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Dear Dr Carpenter

Thank you for your mail of 4 September and the enclosed reviews. Included with this reply is my revised manuscript NIMG2002-0247.

Both reviewers commented to the effect that the paper addresses an interesting question and that our intraparietal result in particular is a significant extension of previous findings. The reviewers' several concerns focussed in general on (1) proper communication of our methods, which are non-standard, and (2) our interpretation, which in its original form gave short shrift to the alternative hypothesis that intraparietal sulcus is involved in preparing shifts of attention to targets in the contralateral hemifield. We will address the issue of interpretation first, since on this point both reviewers concurred.

Both reviewers cited the fact that our observations cannot distinguish between (1) our stated hypothesis that intraparietal sulcus subserves suppression of unattended stimuli, and (2) the alternative hypothesis that intraparietal sulcus prepares attentional shifts into the currently unattended hemifield, and suggested that the shifting hypothesis be given an emphasis on a par with the suppression hypothesis. We have extensively rewritten the discussion in order to accomplish this shift of emphasis.

Although both reviewers also focussed on our methods, the concerns that each reviewer highlighted differed. We will therefore address each specific point from each reviewer separately:

**Reviewer I:**

**'There is no behavioral data indicating that subjects were actually following the instruction and no measure of attending or shifting the direction of attention. The only behavioral data is the latency of moving the finger to the (assumed) attended location, but we do not really know if subjects covertly directed attention to the other field when a target was presented.'**

In fact, as we wrote at the beginning of the results section, the behavioural data in Table 1 show that subjects were performing the task. Only two subjects accomplished fewer than 13 of the 14 nominal target detections in each location to be attended, and only two subjects gave more than a single false alarm to targets appearing at locations to be ignored. In any case, the few false alarms and missed targets in a minority of subjects could not have affected the fMRI averages and statistics, since the intervals surrounding misses and false alarms were

excluded from the fMRI attention analysis. We have added a sentence to the results section in order to make this point clear.

**‘The pictures and figures are sub optimal in quality. The quality of the color picture is poor, and the lines of the time course are hard to see.’**

We have enlarged the time course figure so as to make its lines more clear. The resolution and contrast of the colour figure are those provided by our hardware, and we agree that laser-printing has negatively affected this figure. We have included the colour figure as a separate graphics file with this revised submission, and will provide photographic-quality hardcopy with the final submission.

**‘The design is unusual. The blocks are very long and fall into the 1/f physiological noise frequency. The two active conditions are alternated within a block. A much better design would have been to have shorter blocks (10-20 seconds) interspersed by fixation periods. This would have eliminated the 1/f noise problem, and allowed a more powerful modeling of the responses. I am not sure what are the effects of modeling two effects within a single block. Given the slow hemodynamic response and the presence of multiple targets (visual field to attend to) BOLD response will overlap in time for the two conditions.’**

Our design is indeed unusual, and as we have noted in the discussion, it is this unusual design that has allowed detection of the very subtle intraparietal attention effect that we have demonstrated. Reviewer #1 is of course correct in pointing out that the optimal block length for an alternating block design is far shorter than the 60s duration of our task blocks. However, since we are modelling two effects with two independent statistical analyses, there are two sorts of ‘blocks’ involved. As stated in the methods, in the first functional analysis the 60s task blocks are compared to the 30s fixation blocks that flank them in order to generate a functional map of the effect of the task. In the second functional analysis, though, shorter blocks consisting of periods of directed attention are defined within the task blocks on the basis of behavioural data. As it is the attention effect that is of primary interest, the experiment was designed so that the lengths of the short attention blocks, rather than the longer task blocks in which they were embedded, fell within the optimal range of block length for an alternating block design. We have added text within the ‘analysis’ subsection of the methods section to clarify this aspect of the block structure.

**‘The results presented in figure 2 do not match what is described in the text. Only the time course for left shifts in the left hemisphere in occipital clearly show a deviation from the baseline. A weaker deviation is present in right intraparietal for left shifts as well. All the others do not seem to be significantly different from zero.’**

Again, we must emphasise that our design is an unusual one, using a regions-of-interest approach to highlight very weak – but statistically significant – effects. In addition to the left occipital and right intraparietal effects that Reviewer #1 notes, the time series in Figure 3 and the mean z-score in Table 3 indicate an effect in right occipital cortex: the time series for leftward shifts is consistently below the time series for rightward shifts up to the time at which the shift occurs, and consistently above it thereafter. For the intraparietal region, we agree with Reviewer #1 that the significant difference between the two hemispheres arises

mainly from differential activity in the right hemisphere, and we have inserted in the results section a statement to this effect.

**[Minor] ‘The gender of the subject is irrelevant to the main question. There is nothing in the introduction to justify ‘gender’ as a variable in the analysis, which in turn does not add anything substantial to the results.’**

While it is true that there was no statistically significant effect of sex in our results, there was a possible trend. There have been suggestions in the literature of sex differences in patterns of cerebral lateralisation during visual spatial tasks, and in particular one recent fMRI study [Gur *et al.* 2000] suggesting sex differences in the pattern of lateralisation of parietal activity during a visual spatial task. We therefore took the conservative approach of including sex as a factor in the analysis. We have added to the introduction a brief explanation of this rationale.

**[Minor] ‘I would take out of the analysis subjects that performed less than 80% correct. For instance, there is one subject (# 4) that in the right hemifield had 8 hits, 4 misses and 3 false alarms. It is hard to tell what this subject did during the task (see also subject # 5 - left hemifield).’**

As reported in the revised paper, we have re-analysed the data with subjects 4 and 5 excluded. The significance of the effects was not altered.

**[Minor] ‘Pages 12 and 13: The use of the words ‘early’ and ‘late’ attention stages is not clear. The authors suggested that “early selection of relevant stimuli” caused activation of the contralateral ventral occipital cortex and that the activation in the ipsilateral intraparietal sulcus is an outcome of “a late process of suppression of irrelevant stimuli”. Early and late selection are usually used in a different context. What is the theoretical frame justifying these two stage idea for attending vs., suppressing?’**

We agree that this usage of ‘early’ and ‘late’ is confusing and not necessarily supported, and have removed it.

**[Minor] ‘The analysis might be simplified by using ipsilateral vs. contralateral as factors rather than left and right hemisphere. If this is the only way to analyze the result it should be clearer in the results section (page 10 first paragraph).’**

In the rewritten results section we have clarified the relationship between the signs of z-scores in the left and right hemispheres and activation ipsilateral and contralateral to the attended hemifield.

**[Minor] ‘Page 8 description of methods is not very clear. Authors should clearly state what HRF they used to deconvolve time courses, and how frames were coded.’**

We have completely rewritten this description to make it more clear. In order to avoid assumptions about the HRF, and since the task and fixation periods were relatively long in comparison to haemodynamic response latencies, we used a simple square wave to model haemodynamic response.

**[Minor] ‘Mean z-scores are very low. None of these z-scores would survive a voxel-wise analysis of left vs. right field.’**

We concur that none of these *z*-scores would survive a whole-brain, voxel-wise analysis with correction for multiple comparisons. The very weakness of these attention effects is one reason for the use of a regions-of-interest approach with individual functional mapping, focussing *a priori* on those areas in which we hypothesised effects. We have rewritten the penultimate paragraph of the discussion in order to cover this point.

**Reviewer II:**

**‘...the data are at odds with the results of Martínez *et al.* (*Nature Neurosci.*, 1999), who reported an increase of IPS activity contralateral to the attended stimulus.’**

We thank Reviewer #2 for reminding us of the relevance of the work of Martínez *et al.* In fact, the finding of Martínez *et al.* of intraparietal activity contralateral to the attended hemifield is consistent with our findings and interpretation, and the key to this consistency is a comparison of the locations of distractors in our experiment and in theirs. Whereas our distractors were confined to the unattended hemifield, Martínez *et al.* used closely spaced distractors within both hemifields. As the distractors within the attended hemifield likely would have been more salient than those in the hemifield opposite, the demand for suppression in the task used by Martínez *et al.* would have been greatest in the attended hemifield — and greater than in our study, in which distractors were far removed in the unattended hemifield. Accordingly, Martínez *et al.* found a larger effect in their paradigm than we did in ours, and found it in the contralateral hemisphere rather than the ipsilateral. Both of these differences are readily explained by considering the effect as a product of differing levels and spatiotopic locations of distractor suppression. In our revised discussion section we have added a paragraph to this effect.

