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# Neural basis for priming of pop-out during visual search revealed with fMRI

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## Abstract

Maljkovic & Nakayama (1994, 1996) first showed that visual-search efficiency can be influenced by priming effects. Even 'pop-out' targets (defined by unique color) are judged quicker if they appear at the same location and/or in the same color as on the preceding trial, in an unpredictable sequence. Here we studied the potential neural correlates of such priming in human visual search using fMRI. We found that repeating either the location or the color of a singleton target led to repetition-suppression of BOLD activity in brain regions traditionally linked with attentional control, including bilateral intraparietal sulci. This indicates that the attention-system of the human brain can be 'primed', in apparent analogy to repetition-suppression effects on activity in other neural systems. For repetition of target color but not location, we also found repetition-suppression in inferior temporal areas that may be associated with color processing; while repetition of target location led to greater reduction of activation in contralateral inferior parietal and frontal areas, relative to color repetition. The frontal eye fields were also implicated, notably when both target properties (color and location) were repeated together, which also led to further BOLD decreases in anterior fusiform cortex not seen when either property was repeated alone. These findings reveal the neural correlates for priming of pop-out search, including commonalities, differences, and interactions between location and color repetition. fMRI repetition-suppression effects may arise in components of the attention network because these settle into a stable 'attractor-state' more readily when the same target property is repeated, than when a different attentional state is required.

## Introduction

The way that human observers react to stimuli in their visual environment can be strongly influenced by recent history. Previously viewed objects are often processed more efficiently (faster and/or more accurately) than others, leading to a variety of effects collectively known as 'priming'. These priming effects have long been used as behavioral tools for probing internal representations (e.g. Cooper, Schachter, Ballasteros & Moore, 1992; Biederman & Cooper, 1991; Schachter, Dobbins, & Schnyer, 2004). More recently, neuroimaging studies have analogously investigated how various types of repetition might affect neural responses, often for visual objects (e.g. James et al 1999; Winston et al. 2004; Koutstaal et al. 2001; Vuilleumier, Henson, Driver & Dolan, 2002), but more generally for other types of repetition also. For visual objects, a typical finding has been that the BOLD signal in ventral visual cortex can be reduced

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for repeated (or 'primed') visual stimuli. Such fMRI effects are often referred to as BOLD repetition-suppression, or fMRI adaptation (e.g. see Buckner et al., 1998; Grill-Spector et al. 1998; Kourtzi and Kanwisher, 2001).

In most such studies to date, the stimuli in question were objects presented in isolation, one at a time, unlike the cluttered scenes of daily life where different objects and different features may appear together. However, a separate line of purely behavioral research has examined the possible role of priming effects arising during visual search, among more cluttered displays with multiple stimuli (e.g. Maljkovic & Nakayama, 1994; 1996; Hillstrom, 2000; Kristjánsson, Wang & Nakayama, 2002; Kristjánsson 2006a; Goolsby & Suzuki, 2001; Olivers & Meeter, 2006; Theeuwes, Riemann & Mortier, 2006; see also Chun & Jiang, 1998). For example, Maljkovic & Nakayama had their observers search for a uniquely colored diamond among two other diamonds of a different color, to perform a discrimination on the target diamond. They found speeded responses in the discrimination task when the color or location of the target was unpredictably repeated. Such facilitation effects have now been found in more challenging search tasks as well (e.g. Kristjánsson et al., 2002; Wang, Kristjánsson & Nakayama, 2005).

Although there is a growing literature on the behavioral characteristics of such priming effects in visual search, and their impact on attentional processes (e.g. see Nakayama, Maljkovic & Kristjánsson 2004; Kristjánsson, 2006b; for reviews), relatively little is known as yet about their neural basis. In a recent neuropsychological study (Kristjánsson, Vuilleumier, Malhotra, Husain & Driver, 2005) we found, using a variation of the Maljkovic and Nakayama (1994) paradigm, that priming of pop-out by repeated target color was relatively preserved in two patients with lesions centered on right inferior parietal lobe, implying that the neural basis for such priming of pop-out might lie mainly elsewhere; but location priming depended closely on awareness of the target (whether it was noticed or not) indicating a role for the affected parietal circuits in position priming.

Other data on possible neural substrates of priming during pop-out search come from single-cell recordings in awake behaving macaque monkeys. Bichot & Schall (1999, 2002) recorded activity in frontal eye field (FEF) single neurons, during a visual search task where target features (color or shape) could be repeated across successive trials. They found that single-unit activity in this region discriminated between target and distractors better and earlier on repetition trials, indicating that FEF may show differential response patterns as a function of repeating target features in visual search. They also observed that single-unit FEF responses to distractors were decreased by target priming, indicating that priming of popout by repetition may cause a selective 'pruning' of the FEF population response to a given search display. These studies only probed FEF neurons in the monkey, however, so the possible contribution of other brain areas to priming of pop-out remains unknown.

