

# BOLD Signal in Intraparietal Sulcus Covaries With Magnitude of Implicitly Driven Attention Shifts

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## Abstract

A lot is known about the neural basis of directing attention based on explicit cues. In real life however, attention shifts are rarely directed by explicit cues but rather generated implicitly, for example on the basis of previous experience with a given situation. Here, we aimed at studying attention shifts dependent on recent trial history. While explicitly cued attention shifts involve activity in cortex of the intraparietal sulcus, whether this region is also involved in shifting attention according to recent history is still unknown. We asked observers to detect targets in a stream of visual stimuli with three feature dimensions: Color, shape and motion. Critically, target occurrence probability was always higher in one stimulus dimension than in the others, and probabilities switched between dimensions over blocks of trials. After each probability switch, target detection times decreased exponentially for high-probability targets and increased for low-probability targets, compatible with gradual shifts in attention dependent on trial history since the switch. BOLD signal in left prefrontal and intraparietal sulcus regions was higher in the early phase after the switch, while anterior cingulate, cuneus, precuneus, temporal and more anterior frontal regions showed more activation later after the switch. These findings are compatible with the engagement of regions involved in the establishment and maintenance of attentional sets. BOLD signal in left intraparietal sulcus correlated with the size of the performance changes consecutive to the detected targets, suggesting that it reflects the size of attention shifts induced by updating target probabilities over recent trial history.

**Keywords:** fMRI, trial history, statistical learning, one-back detection task, attentional set.

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## Introduction

Attention can be directed to a particular location, object or aspect of a stimulus by an explicit cue (e.g., a central arrow pointing to the hemifield to be attended). However, in many real-world situations, there are no explicit cues telling us where or what to attend to. Instead, we often rely on recent experience of a particular situation to guide our attention, as in the following example: A newcomer arrives in London. The first time she tries to buy a ticket for the London Underground, she is bewildered by all the buttons available on the different ticket machines. After using the machines a few times, she has learned to direct her attention only to the buttons needed to buy her ticket and to ignore the others. The information she accumulated over time now determines where she directs her attention, adequately for her task. In the current study, we investigated the neural mechanisms involved in shifting the attention bias according to information accumulated in recent history.

A number of studies have shown that a higher likelihood of target occurrence in one spatial location or stimulus dimension can attract attention and increase detection performance. This phenomenon has been previously described as priming of pop-out, feature-based facilitation of return, probabilistic or contextual cueing depending on the exact paradigm (Chun and Jiang, 1998; Fecteau, 2007; Found and Muller, 1996; Geng and Behrmann, 2005; Huang et al., 2004; Kristjansson et al., 2001; Maljkovic and Nakayama, 1994; McPeck et al., 1999; Soetens, 1998; Theeuwes et al., 2006). This effect can also be influenced by top-down attentional control (Muller et al., 2004; Muller et al., 2003). The effect has been reported in the monkey also (Dorris et al., 2000; Fecteau and Munoz, 2003; Fecteau et al., 2004).

A fronto-parietal network is known to be involved in top-down control of attention (for recent reviews, see: Behrmann et al., 2004; Corbetta and Shulman, 2002; Yantis and Serences, 2003). When shifting attention from one dimension of a visual stimulus to another (say, from color to shape), transient increases in Blood Oxygen Level - Dependent (BOLD) signal are found in cortex of the superior parietal lobule and intraparietal sulcus (Giesbrecht et al., 2003; Le et al., 1998; Liu et al., 2003; Peuskens et al., 2004; Pollmann et al., 2006; Rushworth et al., 2001; Serences and Yantis, 2007). Shifting attention between stimulus dimensions as in the extradimensional shifts in the Wisconsin Card Sorting Test involves the (lateral) prefrontal cortex (e.g.: Hampshire and Owen, 2006; Owen et al., 1991; Rogers et al., 2000). More posterior regions of the dorsolateral prefrontal cortex, particularly the junction of IFS & precentral sulcus, are associated with activation of the currently relevant task representation (Brass and Von Cramon, 2002; Brass and Von Cramon, 2004a; Braver

et al., 2003; Bunge et al., 2003; Derrfuss et al., 2005; Konishi et al., 2001), whereas more anterior regions are thought to be involved in sustaining the attentional set required by the current cognitive goals (Luks et al., 2002). Both prefrontal and parietal regions are also involved in task switching (Brass and Von Cramon, 2002; Braver et al., 2003; Miller and Cohen, 2001; Serences et al., 2004; Sohn et al., 2000; Yeung et al., 2006)

In this study, our aims were to (1) use target probability to induce implicitly generated shifts in subjects' visual attention and (2) investigate whether neural structures known to be involved in attention shifts are also involved in these implicitly generated attention shifts. Specifically, we hoped to find higher detection performance for targets appearing most frequently, with gradual increases in performance as targets accumulate in recent trial history. We hypothesized that these changes in performance would be due to successive shifts in attention towards the stimulus dimension containing most targets in recent history. We expected the BOLD responses in intraparietal sulcus and possibly in prefrontal cortex to reflect the size of these attention shifts (as measured by their effect on behavior). To test this, we quantified the changes in attention bias from the changes in behavior over time and created BOLD predictors to identify signal correlated with the size of the attention shifts.

## Materials and Methods

### Participants

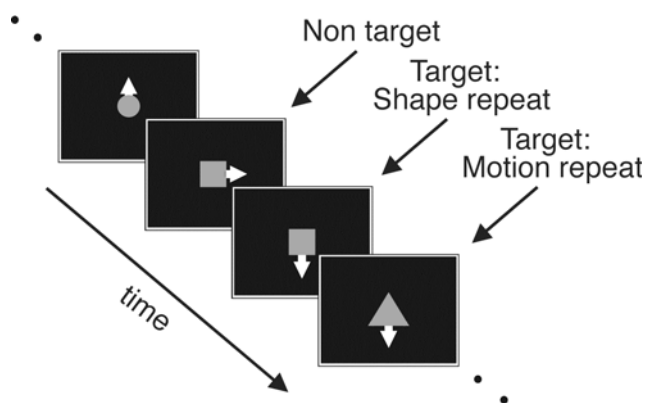
Eleven human volunteers (eight male, aged 21 to 29 years) from the Tübingen community participated in the experiment. All participants had normal color vision, normal or corrected-to-normal visual acuity, no history of neurological or psychiatric illness and gave full written informed consent. The study was approved by the local ethics committee.

### Experimental Design and Analysis

#### One-back Repetition Detection Task

Participants were to detect targets in a rapid serial visual presentation of simple visual stimuli. Targets were consecutive visual stimuli that matched in one of their features: color, shape, or motion direction (see Figure 1). Features of a given stimulus were randomly sampled from four easily distinguishable states per dimension (color: red, blue, green or yellow; shape: square, disk, cross or triangle; motion direction: vertical up, vertical down, horizontal left and horizontal right). N.B., we refer to the terms 'dimension' or 'feature dimension' of a stimulus to mean its color, shape or motion direction. For each particular stimulus, each dimension is in one state out of several (e.g., in the dimension 'color', one stimulus could have one of the states red, blue, green or yellow). By contrast, when we refer to 'stimulus feature' or 'feature state', we mean the state of one dimension of a particular stimulus; for example, we say the 'feature state' of the 'color dimension' of a given stimulus is red. In our experiment, there were never repetitions in more than one dimension at the

same time over consecutive stimuli. For example, color targets were defined by having the same color (e.g., red) as the stimulus immediately preceding it, while shapes and motion directions differed. In non-target trials, all three stimulus features were changed from one stimulus to the next (i.e., the stimulus had a different color, shape and motion direction than the preceding stimulus). The duration of each trial was 1.5 s and started with presentation of the stimulus for 300 ms (spanning  $1.7^\circ$  of visual angle and moving by  $0.8^\circ$  with a constant speed of  $2.7^\circ/s$ ) at the center of a black background, followed by a fixation cross until the start of the next trial. Participants were free to respond at any time during the trial, but before the onset of the next trial. A single button was used to report all three types of targets and no feedback was given.



**Figure 1: Experimental Design.** Participants' task was to report targets consisting of repetitions of a stimulus feature from one trial to the next (one-back repetition detection). In the example shown, the first stimulus represents a blue circle moving up (arrow not shown in the real stimulus, color not shown in this figure) and the second, a red square moving right. The second stimulus is not a target because all its features are different from those of the first stimulus. The third stimulus has the same shape (square) as the second stimulus, and is therefore a shape target. The fourth stimulus is a motion target. Color targets also appeared but are not shown here. Importantly, target occurrence probabilities were unequal and varied across blocks of trials.

#### Target Probability

The probability of target occurrence was determined by one Poisson process per stimulus dimension (color, shape and motion direction), all running simultaneously. On a given trial, one of the Poisson processes had a high probability (0.29) while the other two processes had a small probability (0.032), thereby giving a bias to the occurrence of a particular type of target. Each trial could contain only one type of target (priority was given to the high-probability targets), and targets were spaced at least one non-target trial apart (i.e., the occurrence of a target excluded the possibility of a target in the next trial, thus avoiding long repetitions of a particular stimulus feature state). Probabilities were switched between stimulus dimensions every 20-30 trials (determined by a random process with flat distribution), thus forming

blocks in which the probability of one type of target was higher than for the others (Figure 2A). Each 5-minute run contained 207 trials, of which an average of 67 were targets (high and low probability confounded); there were on average 7.45 targets per block, or 0.32 per trial. There were 6.71 high probability targets per block or 0.29 per trial, and 0.74 low probability targets per block or 0.032 per trial. A cue (four white stars shown in the center of the screen for 500 ms, 2° by 0.4° of visual angle) indicated when target probability switches occurred, but did not reveal which dimension would contain more targets in the coming block.

#### *Effects of Target Probability on Detection Performance*

The experiment was designed to induce implicitly-generated shifts in attention through variations in target occurrence probability. Target probabilities were changed between blocks: E.g., at the transition from a color to a motion block, color targets would switch from high to low probability and motion targets would see the reverse change. We told participants *when* changes in target probability happened, but not *what* these were (see Target Probability section above). We expected subjects to respond faster and more accurately to targets occurring with higher probability. Furthermore, we hoped that detecting targets would gradually shift subjects' attention to the dimension containing most targets since the last change in target probabilities. We expected that these gradual changes in attentional bias would be reflected in performance changes as a function of target history in the current block of trials. As the task was to respond as quickly and to as many targets as possible, we expected that participants would integrate information over the course of each block in order to find out which stimulus dimension would contain more targets for the remainder of the block, and bias their attention towards that stimulus dimension while still keeping some attentional resources for the other dimensions in order to detect the low-probability targets. We therefore considered differences in detection performance between stimulus dimensions to be an indication for the relative attentional weight given to these stimulus dimensions. Of course, although our subjects reported after the experiment that they did bias their attention to the dimension where they thought more targets would occur, we cannot be absolutely certain that subjects actually spread their attention exactly in the way that their differences in performance suggest. Other possible explanations for differences in detection performance between stimulus dimensions are covered in the Discussion section.