**‘...it would be helpful if the labels “task period”, “fixation period”, and “baseline period” were more precisely defined – are “fixation period” and “baseline period” identical?’**

We agree with this criticism of terminology. We have added to the methods section more explicit definitions of ‘task period’ and ‘fixation period’, and have eliminated the use of ‘baseline period’ as a synonym for ‘fixation period’.

**‘...any visually responsive areas (not only three) should be activated. If this was the case, how were the present ROIs selected?’**

ROI’s were constrained *a priori* to be within three general anatomical regions, and the functional map for each subject was used to specify precisely the location of each ROI within these general anatomical regions. We have extensively rewritten the ‘analysis’ subsection of the methods section in order to make this methodology more clear.

**‘Which statistical model is included in the permutation test of the AFNI software package?’**

The combination of within-subjects measures derived from the permutation test with a between-subjects analysis of variance implements a mixed-effects model. (Mixed-effects models are often referred to in the context of fMRI as ‘random-effects’ models since they account both for fixed effects and for the random effect of between-subjects variance.) We have added a statement to this effect to the methods section.

Though we could delve into a detailed description of permutation testing as applied to fMRI, this is more properly the subject of a separate paper – and in fact has been the subject of several! Therefore, for detailed information on nonparametric statistical modelling we refer the reader to our paper on the subject [Belmonte & Yurgelun-Todd 2001a] and to the several others which it cites.

**‘What are the complete coordinates of the selected ROIs? Can they be displayed on a few more slices?’**

We have expanded Figure 1 to illustrate ROI’s in all subjects, and included Talairach coordinates in the results section.

**‘It would be nice if the hypothesis was derived from previous evidence and/or models and if it was made more explicit. Where does the hypothesis of suppressive effects in visual selection originate from? Where are the expected sources and sites of suppression located in the brain? In particular, where does the hypothesis of suppression by PPC originate from?’**

Although the idea that attentional suppression may be localised in intraparietal sulcus is a new one, the idea of suppressive processing in selective attention is a rather old one, founded on phenomena such as negative priming [Tipper 1985] and inhibition of return [Posner & al. 1985]. The idea the suppression of distractors may take place in intraparietal cortex in particular was advanced by Wojciulik and Kanwisher [1999], on the basis of the diversity of attentional tasks that evoke intraparietal activation. Our rewritten introduction and discussion expand our original treatment to address these questions of background and context of the suppressive hypothesis.

**‘The reason for the rather unusual behavioral response (finger movement) should be substantiated.’**

Finger movement is unusual only because electromechanical switches are more widely available as response devices than are optical switches. Finger movements are simpler since there is no force-feedback involved. In addition, the use of leftwards and rightwards finger movements as responses may decrease the demand on working memory, since the current position of the finger serves as a mnemonic for the direction in which the subject’s finger and the subject’s attention should next be moved. We have added a sentence to the methods section noting this.

**‘The report of behavioral results lacks the eye movement data – the number of saccades should be reported for each subject. Besides, were saccade time points correlated to time points of attention shifts or did saccades occur randomly during the task performance?’**

We have revised the results to include these saccade data. Averages of point-of-regard versus time indicate no systematic deviation of gaze direction associated with shifts of attention.

**‘A report of mean d' rather than uncorrected mean accuracy (here, SDs are missing) would be more convincing since the single subject data suggest differences between the individuals’ criteria.’**

We agree that the single subject data suggest differences in criteria. However, with seven of the eleven subjects at ceiling in terms of hits versus misses, and six at ceiling in terms of correct rejections versus false alarms,  $d'$  ceases to be meaningful.  $d'$  can be defined as  $N^{-1}(p_H) - N^{-1}(p_{FA})$ , where  $p_H$  is the ratio of hits to the total of hits and misses,  $p_{FA}$  is the ratio of false alarms to the total of false alarms and correct rejections, and  $N^{-1}$  is the inverse cumulative standard normal distribution. If the number of misses is zero, then  $p_H$  is estimated as 1, and of course as  $p$  approaches 1,  $N^{-1}(p)$  increases without bound. Similarly, if the number of false alarms is zero, then  $p_{FA}$  is estimated as 0, and as  $p$  approaches 0,  $N^{-1}(p)$  decreases without bound. Thus  $d'$  is not well defined in the majority of cases in this study, and mean  $d'$  is therefore not definable.

Were this a psychophysical study, the ceiling effect in these behavioural measures would be a fatal flaw. Since the only purpose of the behavioural task was to ensure that subjects were allocating attention as intended, though, the fact that so many subjects were at ceiling is a positive indication that subjects were performing the task and that the resulting fMRI measures were representative of the intended attentional conditions. We have added a sentence at the end of the ‘stimuli and task’ subsection of the methods section, stating this intent of the design.

**‘Does the task really require a feature conjunction in the sense of FIT and related theories?’**

In order to avoid confusion with the terminology of FIT, we have substituted the term ‘combination’ for ‘conjunction’.

**‘I do not understand the description of the neural network model (p. 14, 3<sup>rd</sup> paragraph) - if it can explain the present findings it should be more fully described.’**

This briefly sketched model is speculative, and an outline only. We do not wish to add unnecessary length to the paper by expounding on models whose truth cannot be readily evaluated; we merely wish to advance the idea that the various roles suggested for intraparietal involvement in selective attention are by no means mutually incompatible. The model that we outline is one way in which these roles might coexist anatomically.

**‘The discussion of sex differences and autism is interesting, but not detailed enough to be comprehensible - it could be left out.’**

Though it could be left out, it does communicate the potentially significant point that activity in ventral occipital and intraparietal cortices may reflect complementary modes of processing. Assuming that there is room, we prefer to leave it in.

We recognise that the non-standard nature of our methods has made the communication of our results something of a challenge, and we thank the reviewers and editors for their valuable work in helping us clarify these methods and the interpretation based on them. We trust that these extensive revisions resolve the issues cited in the reviews.

Yours sincerely,

Matthew Belmonte

# Anatomic Dissociation of Selective and Suppressive Processes in Visual Attention

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**RUNNING TITLE:** Selection and Suppression in Visual Attention

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## ABSTRACT

Visual spatial attention is associated with activation in parietal regions as well as with modulation of visual activity in ventral occipital cortex. Within the parietal lobe, localisation of activity has been hampered by variation in individual anatomy. Using fMRI within regions of interest derived from individual functional maps, we examined the response of superior parietal lobule, intraparietal sulcus, and ventral occipital cortex in 11 normal adults as attention was directed to the left and right visual hemifields during bilateral visual stimulation. Activation in ventral occipital cortex was augmented contralateral to the attended hemifield ( $p < 0.006$ ), while intraparietal activation was augmented ipsilaterally ( $p < 0.009$ ), and superior parietal lobule showed no modulation of activity as a function of attended hemifield. These findings suggest that spatial enhancement of relevant stimuli in ventral occipital cortex is complemented by an intraparietal response associated with suppression of, or preparation of a reflexive shift of attention towards, irrelevant stimuli. The spatial attention system in superior parietal cortex, in contrast, may be driven to equal degrees by currently attended stimuli and by stimuli that are potential targets of attention.



