The physiological basis of attentional modulation in extrastriate visual areas

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Selective attention to color or motion enhances activity in specialized areas of extrastriate cortex, but mechanisms of attentional modulation remain unclear. By dissociating modulation of visually evoked transient activity from the baseline for a particular attentional set, human functional neuroimaging was used to investigate the physiological basis of such effects. Baseline activity in motion- and color-sensitive areas of extrastriate cortex was enhanced by selective attention to these attributes, even without moving or colored stimuli. Further, visually evoked responses increased along with baseline activity. These results are consistent with the hypothesis that attention modulates sensitivity of neuronal populations to inputs by changing background activity.

Substantial experimental evidence from humans and non-human primates implicates the extrastriate visual area V5 (located in the posterior region of the inferior temporal gyrus and sulcus) in motion processing and area V4 (located in the fusiform gyrus) in color processing[1–6]. Research suggests that attention to color or motion enhances activity in V4 or V5 respectively. In non-human primates, the effect of attention on neuronal activity is to enhance both baseline activity[7,8] before a visual stimulus is presented and activity evoked by a stimulus with the attended attribute. Studies of macaque visual cortex suggest that the responses of most V5 cells are reduced when attention is directed to moving stimuli that are outside the cell's receptive field but are enhanced when attention is directed to stimuli within the receptive field[9]. In humans, neuroimaging (positron emission tomography; PET[10] and functional magnetic resonance imaging; fMRI[11,12]) shows that V5 activity is enhanced when subjects attend to motion rather than view moving stimuli passively. V4 responses to color stimuli are also enhanced by attending to their color[10,13,14]. Under conditions of attention, electrophysiology in monkeys reveals that increased selectivity and responses enhanced by ~20% were found in 72% of V4 cells tested[13]. Another electrophysiological study found that V4 cell responses increase and become more selective as a color discrimination task becomes more difficult and requires more attention[14]. These results suggest that extrastriate responses to visual stimuli are modulated according to task demands. In other words, responses to individual attributes can be selectively enhanced by attention.

The above studies show attentional modulation of stimulus-evoked responses. Fewer studies have explicitly investigated attentional modulation of baseline activity. Macaque studies explored baseline shifts in neuronal responses in the context of working memory[8]. They found that both baseline activity and activity evoked by a moving stimulus appear to change with expectation. Even when subjects view a blank screen, baseline activity in 32% of V5 cells doubles. Using direction of motion as the matching criterion, this study employed a delayed match to sample task. Modulation of delay period or baseline activity was not related to specific information in the cue (direction), suggesting that this effect may be modulated, in part, by attention. When interpreting our results in relation to these findings, we assume that baseline attentional modulation is mediated by the same sort of tonic discharge associated with delay period activity evoked by working memory tasks. Monkey electrophysiology also shows that attention can modulate both baseline and stimulus evoked activity in V4, depending on the relative locations of visual stimuli within the cell's receptive field[7].

Enhanced baseline activity is taken to reflect attentional 'set' or expectation, whereas changes in stimulus-evoked activity reflect changes in sensory processing[10]. However the functional significance of and relationship between changes in 'set' and changes in evoked activity is unknown. Because of the long periods of time over which hemodynamic signals are integrated, it has been difficult to unambiguously dissociate activity due to attentional set from stimulus-evoked responses in human functional neuroimaging studies[15]. Here, by using a novel event-related protocol and fMRI, we show such a dissociation in V5 and V4, relating attentional set and evoked activity in accord with

Table 1. Performance of each subject in the color and motion target detection tasks.

	Speed		Color		Overall	
Subject	Correct	Incorrect	Correct	Incorrect	Correct	Incorrect
One	83%	19%	92%	22%	88%	20%
Two	75%	11%	94%	31%	80%	21%
Three	88%	22%	94%	25%	92%	24%

'Correct' denotes events that the subject responded to correctly. 'Incorrect' denotes false-positive responses.