In order to reliably induce attention shifts through target probability, we first had to ensure that subjects could accumulate enough evidence of the asymmetry in target occurrence probabilities during the course of a block. We therefore made the target detection task easy enough to enable our subjects to detect most targets presented (this was done by optimizing stimulus feature contrast, presentation time and asymmetry in target occurrence probability

during pilot experiments not reported in the present paper). The difficulty of our task is similar to those used in the priming of pop-out literature (e.g.: Fecteau, 2007; Geng and Behrmann, 2005; Maljkovic and Nakayama, 1994; Theeuwes et al., 2006).

We expected to find the effects of successive attention shifts in changes of response times during the first few trials of a block, as has been reported in the priming of pop-out literature in humans (e.g.: Fecteau, 2007; Huang et al., 2004; Maljkovic and Nakayama, 1994) as well as monkeys (Dorris et al., 2000; Fecteau et al., 2004). Specifically, we expected that within a block of trials, RTs would decrease with increasing numbers of detected targets in the stimulus dimension where target probability was high, while RTs to less-frequently occurring targets would increase. To test this, we binned RTs according to their history (how many targets of the same stimulus dimension had appeared before a given target since the last change in target probabilities, see Figure 2B and Figure 3C, 3D). Then, for each participant, run and stimulus dimension, we modeled the binned RT means as a function of the position in history using the regression model

$$y = e^{-\lambda x} - \beta x + c$$

composed of an exponential term with decay parameter  $\lambda$ , a linear trend term with parameter  $\beta$  and a constant term or parameter  $c$ ;  $y$  represents the data to be explained (i.e. the means of the binned RTs) and  $x$  represents the position in the trial history. The idea behind this model was to explain the sequence of binned RTs as a linear summation of a constant or baseline term (the part of the RT variance that is independent of trial history) and two terms respectively linearly and exponentially dependent on the trial history. As the number of targets per bin was highly variable, we used a weighted-least-squares procedure in which weights were the numbers of targets per bin. Thus, to calculate the parameters, the weight matrix was integrated in the regression model such that the variance from each bin was weighted according to the number of trials from which the variance was computed:

$$\hat{B} = (X^T W X)^{-1} X^T W y$$

where  $\hat{B}$  is the vector of the three parameters (for the exponential, linear and constant terms),  $X$  is the regression model made of the exponential decay, linear trend and constant term regressors,  $W$  is the weighting matrix and  $y$  is the data. This model explained the data well as can be seen from the regression analysis results (see Behavioral Results).

#### *Procedure*

Prior to the actual experiment, participants completed one practice run commented by the experimenters to acquaint them with the task and stimuli. They were told to report all three types of targets whenever they occurred ("one-back repetitions" in color, shape or motion direction), as fast as possible. Participants were informed that target probabilities were unequal and would change when a cue (four white stars) appeared, and that this knowledge could be used to

help them detect the targets; however, they were not told by how much the probabilities differed nor which stimulus dimension would contain more targets in which block. Participants were placed comfortably in the MR scanner after completing the practice run, their head held in place with foam pads. The stimuli were projected by a JVC D-ILA LCD projector onto a screen placed 140 cm behind participants' head and were viewed through a mirror mounted on the head coil. The Psychtoolbox (Brainard, 1997; Pelli, 1997) implemented in Matlab 7.0 (The MathWorks, Inc., Natick, MA, USA) running on a Windows PC (Pentium 4 at 3.2 GHz, 2GB RAM, NVIDIA GeForce 7800 GTX graphics card) was used for stimulus presentation and collecting participants' responses from a magnet-compatible button box (The Rowland Institute at Harvard, Cambridge, USA). Stimulus presentation was triggered with the 5-Volt pulse of the fifth volume of the fMRI sequence (accommodating for four dummy volumes to eliminate T1 signal artefacts). Participants completed twelve runs of 207 trials (5.4 minutes/run).

*Note: Three Types of Targets Reported by One Button*

Using a single button to collect subject responses eliminated the potential confounding effects on target detection performance that might have resulted from switching between different buttons when reporting different target types occurring closely in time, and thus also avoided contaminating the neural correlates of attention shifts with those of response shifts. Although one button was used to report all three types of targets, we could separate performance according to target dimension because each button press could be assigned to a particular target type almost with certainty, as explained in the following. Subjects had to indicate a target by responding before the next stimulus was shown (the 1.5s inter-stimulus interval proved to be ample enough time as <2.5% of all RTs exceeded 1s), otherwise this target would be considered to have been missed. Because targets could not follow each other immediately, responding too late (i.e. during the next trial) constituted a "false alarm", as would of course any response in a trial without target (anticipating from the results: False alarms were rare, about 1.7%, and their RT distribution very similar to that of the hits, with <5% longer than 1 second). As a target could occur in only one stimulus dimension per trial, we could therefore assign each button press to a particular target and it was therefore possible to calculate hit and false alarm rates separately for the three stimulus dimensions.

The only possibility for the misattribution of a button press we could envisage was the following: If on a particular trial a subject thought he saw a target in one dimension and the target actually occurred in another dimension, we would have failed to record a false alarm in the former dimension and instead wrongly recorded a hit in the latter dimension. This would however be extremely unlikely, as false alarms were rare overall (targets were highly salient when attended to) and there is no reason to assume that perceiving a target in the wrong dimension would

occur more frequently than perceiving a target when there was none at all. Regardless of this possibility, we were interested in *changes* in detection performance as a function of target position and high-versus low-probability targets. As performance was of course measured identically regardless of target position, we do not envisage confounding effects on our data resulting from misattributed button presses.

**FMRI Data Analysis**

*Early and Late Phases of a Block of Trials*

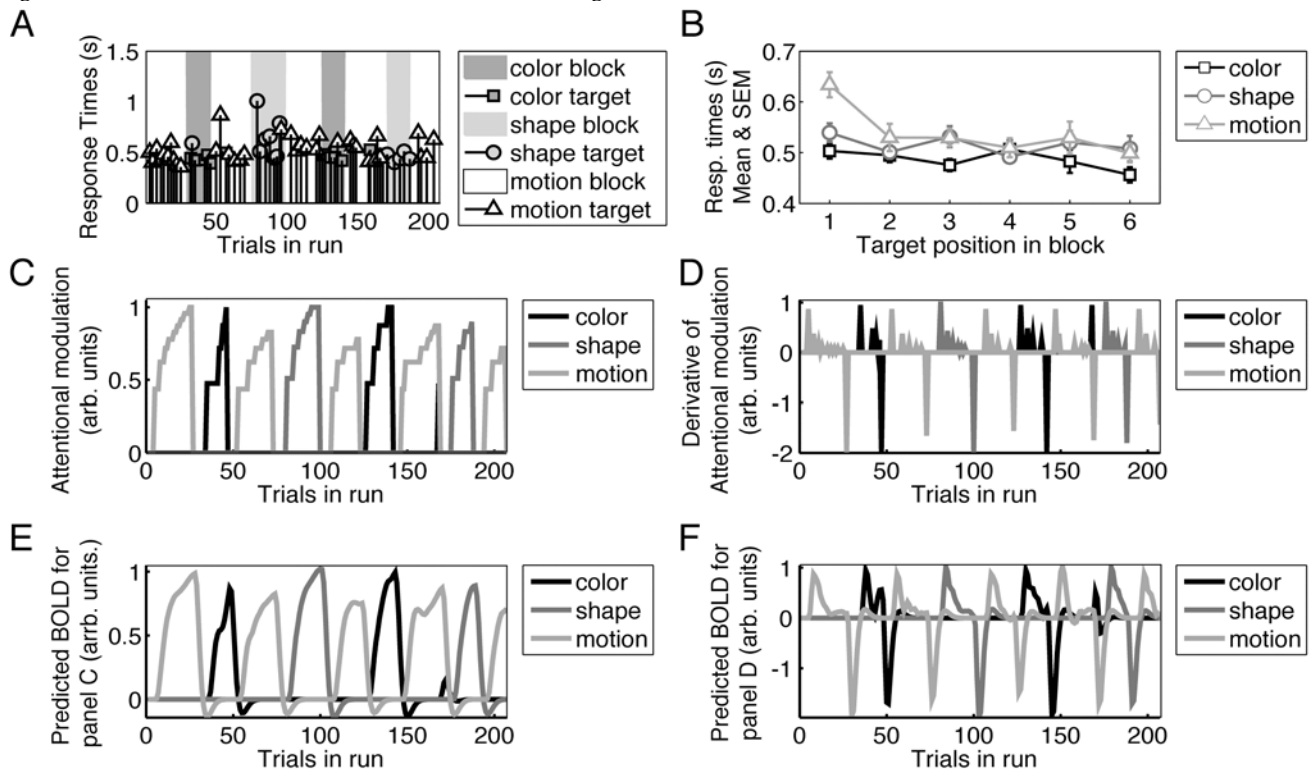
We hoped that after each switch in target probability, subjects' attention would be gradually shifted to the dimension containing most targets in recent history. Thus, we expected performance to change gradually in the early phase of a block of trials until the attention bias is established, then stabilize in the later phase of the block. These two phases would respectively involve the establishment of an attentional set (i.e., subjects would be figuring out which dimension to bias their attention to) and the maintenance of this bias. Therefore, we expected different neural structures involved in cognitive control to respond in the early and late phases of a block, particularly within the dorsolateral prefrontal cortex (see Introduction). This hypothesis was tested in the first analysis (Analysis 1).