Our participants performed a visual search task in the scanner, similar to that used by Maljkovic & Nakayama (1994), and equivalent to that in Kristjansson et al. (2005). The task was to search covertly (without shifting gaze from central fixation) for a briefly displayed, oddly colored (singleton) target diamond, among two distractor diamonds that shared a different color, making a discrimination judgment for the target singleton (specifically, whether there was a notch on the upper or lower corner of the target diamond; see Fig. 1A). Across successive trials, target location (left or right) and target color (red or green) could be repeated or not repeated, unpredictably and independently. We used fMRI to test for any 'repetition-suppression' in the BOLD response (see e.g. Grill-Spector & Malach, 2001; Grill-Spector, Henson, & Martin, 2006, for review) when target location and/or color was repeated, by analogy with previous studies of priming that had exploited BOLD repetition-suppression to investigate repetition effects for various other topics, such as object representations in the ventral visual pathway (e.g. Kourtzi & Kanwisher, 2001; Eger et al. 2004; Henson, Shallice & Dolan, 2000; George

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et al., 1999; Vuilleumier, Armony, Dolan & Driver, 2003). Testing for BOLD repetition-suppression in particular seemed a reasonable *a priori* approach here, given that repetition-suppression has now been found for various types of repetition, in various different brain areas (e.g. for object perception (Schacter & Buckner, 1998; Henson et al., 2003; Vuilleumier et al. 2002; Grill-Spector & Malach 2001) or for semantic processing (Wagner, Koutstaal, Maril, Schacter & Buckner, 2000; Buckner, Koutstaal, Schacter & Rosen, 2000; Simons, Koutstaal, Prince, Wagner, & Schacter, 2003; Naccache & Dehaene, 2001)). Nevertheless, the fMRI correlates of priming for pop-out (i.e. for target repetition during pop-out visual search) have not to our knowledge been previously studied, so it remained unknown prior to our study whether or not any components of the putative 'attention network' (Corbetta & Shulman, 2002; Mesulam, 1999; Kastner & Ungerleider, 2001; Yantis & Serences, 2003) can show BOLD repetition-suppression. Indeed, most prior fMRI studies of the attention network have sought mainly to 'activate' this network, by comparing attentionally-demanding tasks to various baseline conditions (although see Jones, Cho, Nystrom, Cohen & Braver, 2002, for more subtle manipulations in response-conflict paradigms unlike the visual-search task considered here). We sought here to test instead for any repetition-suppression effects (i.e. relative reductions in activation) when varying only trial history, within an otherwise constant visual search task.

In this way, here we were able to: (i) test for any reductions in BOLD signal when a target property was repeated to produce behavioral priming of pop-out; (ii) to examine whether such effects on particular neural populations might be specific to repeating target location, but not color, or vice-versa; (iii) to test for any commonalities in the neural response to repetition of target location and (separate) repetition of target color; (iv) to identify any effects that depended specifically on repeating both target properties together at the same time; and finally (v) to probe for any repetition effects that might be specific to one target hemifield versus another (as might in principle apply to contralateral visual cortex, for example).

In addition to testing for the repetition-suppression effects that we hypothesized *a priori*, we also tested for any repetition-enhancements (i.e. increased BOLD responses when target location or color was repeated) for completeness; but in fact no reliable fMRI effects of this type were observed here.

We used whole-brain fMRI, with our main hypotheses and questions being as follows. Given previous proposals in the behavioral literature that priming of pop-out reflects primarily the operation of attentional mechanisms (e.g. see Maljkovic & Nakayama, 1994; 1996; Kristjánsson & Nakayama, 2003; Nakayama, Maljkovic & Kristjánsson, 2004; Kristjánsson, 2006b), then attention-related networks in parietal and frontal cortex (e.g. Corbetta & Shulman, 2002; Hopfinger; Buonocore & Mangun, 2000; Yantis & Serences, 2003; Labar, Gitelman, Parrish & Mesulam, 1999; Awh & Jonides, 2001; Culham, Cavanagh & Kanwisher, 2001; Jovicich et al., 2001) might show reduced BOLD signal when visual search is 'primed' by repeating target location and/or color. If so, this would indicate that components of the attention network in the human brain can be 'primed' neurally, in a potentially analogous manner to that found for repetition in other brain regions for other contexts (e.g. for object repetition in the ventral visual pathway; see Grill-Spector et al., 2006, for review).

It would then become a further important empirical question whether any such priming (i.e. BOLD repetition-suppression) effects on attentional networks might be common for repeating target location and for color; or instead be different for each property, with color versus location repetition affecting different brain sites. Such issues on the role of location versus other visual features in attentional control have long been of theoretical importance in psychology (e.g. see Treisman, 1988), but are only just beginning to be studied neurally (e.g. Giesbrecht, Woldorff, Song & Mangun, 2003).

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It still remains contentious whether or not some aspects of visual pop-out require any selective attention at all (e.g. see Donner et al., 2002; Treisman & Gormican, 1988; Bravo & Nakayama, 1992; Nakayama & Silverman, 1986). If pop-out is strictly 'preattentive', then priming of such pop-out presumably need not affect attentional networks at all, but rather may just directly affect visual representations of the repeated target property (e.g. just color-related areas, in the case of repeating color). Indeed, Walsh et al. (2000) have shown that lesions to V4 and TEO may impair some forms of priming in monkeys. Moreover, repeating some aspect of a visual-search display can in principle be considered primarily as a visual rather than attentional manipulation, in which case any BOLD repetition-suppression effects here might be restricted to the posterior visual system, rather than affecting components of the attention network.

A further possibility is that both types of effects might apply (see Pollmann, Weidner, Müller & von Cramon, 2000), with priming of search influencing both the representation of specific visual properties, and also the attention networks classically associated with control of visual search and shifts in covert spatial attention. But note that here only trial history was manipulated, rather than different attentional tasks being compared as is usually the case when examining the attentional network (though see Jones et al., 2002). Finally, because the singleton target in the present paradigm could appear in either the left or right visual field (LVF or RVF) unpredictably, we could also identify any fMRI effects of target repetition (for color or location) that were specific to the current target side, versus those that were not.