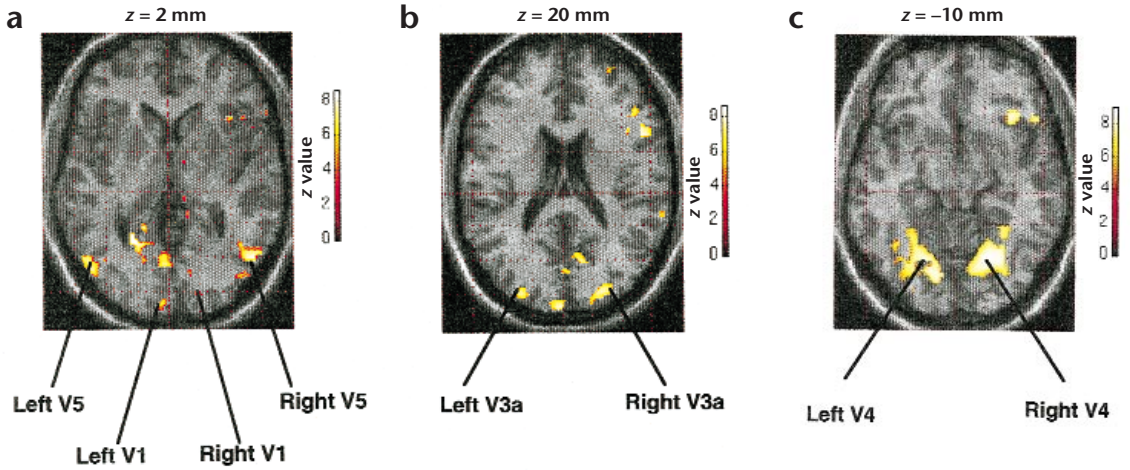

Fig. 1. SPM(*Z*) (threshold, $p < 0.01$, uncorrected) showing the main effect of the stimulus versus baseline over subjects, masked with the main effect from each individual subject (that is, a conjunction of significant effects over all three subjects) and rendered on a structural MRI scan. **(a)** Bilateral regional effects in V1 and V5. **(b)** Bilateral V3a. **(c)** Bilateral V4.

hypotheses based on recent computational studies[16].

Our specific hypothesis was motivated by computational studies of simulated neuronal populations[16] and posits a simple mechanism for attentional modulation. This mechanism addresses important conclusions derived from monkey electrophysiology: single-neuron recordings[7] suggest that when multiple stimuli fall within a cell's receptive field, they compete for the cell's response in a manner that can be biased in favor of the attended stimuli. Computational studies of simulated neuronal populations show that stimulus-evoked rate modulation increases with tonic, background population activity[16]. This suggests that attentional modulation of evoked responses may be mediated by increasing background activity in the appropriate functionally specialized populations, and predicts tonic activation in the appropriate functionally specialized cortical area when attending to a specific attribute of the sensory field. Importantly, this effect should be seen in the absence of any stimuli. Furthermore, computational results predict a specific relationship between changes in background activity and evoked transient activity: areas showing attention-specific increases in baseline activity should also show enhancement of transient evoked responses.

Here we test and confirm these theoretical predictions in humans by separating activity associated with attentional set from that evoked by presentation of a visual stimulus. Using event-related fMRI[17,18], we examined transient V5 or V4 responses to motion or color stimuli under different levels of attention. Subjects viewed a stationary monochromatic random dot display in which dots intermittently changed color and moved radially. By asking subjects to detect and discrimi-

Table 2. Talairach coordinates of the maxima in V1, V5, V3a and V4 testing for the main effect of the stimulus event in each subject.