*Attention Time Course Regressors*

The main interest of our experiment was to study parametric changes in attention bias as evaluated from changes in behavior. We hoped that subjects' attention would be gradually shifted to the dimension containing most targets in recent history. We further hypothesized that this would be the result of attention shifts occurring immediately after the detection of a target. To identify voxels with activity related to these attention shifts, we created "attention time course regressors" to analyze the fMRI data (Analysis 2). These regressors represent the changes in attentional bias occurring through the course of the experiment as a result of the experimental design. We used the regression model described above, fitted to the response time data (Figure 2A and 2B), to create attention time courses for each run. We then created regressors for the fMRI data by convolving these time courses with the expected ("canonical") haemodynamic response function. The procedure is described in the following paragraphs and illustrated in Figure 2.

Starting at the beginning of a block from a baseline representing equal distribution of attention across stimulus dimensions (= no bias), values of the attention bias time course regressor were increased every time a target was detected in a given dimension (say color, shown in black in Figure 2C), and reset to baseline at the start of the next block. This represents our hypothetical stepwise increase in attention bias resulting from the detection of successive targets. The values used to increase the regressors were taken from the model fitted to the RTs: The regressor was increased by a big step for a big decrease in RT (Figure 2A and 2B). As can be seen in Figure 2C, the

regressor values increase with the number of targets



**Figure 2: Attention Regressors used in fMRI Data Analysis (Analysis 2).** (A) Example responses of one run of 207 stimuli. Vertical lines represent detected targets, their height represents response times. The background shading indicates which target type was most probable: White indicates a higher occurrence probability for motion targets, a "motion block". (B) Response time (RT) changes for high probability targets as a function of the position of the detected target in a block (e.g., squares represent data from color targets in color blocks) for one run. Data from one participant, error bars are standard errors of the means across trials. (C) "Attention bias" regressors for the three stimulus dimensions for the run represented in panel A, representing changes in attentional bias due to recent trial history (=number of targets having already occurred in the block). (D) First derivative over time of the regressors shown in panel C, representing the shifts in attention towards or away from a particular stimulus dimension. (E) and (F) Regressors used to analyze the fMRI data (Analysis 2) made by convolution of the regressors shown in panels C and D respectively with SPM2's canonical haemodynamic response function (sum of two gamma functions).

as RTs decrease, then reach a maximum value when RTs do not decrease anymore, and finally drop back to baseline when participants are shown that probabilities switched between dimensions (i.e., start of the next block). This represents our hypothesis about changes in attention in this paradigm: When information about the target probabilities in the current block accumulates, the attentional bias towards the stimulus dimension most likely to contain targets increases. This would result in increasingly short RTs for targets in that dimension but longer RTs for other targets, which is what our behavioral data show.

We hypothesized that a brain region involved in shifting attention would show activation commensurate with the changes in the attention bias (i.e., attention shifts). To compute the regressors representing the predicted BOLD signal for the attention shifts, we first created attention shift regressors by taking the first temporal derivative of the attention bias regressors (one per stimulus dimension, run and participant, for an example see Figure 2D). Each regressor represents the expected

neural activity related to the attention shifts away from equal distribution over dimensions and towards one particular dimension. High positive values following the first few targets in a given block represent increases in firing as attention is shifted strongly, then smaller values when attention is shifted less strongly. Finally, a negative value at the end of a block represents strong decreases in firing below baseline, possibly due to a decrease in firing during a state of neural adaptation or fatigue, as the attention bias is resolved and attention is again spread over all stimulus dimensions. We then convolved these regressors with SPM2's canonical haemodynamic response function (HRF, a sum of two gamma functions) as shown in Figure 2F. Based on the fMRI literature on attention shifts, we expected to find voxels with such activation profiles in the cortex surrounding the intraparietal sulcus. In addition, we hypothesized that some voxels might show BOLD responses related to the attention bias itself: Such voxels might show stronger neural activity (and therefore also high BOLD signal) when attention is directed to a particular dimension of the stimuli.

Therefore, we took the attention regressors (Figure 2C) and convolved them also with the HRF (Figure 2E). Both sets of BOLD signal predictors were inserted into the SPM2 design matrices (see below). These regressors were not de-trended or de-meant before input into SPM2 in order to accurately represent our activation hypothesis; however, SPM2 automatically performs this in order to correctly estimate the mean activity over a scanning run.

As discussed above, the task difficulty was kept low to ensure that subjects detected enough targets and be affected by differences in target probabilities. This also had advantages for our parametric fMRI data analysis: A great number of detected targets allowed us to collect many trials with varying magnitudes of attention shifts, in all positions of the blocks but particularly at the beginning of blocks where the attention bias is gradually shifted from equal distribution over dimensions towards one dimension. Frequent occurrences of trials in different block positions during the whole experiment also shifts the power of induced effects out of the low temporal frequency range where fMRI data are most noisy and thus optimizes the design (Josephs and Henson, 1999).

### *fMRI Data*

#### *fMRI Data Acquisition*

Images were acquired on a 3-Tesla Siemens Trio Scanner (Siemens Medical Systems, Erlangen, Germany) using an 8-channel receiver head coil. The MR sequence used to acquire Blood Oxygen Level Dependent (BOLD) signal data was an Echo-Planar Imaging (EPI) sequence with a repetition time (TR) of 1880 ms, an echo time (TE) of 40 ms, a flip angle of 78°, a field of view of 256 x 256 mm, a matrix size of 64 x 64, and a bandwidth of 2302 Hz/px. Each functional image comprised 27 axial slices with an in-plane resolution of 3 x 3 mm, a thickness of 3 mm and a 1 mm interval between slices, and was positioned to cover the entire brain excluding the cerebellum, based on an anatomical scout image of thirteen sagittal slices. We acquired twelve runs of 5.4 min (179 images) per participant. The first 4 images were discarded to eliminate the T1 saturation effect. T1-weighted anatomical scans were acquired after the functional runs (MDEFT; TR = 10.55 ms, TE = 3.14 ms, flip angle = 22°, image matrix = 256 mm [Read direction] x 224 mm [Phase], 176 slices, voxel size = 1x1x1 mm, scan time = 5.59 min).

#### *Preprocessing*

Preprocessing of the fMRI data was carried out using the SPM2 software package (Wellcome Dept. of Imaging Neuroscience, <http://www.fil.ion.ucl.ac.uk/spm>). To correct for head motion, the functional images were realigned with the first functional image and resliced (Friston et al., 1995a). Estimated motion parameters never exceeded 1 mm. Images were normalized to a standard EPI T2\* template with a resampled voxel size of 3 x 3 x 3 mm (Friston et al., 1995a), then smoothed by convolution with a 9 mm full width at

half maximum (FWHM) Gaussian kernel.

#### *Statistical Analysis: Mixed Effects Procedure*

Processed fMRI data were analyzed using the general linear model framework implemented in SPM2 (Friston et al., 1995b). We performed three successive analyses to test different hypotheses on the same data. Analysis 1 was designed as a simple way to identify brain regions responding differently during the build-up of the attentional bias compared with the period where the bias was established. Analysis 2 was a more sophisticated analysis designed to identify voxels with signal directly related to changes in attention shifts and attention bias as they unfold over time, using the individually-fitted attention regressors described above; this was the analysis of main interest in this experiment. The third analysis was a control analysis on the results of Analysis 2. Each analysis was performed as a two-stage, mixed effects procedure. The first step of each analysis used a fixed-effects model to analyze individual data sets. The second step of each analysis used random-effects *t*-test models to analyze the group aggregates of individual results. We report only results from the group statistics in order to enable inference of our results to the whole population from which the participants were drawn. We will now describe the mixed-effects procedure used in all analyses, and then describe each analysis in detail in the next sections (Analysis 1, 2 and 3).

For each analysis, we created a fixed-effects model for the data of each participant, by modeling each run separately within one GLM ("multiple sessions per participant" in SPM2). A temporal high-pass filter with a cutoff of 128 sec was applied to the preprocessed data to remove low-frequency signal drifts and artefacts, and an autoregressive model (AR 1 + white noise) was applied to estimate serial correlations in the data and adjust degrees of freedom accordingly. Following that, a linear combination of regressors in a design matrix was fitted to the data to produce parameter estimates which represent the contribution of a particular regressor to the data. Each design matrix contained, in addition to our regressors of interest, 6 movement vectors per run obtained during realignment to model signal variance due to head motion artefacts, and a constant term to model each run's baseline signal. Fitting the BOLD time-series of each voxel in the brain with this design matrix gave effect size parameter estimates for each regressor, resulting in 3D maps of parameter estimates for all voxels.

In the second level of each analysis, group effects were assessed by performing one-sample *t*-tests on specific contrast images computed for each participant. These individual contrast images were made by contrasting specific parameter estimate images averaged over all runs of each participant. A mask selecting only those voxels lying within the brain in all participants was used in all second-level models.

Activations were thresholded at  $p = 0.05$  corrected for multiple comparisons across the whole

brain at the cluster level.

#### *Analysis 1: Responses to Early versus Late Targets*

This analysis was aimed at identifying neural structures responding differently when the attentional set was being built up (early phase) compared with the period where the attention bias was established and maintained (late phase). On the basis of our behavioral results, we defined the early phase as the first and second trials of each block (where detection performance was changing: RTs were decreasing, at least in some target dimensions), and the later phase as the third trial and onwards (where the performance was more stable). This separation into early and late phases after the second target was arguably somewhat arbitrary but allowed a comparison of meaningful numbers of targets from both phases. To this end, we modeled separately the following trial types: The first detected high-probability targets of each block, the second detected high-probability targets of each block (for both of these target types we pooled over target dimension due to low numbers per run and because the attentional bias was not yet clearly established), the later detected high-probability targets in the block (i.e. from the third target onwards; for these targets, color, shape and motion targets were modeled separately), the detected low-probability targets (pooled over target dimension due to low numbers), the missed targets and the non-target trials. Block onset cues were not modeled as they were highly correlated in time with the first hits occurring in the block. False alarms were not modeled due to very small numbers per run.

In our group analysis we compared responses to detected high-probability targets early in the block versus late detected targets. This was tested both separately for each target dimension for the late targets and by pooling over target dimensions.

#### *Analysis 2: Effects of Attention Shift*

This analysis was designed to test our main hypothesis: Are there voxels in the brain whose BOLD signal changes can be predicted by our attention-shift timecourse regressors? Thus, the regressors of main interest in the model were the 3 attention shift-related BOLD regressors (for details see Attention Regressors section and Figure 2F). In addition, the model contained 3 attention bias-related BOLD regressors (Figure 2E) which were of minor interest.