## INTRODUCTION

Within the posterior attentional system, the orientation and maintenance of visual spatial attention give rise to activity both in parietal regions that direct attentional signalling and in ventral occipital regions that are directed by attentional signals [Posner & Petersen 1990]. PET studies have associated activity in superior parietal lobule both with shifts of visual spatial attention [Corbetta & *al.* 1993; Vandenberghe & *al.* 2001] and with visual vigilance [Pardo & *al.* 1991; Vandenberghe & *al.* 1996], particularly during conditions that combine high perceptual demand with peripheral presentation of stimuli [Vandenberghe & *al.* 1996, 1997]. Additionally, there is some evidence of sex differences in patterns of parietal lobe activation associated with attention-demanding visual spatial tasks [Gur & *al.* 2000]. More recent fMRI work has focussed on inferior parietal cortex, where activation during shifts of attention has been mapped to anterior and posterior zones of the intraparietal sulcus [Corbetta & *al.* 1998, 2000; Wojciulik & Kanwisher 1999]. It has been suggested that intraparietal sulcus performs a more general role in attentional processing, functionally distinct from simple shifting and possibly related to the active suppression of distractors [Wojciulik & Kanwisher 1999].

In addition to parietal areas, visual spatial attention has effects on the ventral occipital regions that are targeted by attentional modulations. Visual attention augments activation in extrastriate cortex on the inferior surface of the occipital lobe, in a region centred on fusiform and lingual gyri [Pardo & *al.* 1991; Corbetta & *al.* 1993; Vandenberghe & *al.* 1996]. In the case of a lateral focus of spatial attention, this augmentation is contralateral to the attended hemifield [Heinze & *al.* 1994; Hillyard & *al.* 1997; Vandenberghe & *al.* 1997, 2000; Martínez & *al.* 1999; Hopfinger & *al.* 2000]. This well characterised, replicated, and lateralised effect of spatial

attention in higher-order visual cortex can serve as a useful comparison for attentional phenomena in other brain regions. In order to examine differential responses of superior parietal, intraparietal, and ventral occipital cortices during attention in the presence of distractors, we applied fMRI during bilateral rapid serial visual presentation of stimuli in a visual spatial attention task.

Recent fMRI studies have focussed on event-related analysis of periods surrounding shifts of attention [Kastner & *al.* 1999; Corbetta & *al.* 2000; Hopfinger & *al.* 2000]. As our primary interest is not in shifts *per se* but in the effect of shifts on responses to subsequent stimuli, we have instead applied a blocked analysis comparing periods of attention to left and right hemifields. This blocked analysis of stimuli presented in continuous streams affords greater opportunity to examine steady-state visual response than would an event-related analysis of discrete, temporally isolated stimuli. In addition, there is evidence that at TR's of 2s or more, blocked analysis yields an advantage in BOLD signal strength [Buckner & *al.* 1996]. This paradigm of blocked comparison during rapid serial presentation has been previously applied in quantitative electroencephalographic studies of visual spatial attention in normal [Belmonte 1998] and patient [Belmonte 2000] populations.

## **METHODS**

### **Subjects**

Eleven right-handed adults (five men, six women), ages 22 to 35, were recruited from the local community. Subjects had no history of neurological or psychiatric illness, no history of CNS trauma, and no current medications affecting CNS function. The experimental protocol

was approved by the McLean Hospital Institutional Review Board. Informed consent was obtained from each subject, and subjects were paid for their time.

### **Stimuli and Task**

Video was back-projected onto a screen fastened to the front of the head coil, made visible to the subject by a mirror. Red and green coloured squares subtending  $1.8^\circ$  were displayed in the upper hemifield, centred  $5^\circ$  lateral and  $3^\circ$  superior to fixation. Stimuli were flashed at  $9\text{s}^{-1}$  with a 50% duty cycle, for a stimulus duration of 56ms and an inter-stimulus interval of 56ms on each side, giving a total stimulus period of 112ms. Flashes on the two sides were  $180^\circ$  out of phase with each other, that is, the offset of a stimulus on one side coincided with the onset of a stimulus on the other side.

The experiment comprised ten trials, each of which consisted of a 60s period during which subjects received stimulation and performed the behavioural task, flanked by two 30s periods of visual fixation without stimulation, for a total duration of 120s. In order to avoid visual fatigue, subjects were permitted to rest for up to three minutes between trials. Subjects were instructed to maintain fixation at the centre of the display and to begin by attending covertly to one of the two stimulus locations. This starting location was counter-balanced across trials. On detecting the target (red) stimulus in the attended location, subjects had to respond by shifting attention covertly to the newly attended location, and by moving the index finger of the dominant hand in the direction of this shift. (The current position of the finger thus served as a mnemonic for the task.) The rest of the trial then proceeded in the same manner for the newly attended location. Stimuli of the target colour occurred with equal probability both in the attended location and in the unattended location.

The first trial contained four nominally attended targets. We describe these as ‘nominally’ attended since a missed target or a false alarm affected whether or not specific subsequent targets were attended. Of the remaining trials, six contained three nominally attended targets and three contained two nominally attended targets. Targets were uniformly distributed over the final 42s of each 60s period of stimulation, except in the case of the second trial, whose first target occurred at 8.68s. No attended target followed within 12s of a previous attended target, except in the case of one pair of attended targets in the fourth trial which were separated by 6.28s. These variations in number and timing of attended targets were intended to ensure that subjects kept attending throughout each trial. As our interest lay not in psychophysical measures of ability to direct attention but in the neurophysiological effects associated with successful direction of attention, the task was designed so that most subjects would be at or near ceiling.

### **Behavioural Recording**

Fixation was monitored using an infrared eye tracking system (ISCAN, Inc., Burlington, Massachusetts). Infrared illumination of the eye was supplied by an array of LEDs mounted on the head coil and arranged so as to minimise the external magnetic field due to current flow. The eye image was recorded by an infrared camera mounted at the rear of the magnet bore, and transmitted to a computer outside the scanner room for analysis.

In order to avoid magnetic transients associated with electrical switching, an optical signalling device was constructed to transduce behavioural data. A high-output red LED (Radio Shack #276-086A, 5cd at 660nm peak) was mounted at the top of a wooden enclosure, powered from an external supply via a twisted-pair cable so as to minimise external magnetic field. Two strands of DB-1000 1mm plastic optical fibre were mounted in holes drilled at the bottom of this

enclosure. When the subject's finger was positioned on the right side of the enclosure, it blocked the light path between the LED and the fibre ends. When the subject's finger was positioned on the left, the fibre ends were illuminated. The fibres led outside the scanner room through an RF wave guide to a fast-acting Type 7H cadmium selenide photocell (Mouser Electronics #621-CL707H) connected in parallel with a  $100\text{M}\Omega$  resistor, and the voltage across this photocell was digitised and sampled at  $18\text{s}^{-1}$  through a standard PC game port.

## Scanning

During each 120s trial, forty single-shot echo-planar images ( $\text{TR}=3\text{s}$ , effective  $\text{TE}=40\text{ms}$ , flip angle  $90^\circ$ ) were collected in coronal slices perpendicular to the midsagittal line between the anterior and posterior commissures. Images were 7mm thick and spaced 1mm apart, with a 20cm square field of view in a  $64\times 64$  matrix for an in-plane resolution of 3.125mm, and were acquired on a General Electric Signa 1.5T system with a standard birdcage head coil. Scanning was synchronised to the onset of stimulation by using a trigger pulse from the scanner to cue stimulus delivery. Following the functional scan, T1-weighted ( $\text{TR}=500\text{ms}$ ,  $\text{TE}=8\text{ms}$ ) and high-resolution echo-planar (spin-echo,  $\text{TR}=3\text{s}$ ,  $\text{TE}=80\text{ms}$ ) images were acquired in  $256\times 256$  matrices, in the same planes and with the same field of view as the functional images.

## Analysis

Functional images were corrected for head motion using Decoupled Automated Rotational and Translational motion correction [Maas & *al.* 1997], a method that uses a  $k$ -space representation of the images to separate rotational and translational ( $k$ -space phase) components. Linear trend and baseline offset were removed from each trial separately. A thresholding method

was applied to classify voxels as brain or non-brain, and these automatically generated classifications were then manually examined and retouched. In order to avoid any assumptions about haemodynamic response, and since the task and fixation periods were relatively long in comparison to haemodynamic response latencies, the ideal response function was defined as a simple square wave, 1 for time points within each of the 60s task periods and 0 for time points within each of the flanking 30s fixation periods. The first point within each of these periods was excluded, as were all points during breaks in fixation. This task-versus-fixation waveform was applied using the permutation test [Belmonte & Yurgelun-Todd 2001a] component of the AFNI software package [Cox 1996] to generate tail probabilities for task-related activation of each brain voxel.