Subject	Area	*Z*-score (stimulus M. E.)	x	y	z	*Z*-score (motion baseline – color baseline)	*Z*-score interaction (motion > color)
#1	Left V5	7.71**	–50	–74	6	2.78*	1.95*
	Right V5	6.89**	52	–66	6	2.42*	1.86*
	Left V3a	3.92*	–22	–82	28	2.27*	–1.79*
	Right V3a	7.77**	24	–88	26	3.02*	0.72
	Left V1	8.52**	–8	–90	0	1.11	0.84
	Right V1	7.39**	16	–88	6	0.58	–0.80
	Left V4	7.72**	–30	–72	–16	–2.82*	–1.90*
	Right V4	8.37**	30	–64	–14	–2.43*	–1.96*
#2	Left V5	7.43**	–54	–64	0	2.66*	2.22*
	Right V5	7.46**	56	–66	0	2.99*	2.37*
	Left V3a	7.22**	–22	–86	26	2.80*	–0.63
	Right V3a	7.47**	22	–90	22	2.89*	1.47
	Left V1	6.39**	–2	–96	–2	–1.50	0.87
	Right V1	3.84*	10	–94	–2	–2.29*	0.66
	Left V4	7.55**	–30	–78	–16	–2.64*	–1.91*
	Right V4	7.00**	18	–74	–6	–2.70*	–1.89*
#3	Left V5	7.45**	–50	–76	6	2.12*	2.53*
	Right V5	7.03**	44	–58	12	2.07*	2.75*
	Left V3a	7.94**	–20	–88	30	3.05*	–0.78
	Right V3a	6.39**	20	–88	34	2.66*	–0.33
	Left V1	6.92**	14	–98	6	0.43	0.19
	Right V1	3.46*	–8	–98	2	–0.78	1.79*
	Left V4	7.82**	–36	–78	–18	–2.83*	–2.06*
	Right V4	8.25**	38	–62	–18	–2.56*	–2.12*

The table gives the *z*-scores of the maxima from the stimulus main effect ($p < 0.001$, uncorrected). The table also contains the *z*-scores of the main effect (M. E.) of motion/color baseline and the interactions (motion > color and *vice versa*), in that order. These *z*-scores are from the same voxels as in the main effect of the stimulus and are significant at $p < 0.05$. Note that the *z*-scores for the group were much larger, but we elected to show subject-specific *z*-scores to demonstrate reproducibility of these results. *$p < 0.05$, uncorrected; **$p < 0.05$, corrected.

nate between these and sporadic target events using either color or motion cues, attentional modulation of activity evoked by the transient stimuli could be measured. However, our design also allowed us to measure, between stimuli, modulation of baseline activity by attentional set or expectation. During these times, the stimulus did not change position or color. We characterized these two measures of attentional modulation in two functionally specialized extrastriate visual areas (V4 and V5), replicating our findings independently in both hemispheres of three subjects.

Results

Behavior

All subjects reported the task to be demanding, requiring constant attention to the attribute (color or motion) in question. All subjects responded correctly on between 80 and 92% of target events (see Methods) and incorrectly on between 20 and 24% of non-target events (Table 1). These results indicate that the subjects were able to discriminate the target events from the normal events, although the difference was sufficiently subtle that the subjects sometimes mistook non-target events for target events.

The experimental design allowed us to model the effects of attention in terms of baseline changes and stimulus responses separately. Here we present findings that reflect the activity evoked by transient visual events *per se*, the effect of attentional set and the interaction between the visual events and attentional set. The latter reflects the modulation of evoked responses by attention to color or motion.

Neurophysiology

Figure 1 shows the hemodynamic response to the main effect of stimulus events (pooled over color and motion). In each of the subjects, responses were seen bilaterally in the calcarine sulcus (primary visual cortex or V1), in the posterior region of the inferior temporal gyrus and sulcus[3,4] (V5; Fig. 1a), in the superior part of the middle occipital gyrus that extended to the border of the angular gyrus[19] (V3a; Fig. 1b) and in the fusiform gyrus[5] (V4; Fig. 1c, Table 2).

A main effect of motion attentional set was obtained by subtracting the color from the motion attention baseline in areas V5 and V3a in all subjects (Table 2). Likewise, all subjects showed a main effect of color attention in V4 (Table 2). Table 2 shows the *z*-scores of the main effect of attentional set for stimulus main effect maxima. In addition to the areas shown in Table 2, a small number of voxels revealed a main effect of motion attention bilaterally in V4 in all subjects (uncorrected $p < 0.05$). Because these were not observed at the V4 maximum for the main effect of events, these areas are not considered further.

To examine attentional modulation of evoked responses, we tested for interactions in the maxima of regions showing a main effect of events in V5 and V4. In V5 (Fig. 1a), evoked hemodynamic responses were greater under motion attention than under color attention in all subjects (Fig. 2b, d and f). This modulation was expressed above the increased differential motion attention baseline described above (Fig. 2a, c and e). Furthermore, in the maxima of V4 (see Fig. 1c), responses to events were greater under color attention than under motion attention (Fig. 3b, d and f); color attention baseline was also increased (Fig. 3a, c and e). Effects were seen bilaterally in V4 and V5 in all subjects; examples from one hemisphere in each subject are shown in Figs. 2 and 3. These results suggest that attention modulates both baseline activity and evoked responses in agreement with both the functional specializations of V4 and V5 and our predictions.