To anticipate, our fMRI results revealed robust BOLD repetition-suppression effects, by repeating target location and/or color in a pop-out search task, over successive trials in an unpredictable sequence. Some of the strongest BOLD repetition-suppression effects found here clearly arose within components of the attention network (e.g. in the intraparietal sulcus, IPS, and in the FEF), thus affecting structures well beyond the conventional posterior visual system. Moreover, we also found some differential effects (and separately some common effects) for repetition of location vs color. We even found effects for some brain regions that depended on repeating both target properties conjointly.

## Methods

### Behavioral task

The task was to search covertly for the oddly colored diamond (the target) among two other diamonds of a different color (see Fig. 1A), and to make a judgment on the target's shape. The two possible colors were green and red, so the oddly colored target could either be a red diamond among two green ones, or a green diamond among two red ones. The target diamond in the LVF or RVF had a small notch cut off at either its top or its bottom (as did the nontarget in the other visual field, independently, see Fig. 1). The size of each diamond was 1.8 by 1.8 arc deg. Observers had to indicate as fast as they could, by pressing the appropriate key on an MR-compatible button-box, whether the cut-off on just the target diamond was upper or lower. The size of the cut-off was 23 arc min. The target and distractors were all presented at equal distance from a central fixation cross (eccentricity 4 arc deg). The three possible diamond locations were at the top, right and left; at 0, 120 and 240 degrees respectively from vertical around an imaginary clockface (see Fig. 1A). In our version of the Maljkovic and Nakayama (1994) paradigm, the target was always either at the right or at the left, never at the top, with the latter position serving only to produce a search display with a single pop-out target (just as in Experiment 3 of Kristjánsson et al., 2005). Hence each target fell in the LVF or RVF, thereby reducing the number of possibilities to maximize statistical power, and also equating the appearance of LVF and RVF items over trials, regardless of which was currently the singleton target. This aspect was by design; please note that it cannot undermine any of the conclusions reached from our fMRI results. Moreover, this aspect of the design also matches our previous purely behavioral studies (see Kristjansson et al., 2005).

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Display items were presented on a black background. In order to eliminate any confound due to simple differences in shape between target and distractor at the two lateral locations, both the left and the right items always had a notch cut-off. The actual position of the cut-off (i.e. at upper or lower part of diamond) was determined randomly and independently for these two items, but reported only for the singleton target. The stimulus display was visible for only 200 ms (to minimize any tendency for undesired saccades, as confirmed also by eye-tracking here), but the black background and the central white fixation cross were constantly present. The intertrial interval (ITI) varied randomly between 3000 to 5000 ms in steps of 90 ms (this step-size corresponding to the individual slice acquisition times during fMRI, with the varied ITI thereby jittering trial timing relative to volume acquisition).

Each subject participated in 4 blocks of 140 trials during scanning. They were encouraged to respond as quickly as possible while also maintaining a high degree of accuracy. To prevent contamination of results by eye movements, the observers were instructed and encouraged to maintain steady fixation on the central fixation cross throughout the experiment. Eye position was monitored by an infrared eyetracker system throughout scanning, and any trials where eye movements were made were excluded from the fMRI analysis. Our criterion for this was any deviation of gaze > 2 arc deg from center, occurring in the 2 s period from 500 ms prior to display-onset to 1500 ms after this. Such eye-movements occurred on 4.1% of trials only. In the SPM analyses, these trials were modeled out together with any trials where the response was incorrect.

### Participants

Eleven neurologically intact volunteers (5 females), with normal or corrected visual acuity participated, aged 20 to 33 (mean 27.6 years). fMRI results for one subject were not included in the analyses since her behavioral performance was inaccurate and unlike the other observers in many respects (see below). All procedures were in line with local ethical and safety guidelines. All observers gave written informed consent following a briefing session.

### MRI acquisition and other equipment

Blood oxygen level dependent (BOLD) images were collected with echo planar imaging on a 1.5 Tesla Siemens Sonata scanner. We collected 32 slices for each volume (thickness 2.5 mm, separated by 50%, in-plane voxel-size 3 × 3 mm, then resampled to 2×2×2 during preprocessing). TR was 2880 ms (90 ms for each slice). For each of the 4 sessions per participant, 210 volumes were collected, so each session took just over 10 minutes. A standard Siemens head coil was used for whole-brain acquisition. A further T1-weighted anatomical scan of the brain of each participant was collected immediately following acquisition of the functional data.

The experimental display was presented on a rear-projection screen at the back of the scanner and viewed via a mirror mounted above the head of the subject, on the head coil. Stimuli were generated with Matlab using routines from the Cogent software package (http://www.vislab.ucl.ac.uk/CogentGraphics/index.html). A dedicated stimulus PC controlled the display in synchronization with MRI slice acquisition (allowing a random jitter between volume onset and stimulus onset, see above); and collected behavioral responses as well as eye-tracking data via infrared video-oculography (ASL 504 LRO), which allowed us to sample eye position at 60Hz for 2 s on each trial.

### Data analysis

fMRI data were preprocessed and analyzed using the linear regression techniques implemented in SPM2 (http://www.fil.ion.ucl.ac.uk/spm). The BOLD contrast images were realigned, spatially normalized and subsequently smoothed with an 8 mm Gaussian kernel. The first four

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volumes from each of the four scanning sessions were discarded, while the remainder were used for our analysis of all 10 included participants. Individual events were modeled by a standard haemodynamic response function, including eight experimental conditions (targets with repeated color but nonrepeated position; or repeated position / nonrepeated color; or repeated color / repeated position; or nonrepeated color / nonrepeated position; all separately for a target currently in the right or left visual field); plus one regressor for all trials involving either incorrect responses (2.8 % of trials) or eye movements (4.1% of trials). Finally, six additional covariates of no interest modeled any movement artifacts from the realignment correction.