Probability maps generated by this task-versus-fixation comparison were used in combination with each subject's anatomical images to draw regions of interest for a left-hemifield-versus-right-hemifield attention comparison, constructed so as to be independent of the task-versus-fixation comparison. The three regions of interest in each hemisphere consisted of five voxels in ventral occipital cortex centred on middle occipitotemporal gyrus, four voxels just superior to the fundus of the intraparietal sulcus, and four voxels in superior parietal cortex. (Because the study focussed *a priori* only on these three regions, voxels that were activated in the task-versus-fixation comparison but were not located within any of these anatomically defined regions (*e.g.*, voxels in striate cortex) were not considered in the attention comparison.) These regions were drawn on a slice whose anterior-posterior Talairach coordinate was approximately -70mm. Regions of interest for all subjects are illustrated in Figure 1.

For the attention comparison, behavioural data from each subject were used to define a second ideal waveform that described the direction of attention as a function of time. The first

point in each task period was excluded from this waveform, as was the first point following each shift of attention. In addition, all points during breaks in fixation were excluded. In cases of missed targets or false alarms, points were excluded backwards in time to the previous correct response or to the beginning of the task period, and forward in time to the next correct response or to the end of the task period. The points remaining after these exclusions were assigned a value of 1 for leftward attention, or 0 for rightward attention. This behaviour-based procedure thus produced an ideal waveform defining short (~15s) attention blocks, embedded in the longer (60s) task blocks and within the optimal range of block length for an alternating block design [Skudlarski & *al.* 1999]. Because it considered only the task periods, during which the ideal waveform for task-versus-fixation was always 1, the attention comparison was independent of the task-versus-fixation comparison.

The data from the attention comparison were processed in two methods in parallel, one using a conventional measure of percent signal change, and the other using  $z$ -scores derived from a statistical parametric map. For the analysis of percent signal change, for each of the two attention conditions separately, BOLD signal within each region of interest was summed and then expressed as a percentage above the mean baseline signal acquired during the fixation periods. The percent increase for the attend-right condition was then subtracted from the percent increase for the attend-left condition. The resulting attend-left – attend-right differences in percent signal change were subjected to a 2x2x3 (sex by hemisphere by region-of-interest) analysis of variance. *Post hoc t*-tests were applied as indicated by *F* values from this analysis. The strategy of computing within-subjects percent signal change and using it as the independent variable in a between-subjects analysis of variance thus implemented a mixed-effects (often referred to as ‘random-effects’) model [Holmes & Friston 1998].

For the map-based analysis, the regression coefficient between the attention waveform and the fMRI time series was transformed to a  $z$ -score at each voxel, forming an SPM{ $Z$ } [Friston & *al.* 1995].  $z$ -scores from this map were then averaged within each region of interest, to form a  $z$ -score reflecting the degree of attention-related activity in the region as a whole. Since the ideal waveform was arbitrarily chosen to be positive for leftward attention and zero for rightward attention, a positive regional  $z$ -score denotes correlation with leftward attention while a negative regional  $z$ -score denotes correlation with rightward attention. These values were then subjected to the same analysis of variance and *post hoc* tests as specified above for the analysis of percent signal change. Here again, the two-stage analysis (within-subjects  $z$ -score followed by between-subjects analysis of variance) implemented a mixed-effects model.

## RESULTS

Behavioural data, detailed in Table 1, show that subjects had little difficulty performing the attention task. Only two subjects accomplished fewer than 13 of the 14 nominal target detections in each location, and only two subjects gave more than a single false alarm. (Data from intervals surrounding missed targets and false alarms did not affect the fMRI averages and statistics, since these intervals were excluded from the fMRI attention analysis.) The average accuracy, calculated as the ratio between the number of correctly detected targets and the total number of detection opportunities, was 94% for left targets and 96% for right targets. Average response latency was 697ms (SD 119ms) for left targets and 701ms (SD 144ms) for right targets.

Numbers and amplitudes of saccades for each subject are given in Table 2. Because of noise in the eye position recordings, detection of saccades less than  $1.25^\circ$  in amplitude was not reliable. However, this  $1.25^\circ$  detection threshold was only one fourth of the distance between the fixation



point and the targets, and neither real-time video observations nor averages of point-of-regard as a function of time (Figure 2) indicate any systematic deviation in direction of gaze associated with shifts of attention.

The task-versus-fixation comparison yielded regions of interest with average ( $\pm$ SD) coordinates as follows: left ventral occipital,  $-29\pm7$ ,  $-69\pm6$ ,  $-12\pm6$ ; right ventral occipital,  $29\pm7$ ,  $-69\pm6$ ,  $-13\pm7$ ; left intraparietal,  $-30\pm4$ ,  $-69\pm6$ ,  $26\pm7$ ; right intraparietal,  $28\pm5$ ,  $-69\pm6$ ,  $26\pm7$ ; left superior parietal,  $-20\pm11$ ,  $-69\pm6$ ,  $48\pm7$ ; right superior parietal,  $17\pm14$ ,  $-69\pm6$ ,  $48\pm8$ . The  $y$  coordinates are identical because the same coronal slice was used for each region in each subject.

fMRI time series for each region, averaged across subjects, are shown in Figure 3, and  $z$ -scores and percent signal change are detailed in Table 3. The analysis of variance on  $z$ -scores was significant for an interaction of hemisphere by region of interest ( $F(2, 54)=8.81$ ,  $p=0.0005$ ). *Post hoc t*-tests revealed significant interhemispheric differences in the ventral occipital region ( $t(20)=3.08$ ,  $p<0.006$ ), where the mean  $z$ -score was  $-1.00$  in the left hemisphere and  $+0.88$  in the right hemisphere, and in the intraparietal region ( $t(20)=2.90$ ,  $p<0.009$ ), where the mean  $z$ -score was  $+0.18$  in the left hemisphere and  $-0.83$  in the right hemisphere. Both the  $z$ -score magnitudes and the time series indicate that this intraparietal difference arose mainly from the right hemisphere. Since positive  $z$ -scores denote correlation with leftwards attention, this pattern of  $z$ -scores indicates that ventral occipital cortex was activated contralaterally and (right) intraparietal cortex ipsilaterally to the attended hemifield. In the superior parietal region, although the time series contained transient responses in both hemispheres for shifts in both directions, the  $t$  test comparing rightward shifts to leftward shifts was not significant.

No other factors or interactions produced significant effects. We note, however, a possible trend differentiating the sexes: mean  $z$ -scores for ventral occipital cortex were greater in

magnitude for the males (-1.44 left, +1.22 right) than for the females (-0.63 left, +0.60 right), while intraparietal mean  $z$ -scores were greater in magnitude for the females (+0.19 left, -1.14 right) than for the males (+0.18 left, -0.46 right).

The analysis of percent signal change was consistent with the  $z$ -score analysis, though the finding in ventral occipital cortex was somewhat weaker. The analysis of variance was again significant for an interaction of hemisphere by region of interest ( $F(2, 54)=5.03, p=0.0095$ ). *Post hoc t*-tests showed a trend in the ventral occipital region ( $t(20)=1.94, p<0.07$ ), where the mean difference in percent signal change was  $-0.239$  in the left hemisphere and  $+0.209$  in the right hemisphere, and in the intraparietal region ( $t(20)=3.01, p<0.007$ ), where the mean difference was  $+0.057$  in the left hemisphere and  $-0.159$  in the right hemisphere. Data from the superior parietal region were again not significant.