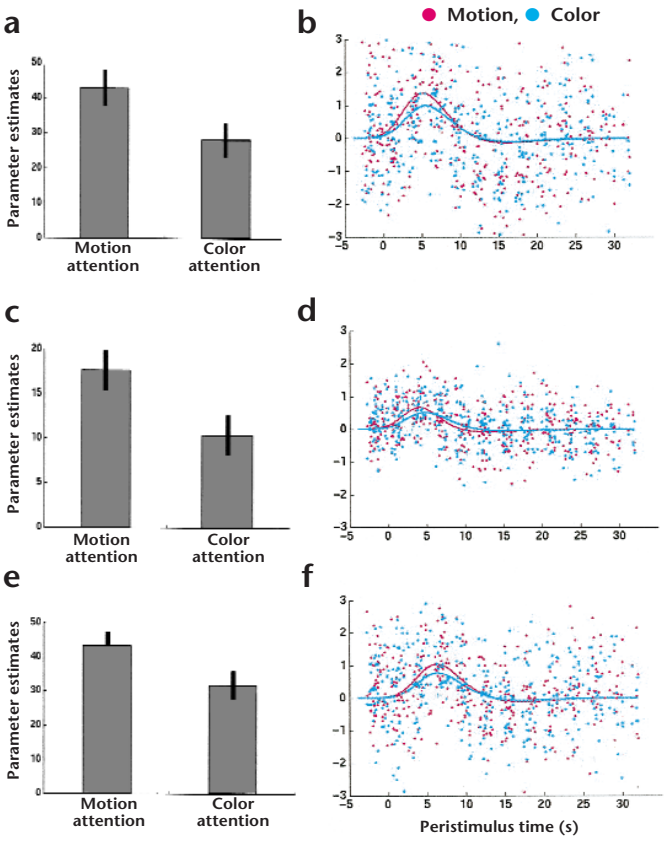

Fig. 2. Activity and responses in V5 as a function of attention in all subjects. **(a)** Parameter estimates with standard errors for baseline effects under both levels of attention in left V5 in subject one. **(b)** Adjusted data and fitted hemodynamic responses following the stimulus events under each attentional context (having adjusted for baseline effects) in left V5 for subject one. **(c,d)** Same as **(a)** and **(b)** but in left V5 for subject two. **(e,f)** Left V5 in subject three. The units are dimensionless and represent percent whole brain mean signal. The magenta and cyan lines in **(b)**, **(d)** and **(f)** represent evoked responses under motion and color attention, respectively.

Discussion

This event-related fMRI study revealed regionally specific effects of attention at two levels. First, we observed baseline responses to motion attention bilaterally in V5 of all subjects and to color attention in V4. Second, discounting baseline effects, motion attention evoked greater hemodynamic responses in V5 to motion stimuli, and color attention enhanced color responses in V4.

The phenomena reported above are interesting in that activity in V5 was enhanced when the subject attended to motion, even when viewing stationary dots (that is, without motion in the visual field; Fig. 2a, c and e). In the same way, activity in V4 was enhanced when the subject viewed monochromatic dots but attended to color (Fig. 3a, c and e).

The relationship between changes in set-related activity with attention and changes in visually evoked responses suggests that attention increases baseline activity within V5/V4, and in so doing increases the sensitivity to motion/color stimuli. This observation may seem counterintuitive, as increasing background