Parameter estimates of event-related activity were obtained using the general linear model, for each voxel in each condition and each subject. Statistical parametric maps of the t-statistic (SPM) were generated from linear contrasts between different conditions and transformed to a normal distribution (SPM{z}) for each participant at the first stage of analysis. At a second stage, a random-effect analysis was performed using t-tests on the contrast images obtained in each subject for each comparison of interest. In all random-effect analyses, resulting SPMs of the t-statistic (df= 9) at each voxel were thresholded using conventional values of $p < 0.001$ uncorrected, and a conventional cluster size of at least 5 voxels, unless mentioned otherwise (see below in text and tables where any exception are explicitly noted). To explore specific regions of interest (ROIs) that were either predicted *a priori*, or were defined by other contrasts at <.001, we occasionally selected a more liberal threshold of $p < 0.01$ (e.g. see Degonda et al., 2005), specifying this below in each such case.

Additional confirmatory ANOVAs were performed outside SPM where appropriate, using parameter estimates (beta values, proportional to percent signal change) extracted at the peak of selected ROIs, to test specific hypotheses as further detailed below. Similarly, parameter estimates for selected regions were used for an exploratory correlational analysis of BOLD repetition-suppression effects, in relation to behavioral repetition effects on response times, as a function of repeating target color or location. Note that all of the most critical BOLD effects were robust and significant at conventional thresholds; but we occasionally report results at less conservative thresholds for completeness (e.g., for regions that were predicted or relevant based on other contrasts), highlighting this when so.

## Results and Discussion

Behavioral measures obtained during fMRI scanning revealed that all but one of our 11 participants showed a strong priming effect on response times for the repetition of target position, and also for the repetition of target color (see Fig. 1B). The exceptional subject was excluded from the fMRI study, since our goal was to investigate the neural correlates for priming of search, which was reliably observed in all other participants, and since the excluded participant was unusually slow and inaccurate. For the 10 remaining subjects, a repeated-measure ANOVA (on the effects of repeat vs nonrepeat of target location, and orthogonally of target color) revealed strong facilitatory priming of reaction times for repeated target position ($F_{(1,9)} = 19.17$, $p < .001$) and for repeated target color ($F_{(1,9)} = 24.68$, $p < .001$). Just as in the original studies of Maljkovic & Nakayama (1994,1996), there was no interaction behaviorally between position and color repetition ($F_{(1,9)} = .979$, $p = .43$), which were thus additive in their effects (Sternberg, 1969; see also Kristjánsson 2006a, for a recent discussion of this point). These behavioral 'priming of popout' results confirm the findings from many previous, purely behavioral studies of priming in visual search (e.g. Maljkovic & Nakayama, 1994,1996; see Nakayama, Maljkovic & Kristjánsson, 2004), as expected, but as now found during scanning.

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### fMRI results: BOLD activity as a function of target hemifield

We first examined whether the side (LVF or RVF) where the target appeared produced any differential neural responses, irrespective of target-repetition factors. Note that each display always contained 3 diamonds (see Fig. 1A), two in one color and the other in the alternative color, with the singleton target always appearing in the LVF or RVF rather than at the top-central location (see Methods). As a result, the two lateralized items themselves were physically equivalent (when fully counterbalanced, as here) across trials with LVF or RVF targets. Nevertheless, we still found activation in occipital visual cortex contralateral to the current singleton target (see Table 1), consistent with an increased neural response due to covert attention being directed towards the target, as would be expected (e.g. see Kastner & Ungerleider, 2001;Driver & Frackowiak, 2001). We next turned to the more novel issue of any BOLD repetition-suppression effects due to repeating target properties (location or color) across successive trials in the unpredictable sequence. Note that the attentional task was held absolutely constant for the fMRI comparisons here, while the current display was also equivalent across repetition conditions; only trial history varied.

### Reduced BOLD when target location is repeated

We first examined the neural consequences of repeating target location, by comparing all trials where the target occupied a different position relative to the preceding trial, minus those where the target was repeated at the same position as on the previous trial. Initially we did this irrespective of whether the pop-out color defining the target was the same or different as the previous trial; and irrespective of the actual target hemifield. Repetition-suppression of BOLD activity for repeated target location was found primarily in the intraparietal sulcus (IPS) bilaterally, as well as in bilateral FEF (see Paus, 1996, for similar coordinates as those shown in table 2), together with a few other anterior structures (anterior cingulate cortex, ACC; plus middle and inferior frontal gyri), and also the right inferior parietal cortex (see Figure 2 and Table 2).

All these effects appear consistent with location-priming of visual search (i.e. the subtle trial-history manipulation here) affecting components in the network of parietal and frontal areas that has long been implicated in control of spatial attention (e.g. see Corbetta & Shulman, 2002; Giesbrecht et al., 2003, Mesulam, 1999; Kastner & Ungerleider, 2001). Here we found for the first time that several regions in this network can exhibit repetition-suppression effects during priming of visual search by repeated target location. Besides IPS and FEF regions that are associated with top-down attention control (Kastner & Ungerleider, 2001), location-repetition effects also affected right supramarginal gyrus and inferior frontal gyrus (see Table 2), parts of the more 'inferior' attentional network described by Corbetta and Shulman (2002), putatively concerned with attentional capture. Finally, some BOLD suppression following repetition of target position was also observed in peristriate cortex (Table 2) indicating that location repetition may affect even this level of visual processing.

