (24). A third possibility is that late-onset areas were activated both by making a response (in early- and late-target trials) and by withholding a response (in no-target trials). However, in no-target trials, a response was withheld early in the test interval and late in the test interval. In late-target trials, a response was withheld early in the test interval but was made late in the test interval. Any area that signals whether a response is currently being made or withheld would show an early-onset pattern. Finally, it is implausible that a single motor process adequately describes the function of over 20 regions in prefrontal, parietal, and occipital cortex, as well as bilateral thalamus and cerebellum.

Continuous flow models of information processing assert that the output from processes involved in stimulus evaluation is continuously fed into processes involved in preparing an appropriate motor response (6). Similarly, single-unit studies show a continuous growth of activity that predicts the behavioral response in parietal and frontal regions (4, 5). The early-onset activation pattern fits well with this conception, and we have argued that these regions are critical for search and detection.

However, the majority of areas showed a late-onset pattern that does not fit the above conception. These activations were time-locked to a discrete event during the test interval. In hit trials, the discrete event was the detection of the target, which was indexed by the key press. In no-target trials, the discrete event was probably the offset of the dynamic noise, which marked the termination of the search. This is consistent with the slightly delayed fall-off of the BOLD response in both early- and late-onset regions in no-target trials, relative to late-target trials. The most parsimonious explanation for the delayed BOLD signal in late-target and no-target trials is that the two events (i.e., target detection and the offset of the dynamic noise) triggered a similar series of processes that activated late-onset areas.

It is beyond the scope of this study to detail these processes, but there is good evidence for the existence of detection-related processes. Behavioral studies, for example, show that target detection produces prolonged interference with the detection of subsequent targets (7, 8), and this interference is independent of any motor detection response. The offset of the dynamic noise may produce a similar "target-absent" state that also generates interference.

We are not suggesting that all 21 late-onset regions came on line at exactly the same time. As noted above, we believe these areas are involved in a variety of processes. The coarse temporal resolution of BOLD imaging prevents us from distinguishing fine temporal differences between late-onset areas that undoubtedly exist. But the results clearly show that late-onset areas are time-locked to discrete events that reliably occur early or late during the test interval.

Furthermore, it is interesting that most single-unit studies of decision processes in monkey have not recorded from many of the late-onset regions observed in the present study (4, 5). Our data indicate that these areas will be related to detection but will not show a continuous growth of predictive activity during the test period.

Finally, late-onset, prefrontal regions such as dorsolateral prefrontal cortex and the anterior cingulate, often are related to working memory and the control of attention (25, 26). A prior study, however, showed that these regions were not active during the cue period of the current, simple task, in which an attentional set was encoded and maintained (10). Activation in these areas was confined to the test period. The same result was obtained when the attentional set encoded a relevant target location (18). The current work confirms this result and further shows that during the test period these prefrontal regions were not involved in controlling the search for the target or applying the cue information to that search.

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