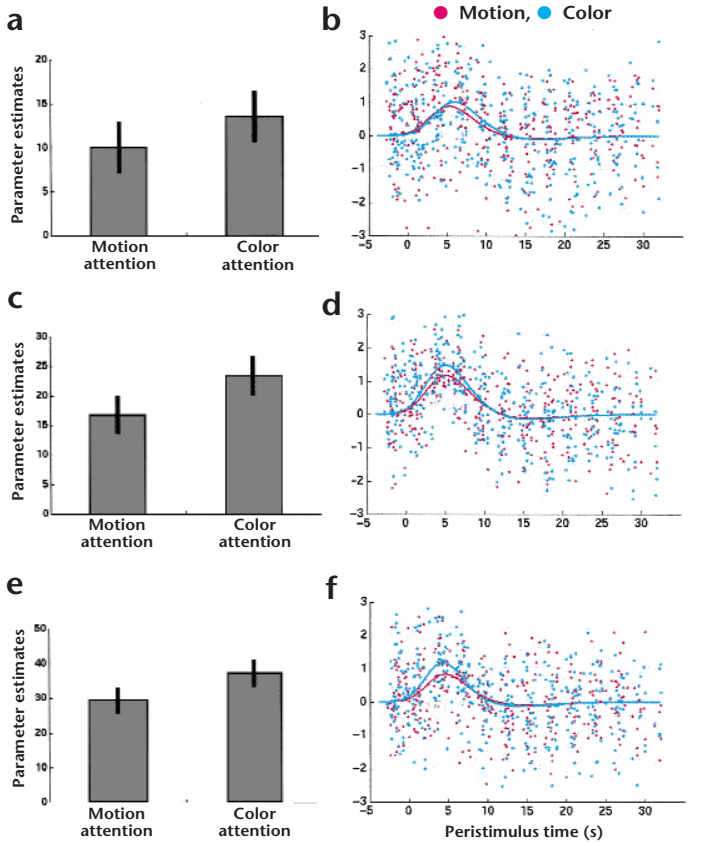

Fig. 3. Activity and responses in V4 as a function of attention in all subjects. **(a)** Parameter estimates with standard errors for baseline effects in left V4 in subject one. **(b)** Data adjusted for baseline effects and fitted hemodynamic response curves following the stimulus events under each attentional context in left V4 for subject one. **(c,d)** Same as **(a)** and **(b)** but in right V4 for subject two; **(e,f)** left V4 in subject three. Magenta and cyan lines in **(b)**, **(d)** and **(f)** represent evoked responses under motion and color attention respectively.

activity might be thought to increase difficulty in distinguishing a transient signal from noise. However, this result was anticipated by our computational work as well as single-neuron recording studies[7,8]. In previous computational studies, we used biologically plausible simulations of coupled neuronal populations to address the relationship between phasic and fast coherent neuronal interactions and macroscopic measures of activity that are integrated over time such as the BOLD (blood oxygenation level dependent) response in fMRI[16]. Our simulations indicated that an attentional 'biasing signal'[7] may mediate its effects in a relatively simple way: increased baseline activity decreases effective post-synaptic membrane time constants (by increasing membrane conductance) and selectively amplifies stimulus-related synchronous interactions (tendency to phase lock)[20]. This reflects an interaction between background activity and stimulus intensity in producing dynamic correlations. In other words, background activity augments stimulus-induced dynamics. This is interesting from a computational perspective, as background activity may have a profound effect on event-related responses. The current experiment explored this background-dependent increase in response sensitivity, as it may constitute a physiological mechanism underlying attention modulation.

The issue of whether attention modulates baseline activity has also been examined electrophysiologically[7]. This study examined the role of attention in monkey areas V1, V2 and V4 using a protocol in which attention was directed to one of two stimulus locations. If the attended stimulus falls within the cell's receptive field (RF) and the ignored stimulus outside the RF, a 30–40% increase in baseline firing rate but no modulation of stimulus-evoked responses is seen in V4. Conversely, when both attended and ignored stimulus locations fall within the cell's RF, evoked responses but not baseline activity are modulated by attention. These results suggest that attentional modulation is mediated by top-down control mechanisms that affect either background or sensory-related activity, depending on the neuron recorded. However, we posit that attentional modulation of baseline population activity is sufficient to enhance population responses to sensory input. The electrophysiology would be consistent with this mechanism if sensory-related responses in a cell population were enhanced by inputs from another set of cells with shifted baseline activity. Thus, the relationship between background activity and stimulus-evoked responses found empirically in this fMRI study and in previous computational simulations need not necessarily exist at the level of single cells, and may be mediated by interactions among cells. Our empirical findings and mechanistic explanation in terms of population dynamics concur with the suggestion that modulation of baseline activity "may reflect a top down signal that gives a competitive advantage to a stimulus" with an attended attribute, that is mediated by "a biasing signal that favors one population of cells over another (reflected by the baseline shift)"[7]. Our results might possibly be explained by sensitization of postsynaptic cells to sensory inputs by presynaptic activity in modulatory projections through voltage-dependent and other non-linear effects. This would preclude a mechanistic role for population dynamics. However, the existence of cells that show a postsynaptic baseline shift argues against purely synaptic modulatory effects as a sufficient explanation.