### Location-repetition effects depending on current target-side

In our initial analysis above of location-repetition effects, we had pooled over target-side, but we next tested for any location-repetition suppression effects that depended reliably on the current target side. A direct interaction test revealed greater repetition-suppressions for repeated-location targets in the RVF than the LVF, for left (and thus contralateral) inferior posterior parietal cortex (xyz = −44 −52 20 [t= 4.13, $p < .002$]) and for left inferior frontal gyrus (xyz = −52 14 8 [t = 6.82; $p < .001$]). The reverse interaction test showed no significant location repetition effects for targets in the LVF relative to RVF. This outcome provides a new line of evidence in accord with traditional suggestions (see Corbetta & Shulman, 2002; Driver & Vuilleumier, 2001; Heilman, Watson & Valenstein, 2002; Mesulam, 1999) that some regions involved in spatial attention in the left hemisphere may deal primarily with just the

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(contralateral) RVF; whereas some analogous regions in the right-hemisphere network may apply for both sides of space similarly, and hence not interact with the hemifield of the target for the current location-repetition effects. Indeed, right inferior parietal cortex showed location-repetition suppression effects here for both the LVF (48 −42 40, t= 5.24, p> .001) and for the RVF (50 −54 46, t= 3.46, p< .005) when these target sides were considered separately. Note, however, that IPS in either hemisphere likewise showed location-repetition suppression effects for targets in either visual field (see Figure 2).

## Reduced BOLD when target color is repeated

The second question of major interest in our study concerned repetition of target color (rather than location) across successive displays. All trials where the target color was the same as on the preceding trial were now subtracted from those where the target color was different to the preceding trial (initially irrespective of current target hemifield, and pooled over the two possible target colors). Such color-repetitions again produced suppression of BOLD responses in regions traditionally associated with visual attention (as found for location repetition), including the intraparietal sulcus bilaterally again, plus the left FEF, and at a lowered threshold (which we report for completeness) the right FEF (see Table 3); together with right anterior cingulate cortex and right middle frontal gyrus.

These repetition-suppression effects again suggest that neural networks involved in attentional control can be modulated (showing BOLD repetition-suppression) as a function of target repetition during visual search, even when this subtle trial-history manipulation now involves color rather than location, with some similar neural effects in both cases. Indeed, many areas showing repetition-related effects for target color (Figure 3 and Table 3) appear to overlap with those exhibiting repetition effects for target position (see Figure 2 and Table 2). Such overlap was tested more formally, as we describe later. For now we note, however, that the right inferior and anterior parietal regions that showed location-repetition effects (Figure 2 and Table 2) did not show any reliable main effect of color repetition here (all $p > .01$ uncorrected for those areas). This suggests that there might be some right-hemisphere specialization for location-priming in particular.

In addition, target color also produced repetition-suppression effects in some extrastriate visual regions, specifically in left inferior temporal regions (see Fig. 3, top two coronal slices in right column of brain images), including the lateral occipital cortex (LOC) and lateral fusiform gyrus (FG); see Table 3. Such effects were not observed for location repetition. These color-repetition decreases in left LOC/FG might relate to cortical regions often associated with color processing (e.g., Bartels & Zeki 2000;Hadjikani et al. 1998; but see also Wade, Brewer, Rieger & Wandell, 2002), although we note that here these left-lateralized regions showed color-repetition effects for targets in either visual hemifield (see Fig. 4 for plots of the parameter estimates separated by visual field). To confirm directly that these effects of color repetition in left inferior temporal cortex were indeed common across the two hemifields, we performed an ANOVA on the activity parameters (SPM beta-values) extracted from both the left fusiform and left LOC peaks, with the following factors: region (i.e. fusiform or LOC); visual field; color repetition; and location repetition. This analysis showed a highly significant main effect of color repetition ($F_{(1,9)} = 93.5$, $p < .001$) but no other main effect and no interaction (i.e. including no interactions of color repetition with target visual field, nor with location repetition [all these $F_{(1,9)} < 1.33$, $p > .22$]). In addition, in whole-brain analysis, there were no significant interactions of color priming with the current field of the target in any region.

## Common areas for location and color priming

We next tested for any regions affected by both color repetition and location repetition (some commonalities are already suggested by comparing Figures 2 and 3, plus Tables 2 and 3). The

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random-effect analysis of location-repetition effects was used as an inclusive mask in SPM (mask threshold at $p < .01$), within which independent color-repetition effects were then assessed by a new random-effect group analysis at $p<.001$ (see Nichols, Brett, Andersson, Wager & Poline, 2005,Friston, Penny & Glaser, 2005, for such an analysis approach to conjunctions). Figure 5 confirms that, as might be expected from the separate results presented above, there were common repetition-suppression effects arising in bilateral IPS plus ACC, found here to be modulated by both location-repetition and color-repetition (see also Table 4). Such common effects presumably reflect the operation of "general" components of the attention network, underlying priming in visual search irrespective of the particular primed feature across successive trials. Note once again that here these anterior attention-related regions were robustly modulated by the subtle trial-history manipulation, despite the constant task and the equivalence of the current display for the conditions compared.