Because the behavioural performance of subjects 4 and 5 was somewhat worse than that of the other subjects, the fMRI data were re-analysed in order to determine whether the exclusion of these two subjects would affect the group results. For the analysis of  $z$ -scores, the data were again significant for an interaction of hemisphere by region of interest ( $F(2, 48)=10.67, p=0.0001$ ), with significant differences in the ventral occipital ( $t(16)=3.65, p=0.002$ ) and intraparietal ( $t(16)=2.44, p=0.027$ ) regions. For the analysis of percent signal change also, the interaction remained significant ( $F(2, 48)=7.85, p=0.0011$ ), with significant ventral occipital ( $t(16)=2.81, p=0.013$ ) and intraparietal ( $t(16)=2.58, p=0.020$ ) effects. In both analyses, the exclusion of these two worst-performing subjects increased the ventral occipital effect and decreased the intraparietal effect.

## **DISCUSSION**

In a comparison of periods of sustained visual spatial attention to left and right hemifields, we have found enhanced activation of ventral occipital cortex contralateral to the attended hemifield, and enhanced activation of posterior ventral intraparietal sulcus ipsilateral to the attended hemifield, while activation of superior parietal cortex showed no effect of attended hemifield. The finding of ventral occipital activation agrees with electrophysiological studies which have demonstrated a small but significant modulation by visual spatial attention of steady-state visual evoked potential amplitude over the occipitoparietal scalp that overlies this area [Morgan & *al.* 1996; Belmonte 1998; Müller & *al.* 1998]. Confirming the attentional nature of this modulation is the observation that the hemispheric pattern of modulation shifts as attention shifts across the midline of the visual field [Belmonte 1998; Müller & *al.* 1998]. Three-dimensional dipole source localisation and fMRI have placed this attentional effect in the areas of posterior fusiform and lateral occipitotemporal gyri [Hillyard & *al.* 1997]. This localisation is corroborated by two studies that combined PET with source localisation of the P100 evoked potential [Heinze & *al.* 1994; Mangun & *al.* 1997]. This convergent evidence suggests that the fMRI and PET effects identified in ventral occipital cortex and the EEG modulation measured at the overlying occipitoparietal scalp sites are manifestations of one and the same neurophysiological process.

Our analysis also revealed effects in parietal cortex. In superior parietal lobe, although there was strong activation both during attention to the left hemifield and during attention to the right, the laterality of attention had no effect on the lateralisation of brain activation. Instead, superior parietal lobe seemed to respond equally or nearly equally to stimuli in both visual fields, attended and unattended. This absence of lateralised activation in superior parietal lobe during lateralised attention replicates the results of other studies that have presented attended and ignored stimuli

simultaneously at fixed, single, peripheral locations in each hemifield [Heinze & *al.* 1994; Vandenberghe & *al.* 1997], but is at odds with a previous finding of lateralised activation during shifts between multiple locations within a hemifield [Corbetta & *al.* 1993]. One possible explanation of this set of findings is that the onset of a stimulus, whether attended or unattended, primes superior parietal cortex to attend to the location of that stimulus. Only in cases where a shift of attention is actually implemented would an additional, shift-related activity be superimposed on this exogenous, stimulus-related activity.

Our finding of intraparietal activation ipsilateral to the attended hemifield – or, equivalently, contralateral to the unattended hemifield – can be explained both in terms of the hypothesis of suppression of irrelevant stimuli and in terms of an alternative hypothesis of spatial orienting. The spatial orienting hypothesis is supported by a convergence of evidence from studies in which a frontoparietal network including intraparietal sulcus is activated by both exogenously and endogenously cued spatial shifting of attention [Nobre & *al.* 1997; Corbetta 1998; Gitelman & *al.* 1999; Hopfinger & *al.* 2000; Nobre & *al.* 2000; Beauchamp & *al.* 2001], by visual conjunction search [Donner & *al.* 2000], and by covert attentive tracking of moving targets [Culham & *al.* 1998]. This same network also seems active during tasks that demand sustained spatial attention during discrimination of orientation [Vandenberghe & *al.* 1996, 1997], form [Martínez & *al.* 1999], internal spatial relationships [Vandenberghe & *al.* 1997], motion coherence [Shulman & *al.* 1999], or visual flow [Büchel & *al.* 1998]. Remarkably, though, even when the factor of sustained spatial attention is controlled, intraparietal sulcus is activated by shifting [Le & *al.* 1998] and conjunction [Wojciulik & Kanwisher 1999] of purely feature-based criteria.

One theory that may explain this generality of intraparietal involvement in attention tasks is the idea that intraparietal sulcus subserves suppression of irrelevant distractors [Wojciulik & Kanwisher 1999]. Behaviourally, the existence of some suppressive process is suggested by the phenomena of negative priming [Tipper 1985] and inhibition of return [Posner & *al.* 1985]. In terms of functional anatomy, suppression within intraparietal sulcus would be consistent with intraparietal activation in spatial and non-spatial tasks that include distractors as discussed above, and with the finding that, unlike frontal activity, parietal activity in Stroop tasks is more sensitive to variations in the task-irrelevant dimension (colour-word versus colour-object) than to variations in the task-relevant dimension (colour-word versus spatial-word) [Banich & *al.* 2000]. In addition, the suppression hypothesis garners some support from studies of selective attention that find an absence of intraparietal activation in the absence of distractors: no activation of intraparietal cortex was detected in a comparison of selective attention to shape, colour, and speed with divided attention to all three attributes [Corbetta & *al.* 1991], nor in a comparison of feature conjunction to simple categorisation [Rees & *al.* 1997], nor during sustained attention to a single, instantaneously moving target [Vandenberghe & *al.* 2001].

These two alternative explanations are difficult to differentiate on the basis of purely correlational methods such as functional imaging, since both predict intraparietal activation contralateral to unattended stimuli. Under the suppression hypothesis this activation reflects active inhibition of distractors, whereas under the spatial orienting hypothesis it reflects the preparation of a reflexive shift of attention evoked by detection of these distractors – a shift that need not actually be executed. Both explanations seem particularly relevant to tasks such as the current one, in which periods of sustained attention are punctuated by shifts. In the task that we have used, subjects are asked to respond selectively to stimuli that satisfy a combination of

spatial and chromatic criteria. Whereas the chromatic criterion is constant, the spatial criterion shifts from time to time: the stimuli to which subjects are responding are always red, but not always in the same hemifield. Under such circumstances, in which one is always anticipating an upcoming shift in the spatial focus of attention, spatial attention may not settle completely on one location. Instead, a somewhat weaker engagement of the spatial filter may yield the best compromise between speed of response to stimuli at the currently attended location and speed of disengagement and shifting to the next attended location. Under the spatial orienting hypothesis, this weak engagement at the current focus may augment the reflexive shifting response to stimuli outside the current focus. Under the suppression hypothesis, weak spatial engagement may demand more vigorous suppression of unattended stimuli that have passed the spatial filter. In this scenario, ventral occipital enhancement and intraparietal suppression would play complementary roles, with the intraparietal suppressive filter plugging the leaks in the ventral occipital selective filter.

This complementary activity between ventral occipital and intraparietal regions may be illustrated by contrasts between certain populations. Although with our small numbers of female and male subjects we did not find a significant sex difference in any of our measures, we did note what appeared to be complementary trends in ventral occipital and intraparietal regions in the two sexes: in the ventral occipital region men's  $z$ -scores tended to be higher in magnitude than women's, while in the intraparietal region women's  $z$ -scores tended to be higher than men's. In a study of subjects with autism performing this same task [Belmonte & Yurgelun-Todd 2001bc], we find that people with autism show no measurable attentional activation in the ventral occipital region, and significantly supranormal activation in the intraparietal region. Both the sex contrast

and the autism contrast suggest that as differential activation in occipital cortex diminishes, differential activation in intraparietal cortex increases, as if to compensate.