Event-related potential recordings in human subjects also demonstrate an interaction between target processing and antecedent attentional shifts. The early component (P1 and N1) of the visual evoked potential are known to be modulated by previous attentional allocation[21]. These attention-related negativities in the cue–target interval are associated with increased stimulus-locked P1 and N1 components[21].

In conclusion, we found both a main effect of attention (V5 or V4 activity was increased by motion or color attention, respectively, even without a motion or color stimulus) and an interaction between attention and the stimulus. This suggests that the main effect of attention (increase in background activity) might engender the interaction (increased sensitivity). Given our simulation results, it is possible that attention modulates responses solely by increasing the background activity within a population. In other words, a simple tonic background effect translated by non-linear neuronal interactions into modulation of evoked transients sufficiently explains attentional modulation. Likely candidates for areas that project to and increase background activity of visual areas have been inferred on the basis of labeling[22] and lesion[23] studies. Areas implicated in attentional modulation include the frontal eye fields, cingulate, premotor, lateral prefrontal, orbitofrontal, opercular, posterior parietal, lateral and inferior temporal, parahippocampal and insular regions as well as

subcortical regions such as the pulvinar. Areas specifically implicated in mediating visual attention include the frontal cortex, occipital cortex, parietal cortex, medial thalamus and the superior colliculus[11]. These afferents could increase the gain of the neurons through the emergent dynamics at a population level, rendering them more sensitive to the attended stimulus.

Methods

Stimulus presentation. Subjects viewed a visual stimulus backprojected onto a viewing screen in the scanner using an LCD video-projector and refreshed at 33.5 Hz. The active screen area was a 37° square. Subjects were instructed to maintain visual fixation on a central point. The stimulus was identical in all conditions and consisted of randomly spaced, stationary, 0.1° green dots on a green background of contrasting luminance. Transient visual stimuli were presented intermittently and consisted of randomly spaced red dots that moved radially on a green background. There were 500 dots on the screen at any time. In a previous fMRI study[1], we characterized V5 activity as a function of stimulus speed and found optimal responses at speeds of around 10 degrees per second. We used this as the speed of our motion stimuli. In 25% of the events, the speed was reduced to 7° per s or the dots were a slightly lighter shade of red.

Subjects alternately viewed the visual display for periods of 98 seconds and a blank screen (a low level control). Before each presentation of the visual display, a visual cue was used to instruct subjects to attend to either the motion or color attributes of the stimulus. In the motion attention condition, the subjects were told to discriminate the slower moving dots from the faster moving dots and respond with a key press. In the color attention condition, the subjects were told to detect the slightly pinker dots. As these events were only subtly different from the normal events, and the subjects were not aware of their 25% sparsity, attention was maintained at high levels. The compound color-motion stimulus events lasted for one second and were presented sporadically where the interstimulus intervals (ISIs) were selected from a random 'uniform' distribution that ranged from one to 36 seconds. One special design problem we faced was to ensure the effects of attention on baseline activity and the modulation of evoked responses were as unconfounded or orthogonal as possible. This was achieved by deleting occasional events such that each attention condition had at least one 'long' ISI of 33 ± 3 s. These intervals were needed to disambiguate attentional effects on the transient hemodynamic response to stimulus events from background activity associated with a particular attentional set[24] (see below).

Data acquisition. A 2T Magnetom VISION (Siemens, Erlangen) MRI system was used to acquire T_2*-weighted fMRI image volumes. Each volume comprised 32 3-mm-thick axial slices (in plane resolution, 3 mm × 3 mm) giving a repetition time per volume of 2.8 s. Each experimental condition lasted for 98 seconds (35 volume scans) and was followed by a blank screen lasting for 19.6 s (7 volume scans). We replicated each condition 10 times in a session, lasting for 39 minutes and 12 seconds. In each session, 840 image volumes (20 replicated conditions) were acquired. Three normal right-handed volunteers (aged 19–26) gave informed consent and participated in the study, which was approved by the National Hospital for Neurology and Neurosurgery Ethics Committee.