Furthermore, the model contained a number of regressors designed to model BOLD signal of no interest. These regressors all represented different possible aspects of the signal without interfering with each other. They were the following: 3 regressors created by convolving the attention shift regressors (modeling BOLD signal related to the level of the attention shift) by the temporal derivative of the HRF to account for deviations in peak latency from the standard HRF shape. To account for variance related to the stimuli shown in the experiment and not related to changes in attention, we included regressors modeling 6 event types: Detected targets (for high probability targets in each target dimension and low

probability targets pooled over all dimensions due to small numbers, i.e., 4 event types), misses and non-target trials. False alarms were not modeled due to very small numbers per run. Each of these event-related regressors was uncorrelated to the attention regressors as it did not include variations related to changes in attention. To account for effects of residual RT variance unrelated to changes in attention due to target position, we added residual RT regressors made by modeling detected high- and low-probability targets as delta functions parametrically modulated by the RTs, then orthogonalized with respect to the fitted attention regressors. This procedure, performed in Matlab using the function `orthog.m`, modified only the residual RT regressors and not the attention regressors. Although this procedure affects the relationship between the residual RTs and the residual RT regressors, it ensured that they could only model variance unrelated to the attention regressors. The event type and residual RT regressors were each convolved with the canonical HRF and separately with the temporal derivative of the HRF.

For our group analysis, we separately tested the effects of attention shifts and the effects of attention bias in one-sample *t*-tests over participants. For both effects, we tested all dimensions (color, shape and motion) combined.

#### *Analysis 3: Effects of Changes in Response Time Independent of Attention (Control Analysis)*

This last analysis was a control analysis, designed to address the following alternative hypothesis: Are the activations found in Analysis 2 *directly* related to changes in response times, *independently* of our attention hypothesis, and thus *not specific* to changes in attention? This analysis was constrained to the cluster identified in Analysis 2, and we hoped to find only small, non-significant effects.

For each run, we computed a histogram of all RTs, and then assigned each RT to one of four 25-percentile-bins, from the fastest 25% to the slowest 25%. Each RT bin was entered as a condition into SPM2, which created regressors by setting delta functions at the timepoints at which these RTs occurred, and then convolving both with the HRF and the temporal derivative of the HRF in separate regressors. Non-target trials were used as a reference condition and were similarly entered into the model, thus resulting in a model with ten regressors of interest per run. We tested the effects of linear decreases in RT in the group data (1-sample *t*-test over participants).

#### *Coordinate System and Anatomy*

Coordinates are reported in the Talairach space, after conversion from SPM2's MNI coordinate output using Mathew Brett's `mni2tal.m` function implemented in Matlab (<http://imaging.mrc-cbu.cam.ac.uk/imaging/MniTalairach>). Anatomical structures were identified with brain atlases and Simon Eickhoff's Anatomy toolbox for SPM2 based on probabilistic cytoarchitectonic maps (Eickhoff et al., 2005).

*Trial-Averaged BOLD Response Time Course*

To describe more precisely the event-related BOLD response in the IPS cluster (identified by the attention shift contrast in Analysis 2, our main interest), we computed the trial-averaged responses to attention shifts following detected high- and low-probability targets, as well as for the three different types of high-probability targets (color, shape and motion) and for the high-probability targets as a function of trial position (pooling over target dimensions). Raw BOLD signal data from all voxels of the cluster identified in the IPS were extracted and filtered by removing low frequencies (cutoff = 128 seconds) and movement artefacts (using the realignment parameters calculated by SPM2), then averaged over voxels. For each run of each participant, the time-series were converted into percent signal change from average activity by dividing the signal measured at each time point by the average signal during the run, subtracting 1, and then multiplying by 100. The event-related responses to each event type were then averaged across all participants and runs from 0 to 17 seconds after stimulus onset. Signal at stimulus onset was used as a reference and thus subtracted from the time courses.

**Results****Behavior***Effects of Target Probability*

Before testing our hypothesis of main interest (gradual changes in performance in the block due to accumulating targets after a change in target probability), we first assessed if there was a difference in detection performance between low and high target probability targets, independently of the target position in the block. As shown in Figure 3A, hit rate was higher for high-probability targets ( $91 \pm 0.9\%$ , mean & SEM over 11 participants, pooled over target dimension) than for low-probability targets ( $79 \pm 4.5\%$ ) ( $F(1,11) = 13.67$ ,  $p < 0.01$ ; 2-way repeated measures ANOVA with factors Target Probability [high, low] and Dimension [color, shape, motion direction]). No significant difference across stimulus dimensions or interaction was found. False alarm rates were low ( $1.7 \pm 0.45\%$ ). As described in the Methods section, these high accuracy values are concordant with our intention to make the detection task easy; this is in order to (1) maximize our chances to observe gradual changes in response times with accumulation of detected targets in a block of trials (see "Effects of Changes in Target Probability" below) and (2) to collect fMRI data from a sufficient number of detected targets for a parametric analysis using the attention regressors.

Figure 3B shows that response times were shorter for high-probability targets ( $570 \pm 24$  ms, pooled over target dimension) than for low-probability targets ( $654 \pm 30$ ) ( $F(1,10) = 86.67$ ,  $p \ll 0.001$ ; same ANOVA design as used for hit rates). In addition, there was a significant difference between stimulus dimensions ( $F(2,20) = 13.78$ ,  $p < 0.001$ ; RTs were longest for motion, then shape, then color) and these differences were more pronounced for low than high probability targets (interaction between target probability and

stimulus dimension:  $F(2,20) = 3.8$ ,  $p < 0.05$ ). The differences between dimensions suggest an unequal target detection difficulty across stimulus dimensions; this is not a concern as the main interest in this experiment was the performance changes occurring *within* each stimulus dimension after the changes in target probability, as discussed in the following paragraph.

The effects of target probability on hit rates and response times are similar to those found in previous studies that have used target probability to induce attentional modulation or priming of pop-out (e.g.: Fecteau, 2007; Geng and Behrmann, 2005; Maljkovic and Nakayama, 1994; Theeuwes et al., 2006).

*Effects of Changes in Target Probability*

The experimental design was optimized to find effects of changing target probabilities between blocks of trials. Specifically, we expected RTs to decrease with accumulating high-probability targets within a block. On the basis of previous findings of such sequential effects (e.g.: Fecteau and Munoz, 2003; Huang et al., 2004; Maljkovic and Nakayama, 1994), we expected the effects to have an exponential shape and stabilize after 3-6 targets.

Indeed, we found that RTs decreased exponentially with increasing numbers of targets of the stimulus dimension in which target occurrence probability was high, irrespective of other interceding target or non-target trials (Figure 3C). This decrease was not due to a change in speed-accuracy trade-off because hit rates for high-probability targets remained stable as target numbers increased (Figure 3D), and was not an artefact resulting from the use of RT means as almost identical results were obtained using medians (not shown). RTs for low-probability targets, initially similar to those for high-probability targets, became longer from the second trial position onwards, while hit rates decreased (Figure 3D). The numbers of high-probability targets for the 6 target positions shown in Figure 3 were: 35.2, 35.2, 34.8, 33.4, 29.3, 22.8 (means per subject, averaged over target dimensions). The corresponding numbers of low-probability targets were: 8.3, 11.1, 9.6, 11.1, 9.1, 7.0 (these were pooled over the three target dimensions).

Our regression model composed of an exponential decay, linear and baseline terms fitted the RT data well: We found significant regressions for all target types (results for color targets:  $F(3,7) = 21.24$ ,  $p < 0.002$ ,  $R^2 = 0.88$ ; shape:  $F(3,7) = 8.33$ ,  $p < 0.015$ ,  $R^2 = 0.72$ ; motion:  $F(3,7) = 181.45$ ,  $p < 0.001$ ,  $R^2 = 0.99$ ). A significant regression was also found for the low-probability targets ( $F(3,6) = 16.84$ ,  $p < 0.005$ ,  $R^2 = 0.91$ ) with an exponential increase instead of a decay, although this increase was only clearly present for the first few target positions (Figure 3C). For both high and low-probability targets, the fitted parameters from each run were used to create attention time course regressors to analyze the simultaneously acquired BOLD signal data (see Materials and Methods).

Note: The effects of target position on the data from

the low-probability targets are more noisy than for the high-probability targets. The results from the low-probability data are to be taken with caution as they are based on less datapoints per subject (see numbers in the previous paragraph), which particularly affects the hit rates as those are based on binary data. With so few trials (less than one low-probability target per block on average), fluctuations of alertness over the dozens of blocks of this long experiment could easily overshadow trial position effects. In addition, there was a large difference in RT across target dimensions in our high-probability target data, and so effects of target dimension could easily have obscured trial position effects in the low-probability target data as these were pooled across dimensions. The further increase in RT for the low-probability targets at position 6 and the accompanying decrease in hit rate

could be an interesting additional effect but as only 7 data points per subject contributed to these data, we will not discuss this effect further.

### fMRI Data

#### Analysis 1: Responses to Early versus Late Targets (Whole-Brain Analysis)

##### The early phase of a block of trials

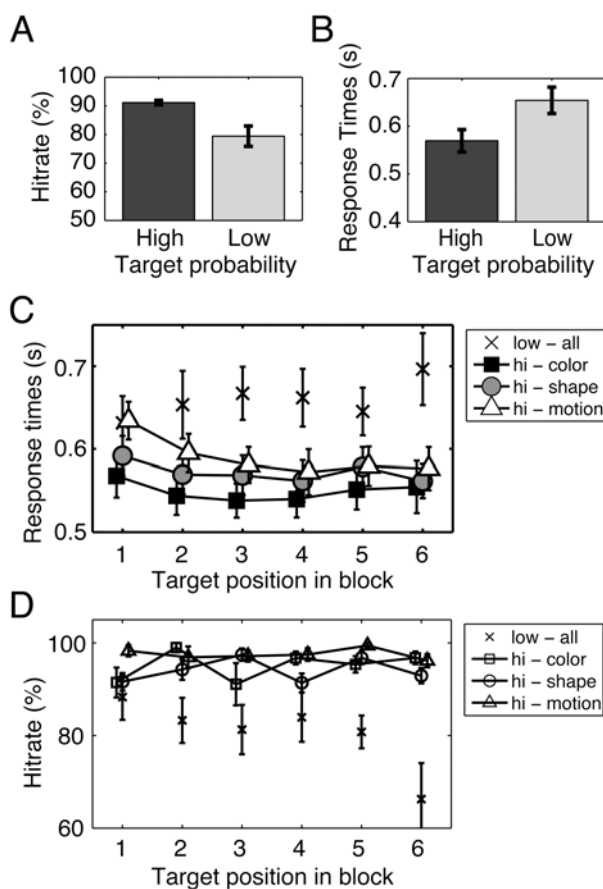
Using the contrast [early targets – late targets in all dimensions], we found activations in middle frontal gyrus (dorsolateral prefrontal cortex, DLPFC) extending into inferior frontal gyrus (IFG), precentral gyrus extending ventrally to the posterior part of the inferior frontal sulcus (IFS) and superior and inferior parietal lobule (SPL and IPL). All activations were in the left hemisphere, are shown in green in Figure 4 and detailed in Table 1.