## Differences between position repetition and color repetition fMRI effects as revealed by direct interaction tests

The above results indicate that the main commonality between location- and color-repetition effects arose in bilateral IPS (see Figures 2, 3 and 5), with notable differences apparently being that left inferior temporal cortex was implicated in color-repetition but not location-repetition effects (see Figures 3 and 4; and the separate analyses of these two orthogonal effects above); while by contrast the location-repetition but not the color-repetition effects affected inferior parietal cortex (see Figure 2, and compare Tables 2 and 3). These differences were confirmed by more formal tests for interactions between repetition (changed minus repeated target feature) and the type of feature (color minus location, or vice-versa), performed voxelwise across the whole brain.

These analyses confirmed that repetition decreases were indeed greater for color than location in left fusiform gyrus (peak at $x=-46$, $y=-58$, $z=-14$; $t=5.58$), as expected from the preceding analysis; and also (albeit sometimes at somewhat lower significance, reported for completeness) in the left FEF ($x=-30$, $y=6$, $z=54$; $t=3.5$, $p<.004$), right IPS ($x=30$ $y=-58$ $z=66$; $t=5.11$, $p<.001$) and occipital cortex ($x=24$, $y=-56$, $z=30$; $t=5.99$, $p<.001$).

Conversely, larger repetition effects for location than color were found in parietal and frontal areas in each hemisphere, but this differential effect varied as a function of target side, in a contralateral manner. For LVF targets, greater location- than color-repetition effects arose in contralateral right inferior posterior parietal cortex ($x=64$, $y=-52$, $z=22$; $t=5.49$, $p<.001$), right anterior intraparietal sulcus ($x=34$, $y=-36$, $z=44$; $t=4.92$, $p<.001$), and right inferior frontal gyrus ($x=40$, $y=34$, $z=-2$; $t=5.49$, $p<.001$). For RVF targets, greater position than color effects were found in contralateral left posterior intraparietal sulcus ($x=-28$, $y=-70$, $z=32$; $t=4.65$, $p<.001$) and left FEF ($x=-20$, $y=-8$, $z=50$; $t=5.49$, $p<.001$), the latter region being slightly more medial than a nearby frontal region showing larger effects for color repetition. Thus, the subtle comparison of different types of repetition in the trial sequence (each of which had similar effects on behavior, see Figure 1B) revealed some contralaterality within the attention network that was specific to location-repetition influences.

Taken together, these data on differential BOLD effects of color- versus location-repetition appear broadly consistent with a role for ventral temporal regions in priming effects that involve color, in contrast with a more pronounced role of contralateral fronto-parietal areas in priming effects that involve location. These differential effects could be separated from the common effects of both types of priming upon bilateral IPS and ACC, with the latter common effects presumably reflecting the more efficient allocation of attention for targets primed by either feature; i.e. less attention demand when appropriate allocation of attention was already 'primed', thus requiring the same attractor-state for the attention network (see Serences &

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Yantis, 2006, for discussion) as for the previous trial, rather than a change to this attentional state.

### Reduced BOLD when both color and position are repeated versus when only one is repeated

Table 5 gives the results of a test for stronger repetition-suppressions when both position and color were repeated, versus when only position or only color was repeated. Such combined repetitions produced a further reduction of activity in similar regions to those found above for the repetition of a single dimension (i.e. color alone, or position alone), including bilateral FEF and IPS.

Furthermore, repetition of both position and color together (and hence repetition of the global "Gestalt" of the whole search display) was also associated specifically with distinct decreases in left fusiform gyrus (anterior to the region shown in Fig. 3 and Fig. 4 that was affected by color repetition per se; see Table 5). In other words, decreases in this anterior fusiform region were found only when both target position and target color were repeated together, not when either feature was repeated alone. This was confirmed outside SPM, by a further analysis of parameter estimates extracted from this region, showing that the effect of combined color-and-location repetition produced a significant reduction in activity (relative to nonrepeat trials with new-color and new-location) that exceeded the sum of the (nonsignificant) trends for the reduction by repeated location alone, plus the reduction by repeated color alone. This indicates that repetition of both color-and-location in the same target was not equivalent to adding the effect of color repetition with the effect of location repetition for this region, but instead produced a super-additive effect, at $p<.00001$). This anterior fusiform region might therefore be involved in processing conjoined object features or the display Gestalt i.e., color combined along with location for all 3 stimuli. Other regions such as IPS and FEF did not show a similarly super-additive repetition-suppression effect for conjoint color-and-location repetition (i.e. their more pronounced suppression with conjoint repetition could be explained as the sum of the two orthogonal repetition effects, unlike the anterior left fusiform).

### Brain-behavior relationships for repeated target properties

Finally, at the suggestion of a referee, we performed an initial exploration of how subject-by-subject changes in visual search performance, as a function of repeating target location or color (i.e. the behavioral priming effects for pop-out search in individuals), might potentially relate to the BOLD repetition-suppression effects observed in critical brain regions (see Macotta & Buckner, 2004; Wig et al., 2005). For each participant, we computed the benefits in median RTs due to color or location priming, as the difference between nonrepeat minus repeat trials, for each feature separately. We then assessed any subject-by-subject correlations of these RT differences with the magnitude of the corresponding BOLD repetition-suppression effects for nonrepeat minus repeated trials. Rather than data-mining the entire brain for any such correlations, we focused on the bilateral IPS and FEF regions already found (independent of the new correlation test) to show substantial color or location repetition-suppression effects. For each subject, we computed the difference in the average parameter estimates (betas) between non-repeat and repeat trials, for IPS and FEF clusters (at $p< .001$) that showed significant position repetition effects (see coordinates in Table 2), as well as for IPS and FEF clusters that showed significant color repetition effects (see coordinates in Table 3), respectively. Correlations between these repetition-related changes in parameter estimates and RTs were then examined using simple linear regression and Pearson tests.