Data analysis and statistical model. Image processing and statistical analysis were carried out using SPM97. All volumes were realigned to the first volume[25]. A mean image was created using the realigned volumes. A structural MRI, acquired using a standard three-dimensional T_1 weighted MPRAGE sequence (1 × 1 × 1.5 mm voxel size), was coregistered to this mean (T_2*) image. This ensured that the functional and structural images were in the same space. The structural image was spatially normalized to a standard template[26], using a non-linear transformation. Finally, the transformed structural T_1 MRI scan was mapped onto the template. The data were smoothed using a 6-mm isotropic Gaussian kernel, full width at half maximum. Our fixed-effects statistical model comprised subject-specific effects (baseline attention effects, responses to stimuli and interaction between these two) and confounds (a constant term for each subject, low frequency components, global activity and responses to stimulus events). This analysis constituted a case study of three subjects, allowing contrasts to be specified both for each subject separately and for averaged effects (Fig. 1).

Our conclusions depend heavily on being able to separate set-related baseline activity from stimulus-evoked activity in the same brain region. To do this, we used multi-linear regression along with statistical parametric mapping at each voxel using SPM97 software[17]. The ensuing regression model is a linear combination of regressors or time-varying variables that best explain the observed time series. We identified three regressors of interest to model effect of attentional set, event-related hemodynamic responses and the interaction between these two factors. The first regressor was set at 1 under attention to motion and –1 for scans acquired under attention to color. Evoked responses were modeled by a delta function ('spike') after each event. The interaction was simply the product of these two and accounts for differential evoked responses under both levels of attention. Hemodynamic responses to these effects were modeled by convolving the regressors with a synthetic hemodynamic response function and its temporal derivative. Variations in cortical activity about the mean of each voxel time series are expressed in terms of the relative contribution of these three effects or, more precisely, the corresponding parameter estimates obtained with least-squares. Statistical inferences are based on *t*-statistics (the parameter estimates divided by their standard error) that are assembled into a SPM(t). The *t*-values were used only to determine significance of the described effects (see below). The effects themselves are presented in terms of the parameter estimates, namely the difference in baseline activity associated with attentional set, the degree of evoked hemodynamic response and the attention-dependent component of these evoked responses (that is, the interaction). To ensure efficient estimation of parameters, it is important to avoid correlations between the explanatory variables. This was a critical aspect of our experimental design and involved at least one long ISI during each attentional condition. The resulting small correlation coefficients (< 0.3) between the attentional set regressors and those modeling attended events do not ensure independence, but make our assessment of separable effects more efficient. Thus, our estimated responses were conservative and, as they remained significant, robust. Without such minimization of regressor colinearity in our experimental design, effect of attention (because it could be modeled by the interaction) and effect of evoked response modulation (because it could be modeled by changes in attention) might have been missed. Actual estimates of activity in Figs. 2 and 3 correspond to parameter estimates in which the constant term was added back to the attentional baseline estimates. Figures 2a, c and e and 3a, c and e show the average baseline activity above which stimulus event effects were seen. In Figs. 2b, d and f and 3b, d and f, the dots surrounding estimated hemodynamic responses correspond to the original fMRI data adjusted for confounds and baseline attentional effects.

By using appropriate contrasts of condition-specific effects, SPM{t}s were created to test for regionally specific main effects and interactions. The SPM(t)s were transformed to SPM(Z) for display and tabulation. Statistical inferences were made using Gaussian random field theory to correct for multiple dependent comparisons. However, because we restricted our hypothesis to V1, V5, V3a and V4 we report maxima only if the areas were at $p < 0.05$ (uncorrected) in all three subjects. The SPMs shown in Fig. 1 represent a conjunction analysis over all subjects; showing an effect only in voxels where it conjointly reached significance in every subject-specific analysis. Because of the separable nature of the design matrix, this corresponds to a significance of $p < 0.05$ (uncorrected)[3].

Acknowledgements

We thank the radiographers at the Wellcome Department of Cognitive Neurology for their help. This work was supported by the Wellcome Trust.

Received 9 November 1998; accepted 20 April 1999

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