These regions are known to be involved in building attentional sets and switching between them. The dorsolateral prefrontal cortex is associated with establishing (Banich et al., 2000a; Brass and Von Cramon, 2002; Brass and Von Cramon, 2004a) and imposing an attentional set (Banich et al., 2000b; Milham et al., 2001), holding cognitive goals in working memory and allocating attention to meet those goals (Luks et al., 2002) as well as switching between attentional sets (Nagahama et al., 2001). It is more involved when the attentional set is difficult to establish due to conflicting information (e.g. in Stroop-like trials when incongruent rather than congruent information is shown, Liu et al., 2006; Milham et al., 2001), and its activity increases with the need for cognitive control (Forstmann et al., 2005; Milham et al., 2003). Particularly, the cortex at the junction of IFS & precentral sulcus is involved in activation of the currently relevant task representation (Brass and Von Cramon, 2002; Brass and Von Cramon, 2004a; Braver et al., 2003; Bunge et al., 2003; Derrfuss et al., 2005; Konishi et al., 2001).

The co-activation of IPS and DLPFC was to be expected: Many prefrontal and parietal activation frequently co-occur in studies of attentional control, especially when subjects establish an attentional set for the particular dimension of interest (e.g.: Banich et al., 2000a; Braver et al., 2003; as reviewed in Corbetta and Shulman, 2002; Nagahama et al., 2001). One recent study (Brass and Von Cramon, 2004b) found that posterior IFS and IPS (at relatively close spatial coordinates to the present study: pIFS: [-41, 18, 26], IPS: [-37, 53, 47], and also only in the left hemisphere) are involved in selecting task-relevant information, and in their block design, their clusters showed higher activity early after a cue indicating which task to perform compared with later, as in the present study. The same group also found lateral prefrontal cortex and IPS to be co-activated when switching between internally-generated task sets (Forstmann et al., 2005).

##### The later phase of a block of trials

When comparing BOLD response to targets late > early in the block, we found activation in the



**Figure 3: Behavioral Results.** Detection performance was higher (A) and response times were faster (B) when target probability was high ( $p < 0.01$  in both cases, see Results section). (C) Response time changes as a function of the position of the detected target in a block (e.g., squares represent data from color targets in color blocks). Connected symbols are means of response times (RT) for high probability targets, unconnected cross symbols are means for low probability targets (e.g., a shape target appearing after the first three motion targets in a motion block would be depicted by a cross at  $X = 4$ ). Error bars are standard errors of the means. (D) Hit rates as a function of the position of the detected target in a block. Similar to panel C except that average hit rates are shown instead of RTs.

anterior and middle/posterior cingulate cortex, anterior prefrontal cortex, anterior temporal cortex, cuneus and precuneus, as well as the parahippocampal gyrus. These activations are shown in red in Figure 4 and also detailed in Table 1. Almost all of these areas have previously been associated with attentional control (anterior cingulate, prefrontal cortex: Cohen et al., 2000), shifts in object-based attention (anterior temporal cortex, precuneus, fusiform gyrus and superior frontal gyrus: Serences et al., 2004) or attentional shifts between

visual dimensions (IFG, ACC, precuneus, cuneus, middle / inferior temporal, fusiform, parahippocampal gyrus: Pollmann et al., 2000).

The activation clusters in prefrontal cortex (in the middle, superior, medial and inferior frontal gyri, extending into the right insula) were more anterior than in the early > late contrast. More anterior regions of the DLPFC are thought to be involved in sustaining the attentional set required by the current cognitive goals (Luks et al., 2002), particularly under conditions where switching between tasks is required compared to when only a single task is to be performed (Braver et al., 2003). On a more speculative note, the anterior mid-dorsolateral, mid-ventrolateral prefrontal activations, which are known to be engaged in verbal episodic memory retrieval (Duncan and Owen, 2000), could also be the neural correlates of verbal strategies that subjects were using to keep their attention focused: Subjects informally reported thinking about the name of the dimension containing more targets to help them attend to that dimension.

The anterior cingulate cortex (ACC) is known to be involved in monitoring of performance and response conflicts (e.g.: Cohen et al., 2000; MacDonald et al., 2000). More specifically relevant to our task, it is also involved in monitoring allocation of attention at the level of activation of competing attentional sets (Luks et al., 2002), which in our experiment should occur more in the later rather than the early part of the block when the attentional set is yet to be established.

While these activations were found by pooling over target dimensions in the contrast [late targets in all dimensions – early targets], at the lower threshold of  $p = 0.001$  uncorrected, some voxels with dimension-specific activity were found in extrastriate visual cortex: In right hMT+/V5 in the contrast [late motion targets - early targets], in medial fusiform (compatible with the location of area V4) in the contrast [late color targets - early targets] and in bilateral lateral occipital areas in the contrast [late shape targets - early targets]. These activations could represent top-down effects of attention on the areas processing the different stimulus dimensions. However, none of these voxels showed significant activation differences when tested by direct comparison between targets of different dimensions (e.g. for motion: [late motion targets - late color or shape targets]), and we will thus not discuss them further.

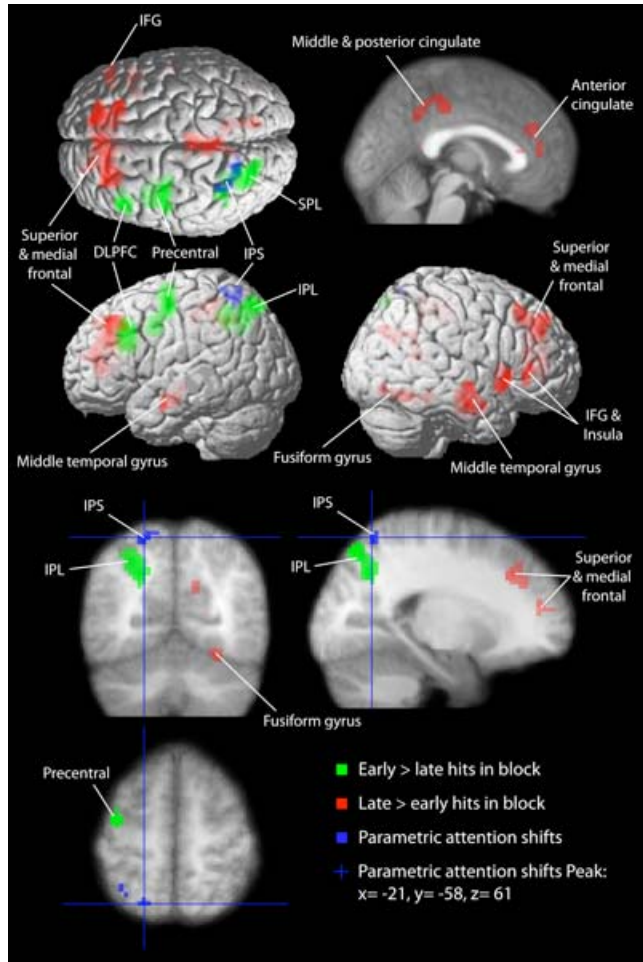
#### Analysis 2: Effects of Attention Shifts (Whole-Brain Analysis)

We found that the *attention shift* regressors (Figure 2F) significantly explained activation only in the left IPS, extending into superior parietal lobule (shown in blue in Figure 4, see details in Table 1). This activation was found by testing for voxels with a significant average response to all three *attention shift* regressors (*attention shift* to color, to shape and to motion), thresholded at  $p = 0.05$ , whole-brain corrected. This cluster was more medial and dorsal than the IPS cluster found in Analysis 1, and these clusters did not overlap. We did not find activation in prefrontal regions, even at the lower threshold of

**Table 1:** Details of clusters found in Analysis 1 (early versus late phases of the block) and Analysis 2 (parametric attention shifts). Threshold is  $p = 0.05$  whole-brain corrected (cluster level). Size column indicates number of voxels, empty cells signify that the cluster is part of the cluster listed above.

Anatomy	H	Coordinates	Size	T	Z
<b>Analysis 1: Early &gt; Late targets in block</b>					
Middle frontal (DLPFC)	L	-50 26 28	114	5.05	4.72
Inferior frontal gyrus	L	-45 21 21		3.96	3.79
Superior parietal lobule (SPL)	L	-24 -67 50	250	4.91	4.61
Superior occipital gyrus	L	-21 -62 39		4.45	4.22
Inferior parietal lobule (IPL)	L	-39 -44 44		3.57	3.44
Precentral	L	-39 -6 61	167	4.76	4.49
Precentral - IFS ("IFJ")	L	-39 -5 33		4.29	4.08
<b>Analysis 1: Late &gt; Early targets in block</b>					
Frontal / Anterior cingulate					
Superior medial frontal	L	-15 36 27	448	11.46	5.05
Anterior cingulate	R	12 30 18		7.92	4.36
Middle frontal gyrus	L	-21 31 34		6.30	3.92
Superior frontal gyrus (SFG)	R	18 42 34	141	6.35	3.93
Middle frontal gyrus	R	24 28 40		5.99	3.82
Superior medial frontal gyrus	R	12 34 34		5.59	3.68
Inferior frontal (triangularis)	R	48 35 4	33	5.28	3.57
Inferior frontal (orbitalis)	R	45 29 -4		4.64	3.31
Insula	R	48 11 -8	85	6.81	4.07
Inferior frontal	R	50 17 -3		5.80	3.75
Putamen	R	33 12 2		5.52	3.66
Temporal					
Fusiform gyrus	R	27 -56 -12	64	7.66	4.30
Middle temporal gyrus	R	45 -4 -20	128	7.55	4.27
Superior temporal gyrus	R	53 -9 -7		7.31	4.21
Hippocampus	R	39 -13 -17		6.44	3.96
Parahippocampal gyrus	R	24 -18 -17	38	6.40	3.95
Hippocampus	L	-39 -12 -15	40	6.37	3.94
Middle temporal gyrus	L	-50 -7 -15		5.23	3.55
Superior temporal gyrus	L	-42 -18 -4		4.42	3.22
Other					
Precuneus	R	9 -46 13	110	7.00	4.12
Cuneus	R	15 -71 34		5.42	3.62
Middle cingulate gyrus	R	3 -24 43	154	6.70	4.04
Middle / posterior cingulate	L	-3 -45 38		5.50	3.65
<b>Analysis 2: Parametric attention shifts</b>					
IPS	L	-21 -58 61	35	6.9	4.1

$p < 0.001$  uncorrected. We did not find voxels with significant responses to our *attention bias* regressors (Figure 2E). As the main focus of interest in this study was to study attention shifts, we will investigate the response of this left IPS cluster in more detail in the next paragraphs.