Remarkably, given that these clusters were not pre-selected based on behavioral performance, there was a positive subject-by-subject correlation (see fig. 6) between the size of BOLD repetition-suppression in right FEF, and the size of the behavioral RT priming effect, for repetitions of target location (Pearson test, $r(9)= .58$, $p= .039$), and to some extent for color

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repetition (r(9)= .54, p= .052). Some trend for a brain-behavior correlation was also found for location-repetition in right IPS (r(9)= .53, p= .057). The other two regions considered showed no reliable correlations or substantial trends (left FEF: r= .26 for location; r=.04 for color, p > .26; left IPS: r= .35 for both location and color, p= .158). The right FEF correlations are striking, given that this region was not pre-selected for showing such brain-behavior correlations, but rather simply for showing overall BOLD repetition-suppression for repeated target features. The exact relationship between BOLD repetition-suppression effects and behavioral priming effects remains contentious in many cognitive domains (see Grill-Spector et al., 2006;Henson & Rugg, 2003 for review). Moreover, behavioral priming effects (as with most aspects of behavior) may presumably often depend on the combined effects of several brain areas, rather than just one, as indicated in several existing combined behavioral-fMRI studies on repetition in other domains, such as visual object processing (e.g., see Vuilleumier, Schwartz, Duhoux, Dolan & Driver, 2005). It is worthwhile to note, however, that Turk-Browne, Yi and Chun (2006), found that behavioural priming correlated with repetition suppression, predicted subsequent scene recognition. In any case, the present right FEF results (see Fig. 6) do indicate some relationship between BOLD effects and behavioral effects, for the new repetition-suppression effects during visual search found here for the first time.

## General Discussion

We used whole-brain fMRI in humans to study the potential neural correlates of 'priming-of-pop-out' in a visual search paradigm, where target location or color could be repeated across successive trials in an unpredictable sequence. To our knowledge, this is the first study to test for any BOLD repetition-suppression effects in this context, and thereby to examine whether components of the attention network may show repetition-suppression effects, as often previously found for other brain areas in very different repetition paradigms.

Behaviorally, we found that location and color repetition each speeded search performance in a similar manner within the scanner (Fig 1B); and that these two effects were additive, as previously reported by Maljkovic & Nakayama in purely behavioral work (1996; see also discussion in Nakayama, Maljkovic & Kristjánsson, 2004;Kristjánsson, 2006a). Within psychology, such additivity has often been used to argue that two effects must reflect distinct internal processes (Sternberg, 1969). Here, by means of fMRI, we were able to assess whether repeating the target's location or color in the search task could indeed each produce any distinct effects on neural activations; but we could also test for any common neural effects, or interactions. We found different outcomes in different brain regions, as described below.

We observed robust BOLD repetition-suppression effects in several brain areas when repeating a target property across successive trials in the search task. Note that this manipulation of trial history is very different to the task manipulations typically used to 'activate' the attention network in many prior studies (e.g. see Corbetta & Shulman, 2002; Mesulam, 1999; Serences & Yantis, 2006; see also Jones et al, 2002, for effects of trial history in the context of response-conflict tasks rather than visual search). Instead, the visual-search task was held constant here, and the current display was also equivalent (i.e. counterbalanced) across the conditions compared, to provide relatively subtle manipulations of trial-history alone during search.

In the sense that BOLD repetition-suppression effects were observed, the current repetition effects in fMRI may seem analogous to those often reported in ventral temporal cortices, when repeating properties of isolated stimuli, such as object identity or shape (e.g. Malach et al. 1995; Grill-Spector et al. 1998; Kourtzi & Kanwisher, 2001; Eger et al. 2004; Vuilleumier et al. 2005). But note that very different brain regions were affected by repetition here, including parietal and frontal cortical regions that are often considered to be important components of an 'attention network' (e.g. Corbetta & Shulman, 2002; Hopfinger; Buonocore & Mangun,

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2000; Yantis & Serences, 2003; Labar, Gitelman, Parrish & Mesulam, 1999; Awh & Jonides, 2001; Culham, Cavanagh & Kanwisher, 2001; Jovicich et al., 2001, Kastner & Ungerleider, 2001). Thus, our study demonstrates for the first time that the repetition-suppression methodology (Grill-Spector & Malach, 2001; Grill-Spector, 2006) can now be utilized with fMRI to probe some of the structures and processes involved in selective attention and visual search.

Specifically, we found (Fig 2A) that repeating target location led to BOLD repetition-suppression in bilateral IPS, anterior cingulate, plus other structures traditionally associated with control of spatial attention, such as FEF and inferior regions of right parietal cortex (Table 2). While the repetition effects in FEF during search found in humans here appear broadly consistent with previous findings from single-cell neurophysiology in monkeys (Bichot & Schall, 1999;2002, see further discussion below), to our knowledge there has not as yet been any physiological study examining priming effects during visual search for more posterior regions, such as the intraparietal sulci. Further invasive neurophysiological work could focus on some of the additional areas identified here. Taken together, our data already show clearly that repeating target location can influence activity in human brain regions involved in directing spatial attention (see also Geng et al., submitted). Future fMRI work could exploit the effects found here, to examine the nature of the spatial coordinates in which attention is directed by these structures (e.g. if the eye moved between successive trials, which was not permitted here, would a 'repeated' location on the screen still produce BOLD repetition-suppression within the IPS and FEF, even though the target would now fall at a different retinal location)? The latter retinal factor would presumably be critical for those regions in peristriate visual cortex which also showed some BOLD repetition-suppression for targets presented at the same location here, indicating that even early visual cortex can show some effects of priming visual search.