Unlike the current study, the work of Wojciulik and Kanwisher [1999] in a series of selective attention tasks found no lateralisation of the intraparietal effect as a function of attended hemifield. This absence of lateralisation is not unexpected, though, since their peripheral spatial attention task included distractors in both hemifields, their peripheral object matching task used distractors that were split across hemifields, and their conjunction task involved only foveal stimulation. The current study, in contrast, used only one irrelevant location which was always in the hemifield opposite to the attended location.

Our intraparietal region of interest is also included in a posterior region identified by Martínez *et al.* [1999] as active in attention to peripheral stimuli. In that study, 3x3 arrays of stimuli were presented bilaterally. Subjects attended to one hemifield at a time, and had to press a button if the stimulus at the centre of the array in the attended hemifield were a rare target. This task demanded selective attention to the central stimulus within the attended hemifield, and suppression of the eight distractors in the attended hemifield as well as the nine stimuli in the unattended hemifield. In this paradigm, the distractors within the attended hemifield likely would have been more salient than those in the hemifield opposite, and thus the demand for suppression would have been greatest in the attended hemifield, and greater than in our study in which distractors were confined to the unattended hemifield. Accordingly, the intraparietal activation detected by Martínez *et al.* was localised contralateral to the attended hemifield, and the effect size exceeded that observed in the current study, reaching significance within a majority of individual subjects.

Too often the conclusions of functional imaging studies are overly specific to the perceptual and cognitive problems presented by a particular experimental paradigm, or by a particular explanatory framework. For this reason we wish to stress that a role for intraparietal sulcus in suppression of irrelevant stimuli would not be incompatible with involvement in the preparation or implementation of attentional shifts, nor with other roles such as attentional integration of object features. One can imagine a neural network architecture in which inputs from various feature detectors, spatial maps, and object representations [Treisman 1993] impinge on interneurons, along with top-down attentional inputs that instruct each interneuron to select or to suppress its particular feature or set of features. This type of architecture would produce increased metabolic demand during conditions of feature integration or selection, feature or object suppression, and shifts of attention between objects, features, or locations. Gross techniques such as fMRI would be unable to detect differences in intraparietal functional anatomy between these conditions. Given the resolution limits typical of current functional imaging systems, one cannot look to fMRI for information on the microarchitecture of neural systems — for the same reason that one does not mend a watch with a sledgehammer.

We can, however, examine single-cell studies for evidence of separate selective and suppressive signals in primate parietal cortex. In macaque monkeys, signals consistent with active processing associated with irrelevant stimuli have been recorded both in area LIP and in nearby visual area 7a. In a memory-guided saccade task, a distractor stimulus presented within the receptive field of an LIP neuron during the delay period evokes a greater response when the target location of the saccade is outside the cell's receptive field than when the target location is inside the receptive field [Powell & Goldberg 2000]: in other words, the cell responds more vigorously when the stimulus is unattended than when the stimulus is attended. In an



exogenously cued attention task, a subpopulation (23%) of LIP cells responded less to the onset of validly cued targets in their receptive fields than to the onset of invalidly cued targets in their receptive fields [Robinson & *al.* 1995]. A smaller subpopulation (13%) showed enhanced response to validly cued targets. Similar results were found with a foveal attention task and peripheral probes, and with a probabilistic attention task with probes in unexpected locations. In recordings from area 7a during a task of delayed matching to location, 55% of neurons responsive to visual stimuli were suppressed (versus 5% enhanced) by attended stimuli as compared to unattended stimuli within their receptive fields [Steinmetz & *al.* 1994]. These findings of greater single-unit response to unattended stimuli have been interpreted in the context of the spatial orienting hypothesis, as indications that parietal tissue is more involved in preparing shifts of attention to previously unattended stimuli than in enhancing responses to currently attended stimuli. However, they are also compatible with the suppression hypothesis. Electrode penetrations in each of these studies have been tangential to the cortical surface, which in these regions lies on the banks of sulci. Given our proposed model of interneuron-mediated suppressive and integrative effects, studies involving radial penetrations of these areas would be of interest. Such studies could categorise neuronal response properties as a function of laminar location and therefore make inferences as to response properties as a function of a cell's position within the local circuit.

In light of the high degree of normal variation in parietal anatomy, several authors [Nobre & *al.* 1997; Corbetta & *al.* 1998; Wojciulik & Kanwisher 1999] have noted the necessity of examining functional anatomy within individuals rather than in a spatial average of individual brains. In a full 30% of the normal population, the intraparietal sulcus follows a distinctly zigzag course through the parietal lobe, sending off varying numbers of small rami as it descends

towards the transverse occipital sulcus [Naidich & *al.* 1995]. Given this degree of variation, spatial averaging based on gross cerebral landmarks would render subtle attentional effects either poorly localised or statistically undetectable. Even aside from the problem of spatial blurring, the attention effects that we have observed are small modulations superimposed on the larger effect of the task: despite the fact that the data when pooled across all subjects yielded a significant result, none of the attention effects were significant within individual subjects. Our alternative to these problems of spatial averaging across subjects and weak attention signals within subjects is to draw regions of interest within individuals, on the basis of individual functional mapping. Basing one's regions of interest on a prior functional analysis may seem at first glance to beg the question of whether an area is activated. The key to resolving this seeming confound is to note that our two functional analyses are completely independent of one another: since the analysis of left attention versus right attention is confined to the task periods, it cannot be affected by the prior comparison of task periods to fixation.

We have demonstrated that spatial enhancement of relevant stimuli in ventral occipital cortex is complemented by an intraparietal response associated with suppression of, or preparation of a reflexive shift of attention towards, irrelevant stimuli during bilateral rapid serial visual presentation. These findings are consistent with those of other functional imaging studies, as well as with those of single-unit recording. Furthermore, the possible suppressive function of intraparietal cortex is compatible with its involvement in other processes such as feature integration and attentional shifting.

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## FIGURE LEGENDS

Figure 1. Attentional regions of interest for all subjects. In each case, functional regions of interest for the attention comparison were drawn in the contiguous areas that were most strongly activated in the task-versus-fixation comparison, within the bounds of the individual anatomical areas of interest. Activations from the task-versus-fixation comparison have been superimposed in one subject in order to illustrate the contribution of functional mapping. (Because subject 10's head was slightly turned within the scanner, some of his regions appear on neighbouring slices. These have been projected on a single slice for purposes of this illustration.)