**Figure 4:** Whole-brain fMRI results. Results from both Analysis 1 which compared responses to detected hits early versus late in the blocks, and Analysis 2 testing for parametric attention shifts. Voxels showing greater BOLD response to the first two detected high-probability targets in a block of trials (early phase) compared with the later detected targets are shown in green, voxels with greater response to late compared with early targets are shown in red, and voxels with BOLD signal correlated with the size of the attention shifts following detected targets are shown in blue. Crosshairs indicate voxel with peak response to attention shifts (coordinates are in Talairach space). Surface renderings are shown on SPM2's template brain, sections are from the mean normalized structural scan across participants. Threshold used is  $p < 0.05$ , whole-brain corrected. Left hemisphere is shown on left (neurological convention).

#### Trial-Averaged BOLD Response Time Courses

We extracted the data from the IPS cluster found in Analysis 2, averaged it over all voxels, and computed the trial-averaged responses for (1) high and low-probability targets (Figure 5A), (2) for high-

probability targets, separately for color, shape and motion targets (Figure 5B) and (3) for high-probability targets binned by target position (Figure 5C; only peak amplitudes are shown). If our IPS cluster is involved in building up the attentional bias to the high-probability dimension, it might show higher responses to high-probability targets, corresponding to the neural correlates of the successive attention shifts. Indeed, high-probability targets elicited greater responses (response magnitude was higher for detected high- than low-probability targets:  $t(10) = 3.9$ ,  $p < 0.002$ ; paired  $t$ -test on peaks of responses) that peaked later (about 2 seconds) and were sustained for longer than low-probability targets. The later response peak after high-probability targets (at about 6 seconds after the onset of the target-containing trial) is compatible with our hypothesis that it is related to neural activity *following* the target detection, and thus possibly related to the attention shift.

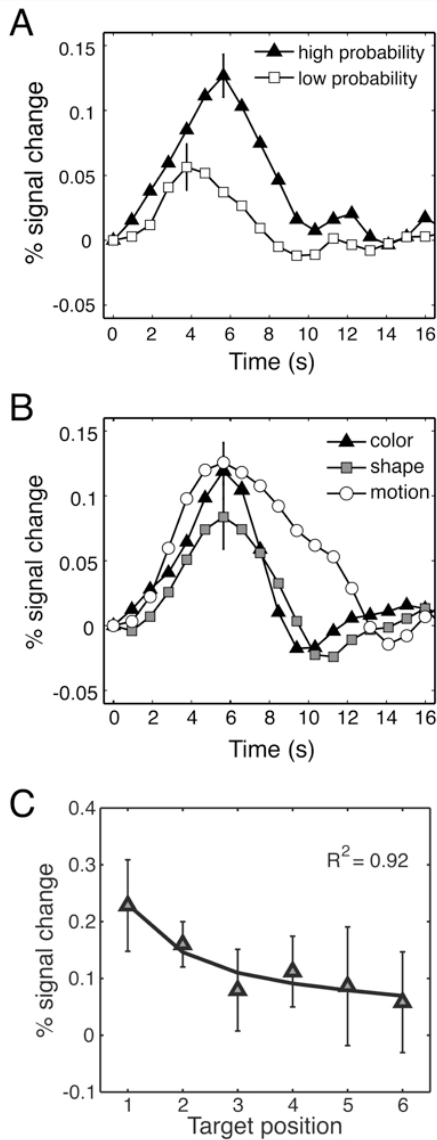
The responses to high-probability color, shape and motion targets were very similar: There was no significant difference between their response magnitudes ( $F(2,20) = 0.20$ ,  $p > 0.8$ ; one-way, repeated-measures ANOVA on peaks of responses).

Confirming the results from the SPM analysis, we found that the BOLD response to high-probability targets decayed exponentially with target position. The regression line in Figure 5C was made using the same regression model also used for the behavioral data and explains 92% of the variance in the between-subjects mean responses.

#### Analysis 3: Effects of RT Changes (Control Analysis)

We hoped that the activation we found in Analysis 2 was not simply related to changes in RT irrespective of attention. Our rationale for this control analysis (Analysis 3) was that the response to RT changes independent of attention should be much smaller than the effect of attention shifts, should not survive the threshold used in the main analysis and thus not constitute a valid alternative explanation for our activation data. Therefore, we tested the effect of decreases in RT on the IPS cluster found in Analysis 2 in SPM and found that no voxel or cluster of voxels survived the threshold of  $p = 0.05$ , whole-brain corrected (the voxel with highest response had a  $t$ -value of 2.08 and a  $Z$  score of 1.86). As both the main and the control analyses were 1-sample  $t$ -tests over subjects, we could directly compare their effect sizes using Cohen's  $d$  for 1-sampled  $t$ -tests (Cohen, 1988), which weights the mean effect by the inverse of its standard deviation. We thus extracted the individual parameter estimates for both effects and found  $d = 2.08$  for the voxel with maximum response to attention shifts compared with  $d = 0.63$  for the voxel with maximum response to RT changes. When averaging over all voxels of the cluster, we found  $d = 2.66$  for the effect of attention shifts and  $d = 0.37$  for the effect of RT change. Next, we assessed the effects of RT changes on the time course data from the IPS cluster, and found no significant differences between response to different RT percentiles ( $F(3,30) = 0.7$ ,  $p > 0.56$ ; same test after subtracting the response of non-

target trials as baseline:  $F(3,30) = 0.31, p > 0.82$ ). In summary, these results indicate that the effect of RT change independently of attention is not significant and much smaller than the effect of attention shifts in our IPS cluster. Therefore, activation in the IPS cluster found in the attention shift analysis cannot be explained by simple variations in RT independently of attention.



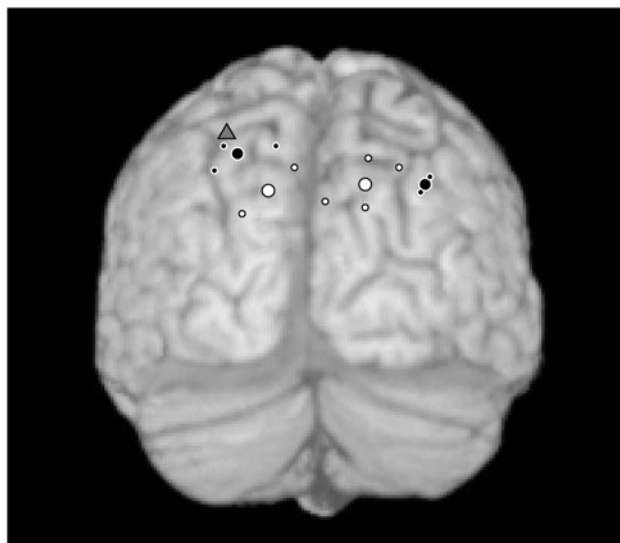
**Figure 5:** Trial-averaged BOLD response time course, time-locked to stimulus onset and using activity at stimulus onset as baseline, averaged across all voxels of the IPS cluster responding to attention shifts shown in Figure 4. Error bars are standard errors of the mean across subjects for each trial type. Data are shown separately for detected high- and low-probability targets (A), for detected high-probability targets separated by dimension (color, shape and motion) (B), and for detected high-probability targets as a function of position in target history (averaged over target dimension; only peaks of responses are shown) (C). The regression line in panel C was fitted using the regression model also used for the behavioral data and explained 92% of the variance in mean signal.

#### Comparison to Previous Attention Shift Studies: Role of Dimension Certainty

Many studies have shown involvement of posterior parietal cortex in shifting attention between spatial locations or stimulus features (dimensions) (Behrmann et al., 2004; Corbetta and Shulman, 2002; for a recent meta-analysis, see Molenberghs et al., 2007). In the present paradigm, at the beginning of a block of trials, the stimulus dimension with the higher target probability was unknown. Therefore, participants did not know towards which dimension they should direct their attention, i.e., their attention shifts occurred under what we will call *dimension uncertainty*. Of previous studies of attention shifts between visual dimensions that reported activation in posterior parietal cortex, some used paradigms where participants were clearly told towards which dimension they would be asked to shift their attention (Giesbrecht et al., 2003; Liu et al., 2003; Rushworth et al., 2001), shifts therefore occurred under what we will call *dimension certainty*. In others, participants had to prepare to attend to or monitor more than one dimension (Asari et al., 2005; Pollmann et al., 2000; Shulman et al., 2002; Weidner et al., 2002), shifts thus occurred under *dimension uncertainty*, and in this they were similar to our present paradigm. We compared the coordinates of the cluster peaks reported in both types of studies with each other and also with the coordinates of the peak of our IPS cluster responding to attention shifts. We found that the peaks of the studies with *dimension uncertainty* are located more laterally in both hemispheres than those with *dimension certainty* (Figure 6), and that our peak was located closer to the left hemisphere coordinates found in studies with *dimension uncertainty*. Specifically, our peak was closest to the average coordinates of *dimension uncertainty* studies in left hemisphere: 14.6 mm vs. 25.4 mm for *dimension certainty*; the average distance to all coordinates was also smaller for *dimension uncertainty* studies: 18.8 (2.1) mm (mean and SEM) vs. 28.2 (6.6) mm; left hemisphere coordinates from *dimension uncertainty* studies were always nearer than coordinates from *dimension certainty* studies, whether considering 1, 2, 3, 4 or all 5 neighbors.

To assess whether these distance values are meaningful, we evaluated the effects of the spatial normalization procedure (warping to MNI space), as follows. We measured, for each subject, the distance by which the anatomical structure located at the peak response in the IPS cluster was shifted by the normalization procedure. While this was performed on the high-resolution anatomical scans for increased precision and easier visual comparison of the structures, results also apply to the functional scans as these were normalized using the same procedure. We found warping effects ranging from 3.7 to 13.1 mm, with only one value greater than 10.5 mm, a median of 6.4 mm, and mean & SEM of 7.3 & 0.9 mm (standard deviation: 2.9). Therefore, all distance values are over 2 standard deviations greater than the average warping effects and greater than all individual warping effects. The differences between

distances to the two types of studies are, at about 10 mm, still greater than most warping effects but should be taken with some caution.



**Figure 6:** *Posterior Parietal BOLD Responses to Shifts of Attention Between Stimulus Dimensions Under Dimension Certainty and Dimension Uncertainty.* Posterior view of a standard brain showing coordinates from the current study (gray triangle) and the strongest activations per hemisphere reported in the following studies. In white (with black outline): Studies of attention shifts between stimulus dimensions occurring when subjects knew to which dimension they had to shift their attention, what we call here *dimension certainty* (Giesbrecht et al., 2003; Liu et al., 2003; Rushworth et al., 2001), bigger white dots represent average coordinates in each hemisphere: [-17 -68 39] and [15 -69 41]. All coordinates: [-8 -60 46]; [26 -60 46]; [2 -75 35]; [-25 -76 31]; [15 -70 33]; [16 -70 49]. In black (white outline), studies of attention shifts occurring under uncertainty about the dimension to attend, what we call *dimension uncertainty* (Asari et al., 2005; Pollmann et al., 2000; Shulman et al., 2002; Weidner et al., 2002), bigger black dot represent the average coordinates in each hemisphere: [-26 -68 50] and [35 -54 41]. All coordinates: [-34 -58 45]; [36 -60 43]; [33 -48 38]; [-31 -70 53]; [-14 -76 53]. Left hemisphere is on left side of figure.

## Discussion

The aim of this study was to induce history-dependent, implicitly generated attention shifts and study their neural correlates. The results show that more frequently-occurring targets are detected increasingly quickly, that BOLD signal in left intraparietal cortex following the detected targets is greater following high- than low-probability targets and reflects the size of the changes in detection performance. Supported by psychophysical studies indicating that target probability can bias attention (Geng and Behrmann, 2005), we conclude that our results are consistent with our hypothesis that detected targets were followed by implicitly generated attention shifts towards the dimension in which the target appeared, gradually building up an attention bias to the dimension in which most targets

appeared in recent history and thereby increasing detection performance of targets in that dimension (but see the next subsection for a detailed discussion and alternative explanations).

This interpretation is supported by our fMRI results: The location of the cluster responding to attention shifts in left intraparietal cortex was close to previously reported activations related to attention shifts, particularly shifts occurring under uncertainty about the stimulus dimension in which a target would appear (*dimension uncertainty*). Furthermore, we found greater involvement of areas associated with the establishment of an attentional set (DLPFC, IFS, IPS region) in response to targets occurring early after a change in target probabilities compared with targets occurring later in the blocks, and higher activity in regions associated with sustaining an attentional set (more anterior prefrontal regions) and monitoring of task performance (ACC) in the opposite contrast.

Thus, we believe that our experiment allowed to study history-dependent, implicitly generated attention shifts with different behavioral effect magnitudes. Our fMRI results suggest that the prefrontal cortex and intraparietal sulcus are involved in establishing the required attentional sets, with one part of the intraparietal sulcus particularly involved in the generation of the successive shifts of attention building up the attentional set.

### *Stepwise Decreases in Response Times: Related to Successive Attention Shifts?*

After a change in target probabilities, participants' response times decreased exponentially with every additional target in the block for frequently occurring targets and increased for rarely occurring targets. This is in accordance with previous studies showing that targets occurring more frequently at one particular location are detected faster (e.g.: Dorris et al., 2000; Geng and Behrmann, 2005), and studies reporting exponential decreases in response times when targets of the same type follow each other directly (Bichot and Schall, 1999; Kristjansson et al., 2001; Kristjansson and Nakayama, 2003; Maljkovic and Nakayama, 1994; Wang et al., 2005). In line with reports that spatial probability can act as an attentional cue (Geng and Behrmann, 2005), we propose that the asymmetric target occurrence probabilities in our paradigm induced an attentional bias towards the dimension in which most targets were likely to appear according to recent trial history. More precisely, we propose that detecting a target (briefly) shifted participants' attention towards the stimulus dimension in which the target appeared, and these successive shifts lead to a stepwise build-up in attentional bias, resulting in increasingly fast detection of targets appearing in that dimension.

We have to formulate some caveats regarding our use of attention shifts as an explanation for our effects. The differences in behavioral performance and BOLD responses to high- versus low-probability targets is necessarily related to their probability, as no other aspect of these targets distinguished them. However, in our experiment, we cannot determine

with certainty whether the accumulation of targets led to voluntary shifts of attention as subjects gradually realized which dimension to attend to (top-down attention), or whether the attention shifts were externally-driven without subjects' control (bottom-up attention), or whether both processes were involved (and if yes, to what degree). One could also attribute our effects to sensory-evoked modulation of target responses, which might act through a mechanism different from bottom-up attention shifts. The interplay of bottom-up and top-down attention and / or priming is a complex issue that we will not go into here (for a discussion, see for example Theeuwes et al., 2006).

One could also describe our trial-history effects as a reduction of uncertainty about the dimension in which the next target will appear (which we call *dimension certainty* in the present manuscript): Seeing more targets in a particular stimulus dimension could produce an expectancy regarding the dimension in which the targets are likely to appear and this expectation could bias visual processing. Uncertainty reduction is one of the main mechanisms proposed to explain how cues increase sensitivity in detection tasks (e.g., Gould et al., 2007; Pelli, 1985; Tanner, 1961). Uncertainty reduction can also occur without an explicit cue, as in perceptual learning: Here, before learning, subjects are uncertain as to which cues are important for the task they have to perform. With practice, they increase their weighting of the informative cues and ignore the others, leading to increased performance (e.g., Eckstein et al., 2004; Goldstone, 1998). In our current task, one could thus argue that detecting more targets in a given dimension reduces subjects' uncertainty as to which dimension is likely to contain the next targets (*dimension uncertainty*) and thus increases performance. Asymmetric target probabilities in recent trial history would therefore decrease uncertainty about the dimension in which the next targets will appear and influence detection performance consequently. Seeing more targets in a particular stimulus dimension could produce an expectancy regarding the dimension in which the targets are likely to appear and this expectation would bias visual processing. Again, that this bias is mediated through attention seems the most plausible explanation to us but this merits further investigation in more detailed studies.

#### ***Explicit Block Cues: Advantages and Disadvantages***

Our experiment was designed to study the development of an implicitly-cued attentional bias from a time point where attention is spread over all stimulus dimensions to a clear bias to one dimension. We used explicit cues that informed subjects of the time points when a change in probability could occur and thus a new attentional set might need to be developed, without informing subjects about which stimulus dimension they should attend. Thus, these cues cannot account for the gradual development of an attentional bias towards a particular stimulus dimension in each block. Nevertheless, the use of an

explicit cue could be seen as clashing with the aim of studying implicitly-cued attention, as these explicit cues were distinct events that most probably triggered cognitive processes in addition to the implicit attentional set-building (this is discussed in the next paragraph), and obviously, a more elegant way of investigating the development of an implicit attentional bias would have been to forgo the use of these cues and manipulate subjects' attentional bias only through changes in target probability. However, these cues allowed to "reset" subjects' attentional focus at a defined time point, facilitating the analysis of gradual changes in performance accompanying the build-up of an attentional bias by providing clear starting points in time. Detecting the effects of changes in attention on behavior without the block cues and identifying the associated neural correlates would be more difficult and less precise in time as many factors would need to be taken into account, such as long-term learning of the occurrence probabilities, the involvement of error-monitoring processes in case we had used feedback to influence subjects' attention as for example in the Wisconsin Card Sorting Test, as well as other uncontrolled variations of target detection performance across dimensions, runs and subjects.

It is probable that consecutive to a block cue, other cognitive processes in addition to the gradual development of an attentional bias would get suddenly engaged and then gradually disengaged as the attentional bias develops with consecutive targets. These processes could include active disengagement from the previous attentional bias, engagement of working memory to keep track of the dimensions in which the targets appeared and increased general arousal or alertness accompanying the additional effort involved in selecting the stimulus dimension. All of these processes would become engaged regardless of the stimulus dimension in which the targets appeared. Working memory and attention are not always easy to fully dissociate both in terms of cognitive processes and neural structures involved (Awh and Jonides, 2001; Lebedev et al., 2004). The activation we found early in the block in DLPFC (associated with working memory) and in intraparietal sulcus region (associated with disengagement and reorienting of attention, e.g.: Thiel et al., 2004) could thus represent the neural correlates of more than just the attentional processes we set out to study.

However, we believe that our fMRI analysis approach based on individually-fitted behavioural modeling (Analysis 2) allowed to identify the neural correlates of attentional set-building, as activity of this cognitive process is more likely to vary in accordance with the parametric changes in RTs that we used to model the fMRI data compared with working memory or the other processes mentioned above. This high specificity is compatible with the smaller number of activated regions we find using the individually-fitted attention regressors compared with the more classic analysis (Analysis 1), and is the reason why we focus particularly on the results of Analysis 2 in this

paper. We assume that similar fMRI results would have been obtained in an adequately-controlled experiment without explicit block cues, but of course this cannot be guaranteed without actually performing the experiment, which goes beyond the scope of the current paper.

### ***Magnitude of Attention Shifts Reflected in Left Intraparietal Cortex Activation***

We found activity in left intraparietal sulcus (IPS) extending into the superior parietal lobule (SPL) correlating with the size of the successive attention shifts building up the attentional bias. Many previous studies have found involvement of SPL in shifting between spatial locations or dimensions of a visual stimulus (see Behrmann et al., 2004, for a review). BOLD responses in SPL were even found to correlate with the size of spatial attention shifts (Vandenberghe et al., 2001). In most of these experiments, participants received clear cues about the location or the dimension in which the next target would appear, there was thus little uncertainty about the dimension in which the target would appear.