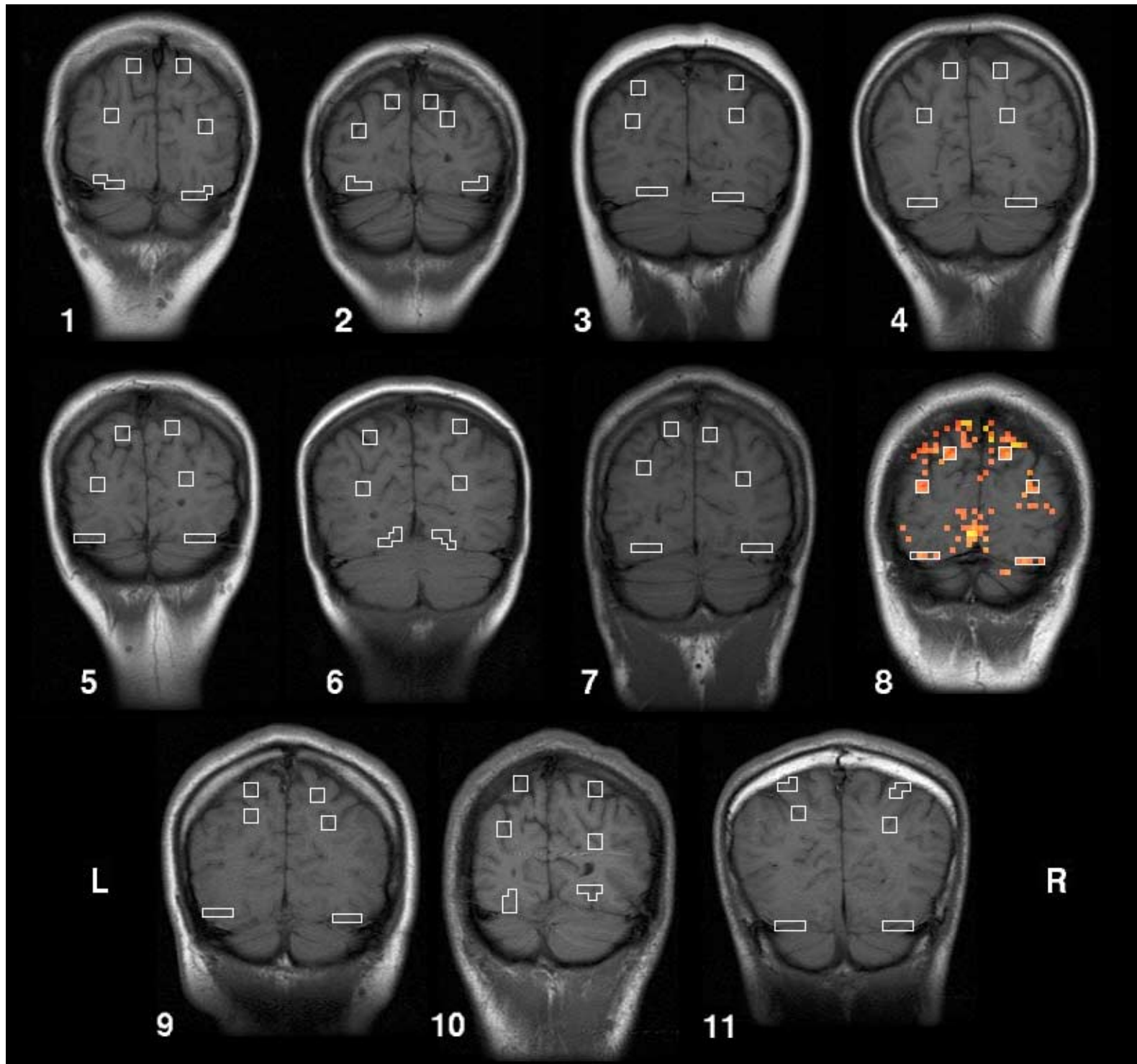
Figure 2. Grand average of gaze direction as a function of time during the intervals surrounding responses. Solid line, rightward shifts. Broken line, leftward shifts. There was no systematic deviation in gaze direction towards either of the target locations, which were positioned at  $\pm 5$  degrees.

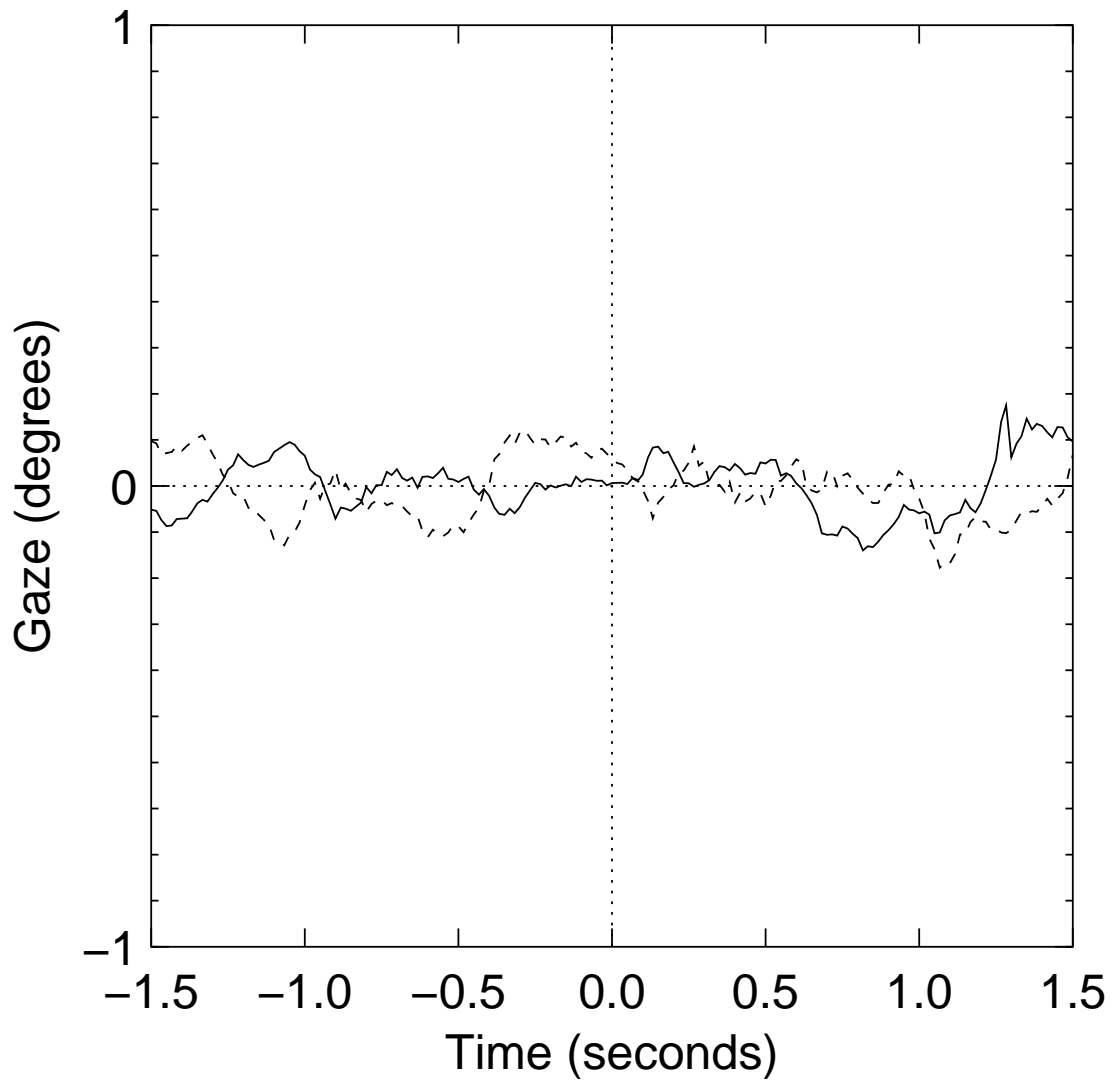
Figure 3. Grand averages of fMRI time series from left (left column) and right (right column) hemispheres, centred on the time of occurrence of an attentional shift. The vertical axis is percent above the mean signal acquired during the fixation periods, when no attention task was being performed. Time series were averaged from six seconds following the preceding shift or the beginning of the task period, up to the time of the next shift or the end of the task period. Solid line, rightward shifts. Broken line, leftward shifts. Note the large contralateral effects in ventral occipital cortex, the ipsilateral effect in right intraparietal sulcus, and the transients in superior parietal cortex.