In contrast, when subjects must monitor more than one rather than just one dimension, increases in BOLD responses to cues and targets have been found more laterally in the intraparietal region (Pollmann et al., 2006; Pollmann et al., 2000; Weerden et al., 2006; Weidner et al., 2002). In these cases, there was a higher uncertainty about the dimension likely to contain the target (i.e., there is *dimension uncertainty*). Greater activity in the left lateral IPS for dimension switches compared with dimension repeats or feature changes was also found by Asari and colleagues (Asari et al., 2005) using a version of the Wisconsin Card Sorting Test controlled for spatial attention shifts. Further, Shulman and colleagues found greater activation in left lateral IPS to attention shifts when subjects were prepared to attend to both color or motion compared with preparation to attend to either one of these dimensions (Shulman et al., 2002). This is in agreement with recent findings (Vickery and Jiang, 2008) suggesting that the IPL is involved in decision-making under uncertainty (in this particular case: uncertainty about the outcome of a decision), even independently of attention, as well as with exploratory decisions (Daw et al., 2006). In Figure 6, we compared spatial locations of parietal clusters reported in the studies mentioned above (studies with attention shifts under what we call *dimension uncertainty*) to those obtained when participants were told by an explicit cue to attend to a visual feature dimension defined in advance (shifts with *dimension certainty*) (Giesbrecht et al., 2003; Liu et al., 2003; Rushworth et al., 2001). In our present study, after a probability switch, participants were uncertain about which stimulus dimension would contain a target (they were thus preparing to shift their attention under *dimension uncertainty*), and the response in IPS was higher during these periods than once an attention bias to one stimulus dimension was established. Correspondingly, the location of our cluster in left IPS is closer to the average coordinates

reported in studies of attention shifts under *dimension uncertainty*. This suggests that slightly different neural populations are involved depending on the certainty of the next dimension to attend.

A recent study reported differences between the roles of the SPL and IPS in attention shifts: Intraparietal sulcus was particularly active when shifts between stimulus dimensions did not have a spatial component and were directed by internal rules of relevance, SPL in contrast was active during spatial shifting (Molenberghs et al., 2007). It was concluded that IPS activity is related to compilation of an attentional priority map, including endogenous recalibration of attentional weights. This is closely related to the successive shifts in attention we induced in our current experiment, and the location of our cluster is close to Molenberghs and colleagues' activation in left IPS.

As in the present study, others have found left hemispheric specialization in posterior parietal for attention shifts between stimulus dimensions (Asari et al., 2005; Shulman et al., 2002; Weidner et al., 2002). Previous studies have also shown more left than right parietal cortex involvement when switching between well-practiced task sets (Brass and Von Cramon, 2004a; discussed in Corbetta and Shulman, 2002; Forstmann et al., 2005; Kimberg et al., 2000; Rushworth et al., 2001; Sohn et al., 2000). In contrast, right posterior parietal cortex is thought to be part of a right hemisphere network involved in visuospatial attention and disrupted during spatial neglect and extinction, as evidenced by findings from neuropsychology (e.g., Mesulam, 1981), neuroimaging (e.g., Çiçek et al., 2007) and temporary deactivation combined with neuroimaging (Sack et al., 2007).

### ***Greater BOLD Response to High- Than Low-Probability Targets in Left IPS***

We found event-related BOLD responses that were higher and peaked later following high- than low-probability targets. This is consistent with high-probability targets eliciting a stronger attention-related increase in neural activity (Bichot and Schall, 1999; Bisley and Goldberg, 2006) than low-probability targets. This greater response transient could lead to the build-up of an attentional bias when successive shifts to the same dimension occur, reflected in gradual decreases in RTs for high-probability targets, but not for low-probability targets.

Once the stimulus dimension with the highest probability was identified, our low-probability targets functioned somewhat like distractors, briefly forcing participants' attention away from the high target probability dimension. Low-probability targets would then be quickly followed by shifts back to the target stream in order to maximize chances of detecting the next targets. With this interpretation, our findings are compatible with previous reports of higher BOLD responses in IPS (Kincade et al., 2005) following cues inducing voluntary attention shifts compared with stimulus-driven attention shifts. Similarly to our interpretation, the authors of the latter study proposed that attention shifts induced by distractors

were quickly followed by shifts back to the target stream, while attention cues led to periods of sustained attention.

This comparison between high and low-probability targets was not the main interest in our study. We mostly used the low-probability targets to force subjects to attend to all three dimensions, and used the RTs from the low-probability targets mainly as a measure for the efficacy of target probability in influencing detection performance irrespective of trial position. We investigated differences between these target types in the BOLD time-courses in our IPS cluster responding to parametric attention shifts because we hypothesized that if this region is involved in building up the attentional bias to the high-probability dimension, it might show higher responses to high-probability targets corresponding to the neural correlates of the successive attention shifts building up the attentional bias. Our results confirmed this hypothesis.

#### ***Changes in Attention Shifts and BOLD Adaptation***

After the start of a block of trials, we found stepwise decreases in RTs for high-probability targets, indicative of a gradual increase in attention bias towards the dimension with most targets. We found the greatest decreases in RT from one target to the next after the first few high-probability targets in a block, accompanied by the greatest attention shifts and the greatest BOLD responses in left IPS. This decrease of shift-related activation as the number of targets increase within a block could be seen as a form of adaptation of the BOLD response following attention shifts (Kristjansson et al., 2007). In their study, Kristjansson and colleagues induced priming of a target location or color by showing two successive targets with the same color or at the same location, and found reduced detection times and adaptation of the BOLD signal in bilateral IPS and FEF as well as other areas. Adaptation was even stronger when both color and location were repeated. In our experiment, after attention had started to be shifted towards one dimension, the next shifts were smaller and led to smaller BOLD changes. This is indicative of decreasing neural activity as trials accumulate in the block, and could be attributed to the fact that early targets were most informative about the dimension in which targets would occur with a high probability in the remainder of the block.

On the other hand, the effect reported by Kristjansson and colleagues can also be interpreted in the context of the model described in the present study: In their study, faster detection of a target occurring at the same location or with the same color as the preceding target could be due to the preceding target having induced a bias towards that location or color. A target following another target with the same location or color would thus be followed by a smaller shift of attention than the previous target as a bias had already started to be built up. Neural activity in IPS and FEF would be smaller after the second target, thus leading to the BOLD adaptation they observed.

One difference that remains between their study

and ours is the nature of the target characteristic that was repeated, as follows. Kristjansson and colleagues found adaptation when the color or location was repeated. In our case, although targets in our experiment consisted themselves of repetitions of feature states in one stimulus dimension, it is the *dimension* of the target that was repeated across targets within a block, not the *feature states* themselves (e.g., with color as dimension with high target probability, a color target made of two red stimuli might follow a color target made of two green stimuli, thus targets occurred more frequently in the color *dimension* but not with any *particular* color). Therefore, the decrease in BOLD responses to attention shifts that we observe when targets accumulate in the block cannot be simply explained by adaptation to stimulus feature states.

#### ***BOLD Signal Modeling Based on Fitted Response Times***

A possible criticism of our modeling approach based on fitted response times is that our results could be driven by other factors than attention also affecting response times, such as varying levels of arousal, motor preparation, speed-accuracy trade-offs or random motor variability. In the analysis of main interest (the attention model, Analysis 2), we created BOLD response regressors based on the variance in the response times explained by target sequence. Therefore, only a part (albeit significant) of the response time variance was used as a measure of the effects of attention. We modeled the haemodynamic correlates of the residual variance in response times (due to trial-by-trial motor variability and not to target sequence) as separate regressors, orthogonalized with respect to the attention regressors in order to not absorb effects of attention. This increased the quality of the fit of the data to the model by explaining signal variance related to the residual RT variance and thus reducing residuals, thereby increasing the sensitivity of our model.

The residual RT regressors did not protect us from the possibility that our results were directly explainable by RT variations, and therefore we performed a control analysis based on another design matrix (Analysis 3), testing whether decreases in response times irrespective of our experimental design could explain activity in the voxels we identified with the attention model. We found no significant effect in any voxel of our left IPS cluster nor in our cluster-averaged time course data. We believe that these measures, along with the consistency of our results with the literature, allow us to be relatively confident that our results are really due to changes in attentional modulation induced by our paradigm and not artefacts of response time variability.

#### ***Weak Effects of Attention Bias in Extrastriate Visual Cortex***

We only found non-significant effects (i.e. not surviving corrections for multiple comparisons) in areas processing the different stimulus dimensions:

hMT+/V5 for motion, LO for shape and V4 for color. The detection of top-down attention modulation in regions processing the different stimulus dimension was not the focus of main interest in our study and thus our paradigm and analysis approach were not optimized to detect such effects. Nevertheless, these areas are all known to be modulated by attention (e.g., Bartels and Zeki, 2000; Buchel et al., 1998; Corbetta et al., 1991; Liu et al., 2003) and we therefore believe that the absence of those effects in our data should be discussed. This absence could be due to at least two factors. First, the task might have been too easy to induce detectable modulation in these areas (see Methods and Results sections for task difficulty motivations). Greater attentional modulation is obtained with stimuli close to the detection threshold (Bisley and Goldberg, 2006; Corbetta et al., 1991; Duncan and Humphreys, 1989; Ress et al., 2000). In addition, the modulatory effects of attention are known to increase as one goes up from one cortical area to the next in the visual processing hierarchy (see Maunsell and Cook, 2002, for a review); this could explain why we found effects in parietal cortex (high in the hierarchy) but not in temporal or occipital areas (lower in the hierarchy).

Second, the low modulation in temporal and occipital cortex could be due to two opposing effects simultaneously induced by our paradigm. Repetition of the stimulus features could lead to BOLD adaptation after each target in the area processing that stimulus dimension (e.g., V4 for repetition of color, LO for repetition of shape). However, this reduction in signal might be compensated by an increase in response gain resulting from the top-down attentional modulation induced by parietal or frontal areas. Again, functional localizer scans would be more adapted to address this question.

### Conclusion

Our data show (1) behavioral effects compatible with an attention bias built up gradually towards one stimulus dimension as a consequence of detecting more targets in this dimension than in the others, even in the absence of explicit cues inducing the attention shifts; (2) that regions involved in establishing an attentional set are engaged early after a change in target probability, while regions involved in sustaining an attentional set are engaged later, once the performance is more stable; (3) that BOLD signal increases in left intraparietal cortex are greater after high- than low-probability targets, consistent with their different effects on the attention bias; and (4) that the BOLD responses in left IPS directly correlates with the size of the change in attentional bias consecutive to each detected target. These findings might reflect how neural populations modify attentional top-down modulation when attentional priorities are updated by recent experience. This is an important process for a brain with limited processing power trying to optimize its behavior in a forever-changing environment.

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