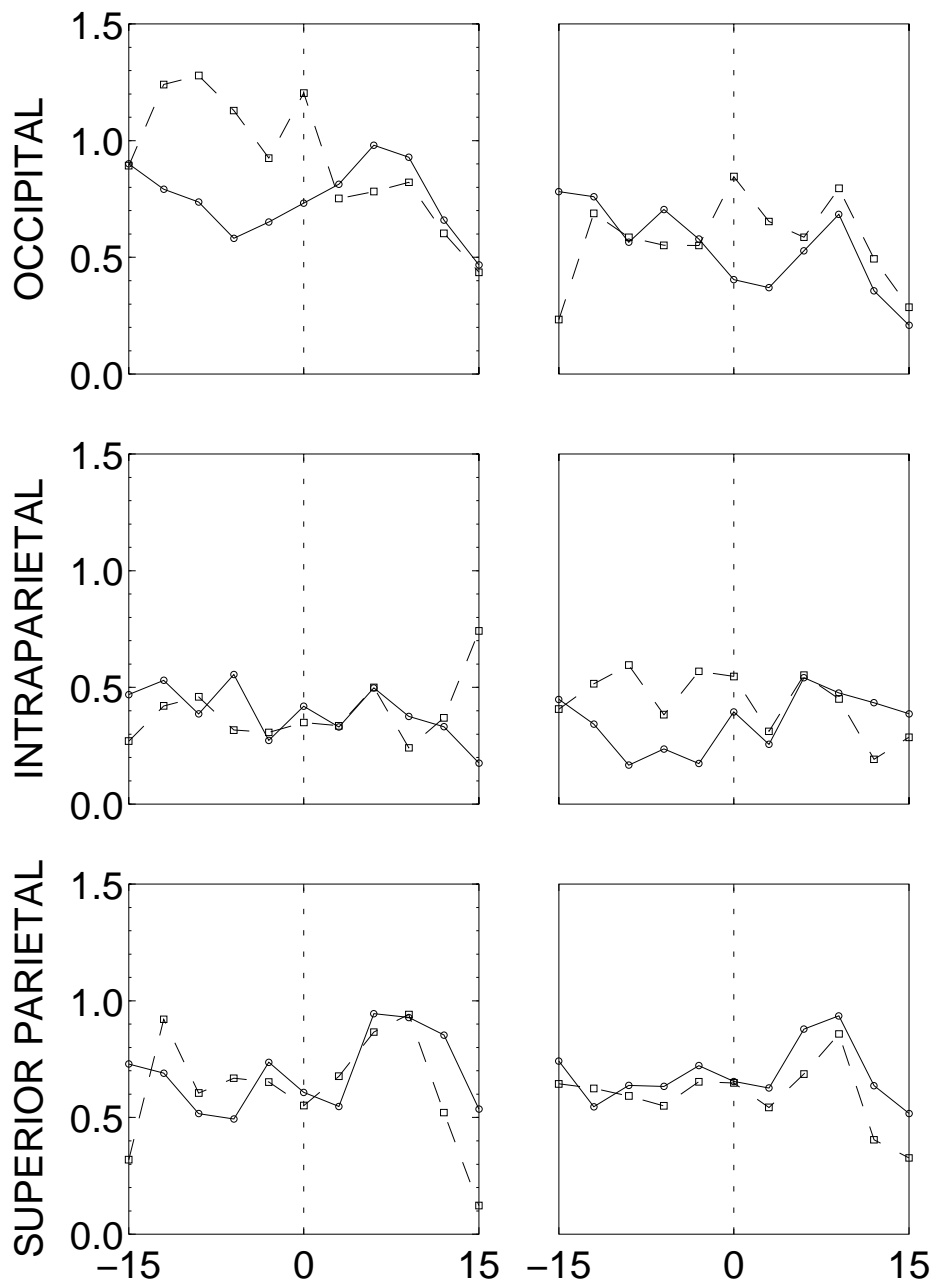
Table 1. Behavioural results. Accuracy, response latency, and numbers of hits, misses, and false alarms for each subject. As the task was designed so that most of the subjects performed at ceiling,  $d'$  scores are not mathematically well defined and therefore are not given.

Table 2. Numbers of leftwards and rightwards saccades for each subject, with average saccade amplitude and standard deviation in degrees of visual angle.

Table 3. Activations for each region of interest, as z-scores and as left-right differences in percent signal change, for individual subjects and as group averages.







L E F T    T A R G E T S						R I G H T    T A R G E T S						
	H	M	FA	accuracy	latency (SD)	H	M	FA	accuracy	latency (SD)		
1	14	0	0	100%	726ms (319ms)	13	1	0	93%	640ms (77ms)		
2	14	0	4	100%	640ms (167ms)	14	0	4	100%	759ms (256ms)		
3	14	0	0	100%	735ms (265ms)	14	0	0	100%	676ms (79ms)		
4	9	2	0	82%	841ms (178ms)	8	4	3	67%	1102ms (254ms)		
5	11	6	1	65%	711ms (181ms)	13	0	0	100%	713ms (192ms)		
6	14	0	0	100%	646ms (101ms)	14	0	0	100%	626ms (110ms)		
7	14	0	0	100%	950ms (279ms)	14	0	0	100%	742ms (108ms)		
8	14	0	1	100%	579ms (89ms)	14	0	0	100%	583ms (92ms)		
9	13	1	1	93%	582ms (57ms)	15	1	0	94%	653ms (107ms)		
10	14	0	0	100%	702ms (89ms)	14	0	0	100%	624ms (74ms)		
11	14	0	0	100%	554ms (52ms)	14	0	0	100%	598ms (85ms)		
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								94%	697ms (119ms)			
								96%	701ms (144ms)			

Subject	L E F T S A C C A D E S			R I G H T S A C C A D E S	
	N	amplitude		N	amplitude
1	0		0		
2	9	1.70 (0.60)	7	1.57 (0.40)	
3	2	1.34 (0.05)	0		
4	2	1.68 (0.26)	6	2.11 (0.89)	
5	2	1.77 (0.29)	0		
6	3	2.06 (0.24)	1	1.27	
7	0		0		
8	0		0		
9	2	1.70 (0.25)	3	1.65 (0.27)	
10	0		0		
11	6	1.55 (0.26)	4	1.55 (0.30)	

## Z-SCORES

## PERCENT SIGNAL CHANGE

## F E M A L E S

	L VO	R VO	L IPS	R IPS	L SPL	R SPL	L VO	R VO	L IPS	R IPS	L SPL	R SPL
1	-0.63	+2.30	+0.87	-2.10	+0.04	-0.05	-0.227	+0.657	+0.086	-0.345	+0.021	-0.021
2	-1.53	-0.46	-0.13	-0.92	+2.14	+0.22	-0.369	-0.098	-0.042	-0.095	+0.281	+0.104
3	-2.38	+0.63	-0.77	-1.77	-1.20	-0.92	-0.633	+0.174	-0.048	-0.191	-0.212	-0.098
4	-2.07	+1.87	-0.10	-1.79	+0.90	+0.01	-0.823	+0.476	-0.067	-0.351	+0.110	-0.011
5	+2.78	+0.68	+2.09	-0.06	+2.39	+2.08	+1.426	+0.306	+0.425	-0.033	+0.551	+0.334
6	+0.04	-1.42	-0.84	-0.22	-1.63	-0.53	+0.005	-0.741	-0.337	-0.086	-0.666	-0.314
MEAN	-0.63	+0.60	+0.19	-1.14	+0.44	+0.13	-0.104	+0.129	+0.003	-0.184	+0.014	-0.001
SD	1.90	1.39	1.12	0.87	1.67	1.04	0.805	0.498	0.249	0.137	0.420	0.215

## M A L E S

	L VO	R VO	L IPS	R IPS	L SPL	R SPL	L VO	R VO	L IPS	R IPS	L SPL	R SPL
7	-1.80	+2.09	-0.77	+0.21	+0.03	+0.77	-0.208	+0.318	-0.053	+0.079	+0.040	+0.071
8	-2.64	+1.31	+0.27	-0.19	-0.93	-0.08	-0.587	+0.236	+0.140	-0.067	-0.087	-0.027
9	-2.38	+0.54	+0.17	-1.03	-0.04	-2.11	-0.899	+0.226	+0.180	-0.232	-0.074	-0.527
10	-1.55	+1.00	+0.50	-0.67	+0.04	+0.17	-0.709	+0.421	+0.177	-0.247	+0.011	+0.047
11	+1.17	+1.17	+0.71	-0.63	+0.83	+0.07	+0.395	+0.326	+0.167	-0.177	+0.227	+0.015
MEAN	-1.44	+1.22	+0.18	-0.46	-0.01	-0.24	-0.402	+0.306	+0.122	-0.129	+0.023	-0.084
SD	1.52	0.57	0.57	0.48	0.62	1.10	0.512	0.079	0.099	0.136	0.126	0.250

MEAN	-1.00	+0.88	+0.18	-0.83	+0.23	-0.03	-0.239	+0.209	+0.057	-0.159	+0.019	-0.039
SD	1.71	1.10	0.87	0.78	1.27	1.03	0.673	0.368	0.197	0.133	0.308	0.224