While fronto-parietal areas are well known to play a role in attention (Corbetta & Shulman, 2002; Mesulam, 1999; Kastner & Ungerleider, 2001; Yantis & Serences, 2003), the present results for these structures are novel in several respects. Most prior studies on the attention network have sought to 'activate' this network, by comparing attentionally-demanding tasks to control tasks. By contrast here we manipulated only trial history, and tested specifically for repetition-suppression rather than overall 'activation'. Our results therefore implicate frontal and parietal areas specifically in priming effects during search for pop-out targets, for the first time in the human brain. Furthermore, they also revealed some specificities within the attention network for the subtle trial-history manipulation (e.g. some contralateralities only for location repetition, when compared directly to color repetition). Moreover, in the particular case of the right FEF, our results even showed some brain-behavior relationship between BOLD repetition-suppression and the individually observed behavioral priming effects.

Another implication of our findings in parietal and frontal cortex is that components of the attention network are evidently involved in pop-out search. Within psychology and the behavioural literature, processing of pop-out stimuli was traditionally thought to be strictly 'preattentive' (e.g. Treisman & Gelade, 1980), rather than to involve attentional mechanisms as indicated here. More recent behavioral work had suggested possible attentional involvement in popout (see, for example discussion in Nakayama & Joseph, 1998), though some controversies still exist concerning this (e.g. Donner et al. 2005). Our fMRI findings provide unequivocal new evidence that the neural substrates underlying modulation of visual search for pop-out targets by repetition do in fact involve some of the parietal and frontal areas long implicated in attention control.

More generally, our study reveals that BOLD repetition-suppression effects may not be restricted solely to visual representations within the ventral object recognition system (Tong,

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Nakayama, Vaughan, & Kanwisher, 1998; Malach et al. 1995), but can also arise elsewhere, selectively affecting those brain areas where the particular repeated property is encoded for the task at hand. The exact neural mechanisms underlying BOLD repetition-suppression effects are still debated, even for some of the most extensively studied examples, such as effects of repeating visual objects on ventral visual cortex (e.g. see Grill-Spector et al., 2006). In that particular context, it has been proposed that BOLD repetition-suppression might potentially correspond to several different types of phenomena at the neural level, including: a reduced extent or 'sharpening/pruning' of activated populations; a reduced firing rate or fatigue/habituation in activated neurons; and/or an earlier activity peak, possibly corresponding to shorter processing time (e.g. see Grill-Spector et al. 2006; Wiggs & Martin, 1998).

Our new fMRI findings of repetition-suppression within the attentional-control network accord particularly well with a new emerging framework for activations of this attention network. Serences and Yantis (2006) recently proposed that components of the attention network are activated primarily when there is a need to 'reset' perceptual systems, in order to force them into a different 'attractor-state'. This could explain why we found reduced activity here when the same attentional state was required (as on a repeat trial), as compared with when a new attentional state was required (on nonrepeat trials, with a different location and/or color to be selected). In terms of the underlying neural events, further invasive work may be required to determine exactly how individual neurons are affected by such attentional repetition; this work can now be guided to the regions we have implicated. Given the existing single-cell findings of Bichot & Schall (1999, 2002) from monkey FEF in particular, we would hypothesize that the present BOLD repetition-effects in human FEF may reflect both sharpening and speeding of the population response there (since both aspects were found by Bichot & Schall at the single-unit level), rather than the fatigue/habituation possibility that Grill-Spector et al. (2006) additionally raise.

Some of the BOLD repetition- suppression effects found here, for repeated target location, notably occurred regardless of the current visual hemifield of the target, including in particular for bilateral IPS (see Figure 2B). By contrast, in left inferior parietal cortex and left inferior frontal gyrus, suppression for repeated target location only arose for contralateral targets, whereas the right-sided homologous regions did not show such asymmetry. This provides a new line of evidence, from the subtle trial-history manipulation, consistent with longstanding suggestions from the clinical neurology literature that some areas associated with spatial attention in humans might be involved only for the contralateral side of space in the left hemisphere, unlike right-hemisphere regions (e.g. right inferior parietal cortex here) that might play a role for both sides of space (e.g. Heilman et al. 2002; Corbetta & Shulman, 2002; Mesulam, 1999). However, here we found that such asymmetry applied only for inferior parietal and frontal regions, whereas the left IPS seemed to be involved for both sides, just as for right IPS also.

Repeating target color instead of target location across successive trials in the unpredictable search sequence led to separable BOLD repetition-suppressions in brain regions that were largely common with those affected by location repetition, but also in some distinct regions (Fig 3). Regions in bilateral IPS and FEF were again strongly affected by repetition. Formal tests for commonality of repetition-suppression effects, applying for both color and location repetition, confirmed that this overlap was most reliable for bilateral IPS, but also to some extent for ACC. These results highlight the general involvement of these parietal and cingulate regions in attentional networks (Mesulam, 1999;Corbetta & Shulman, 2002;Nobre, Coull, Walsh & Frith, 2003;Donner et al., 2002) that appear to be implicated in priming of selective attention regardless of the particular feature (color or location here) that was repeated.

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In addition, however, color-repetition produced some unique BOLD repetition-suppression effects, not seen for location repetitions. These color-related effects arose notably in the left inferior temporal cortex, close to a region previously associated with color cognition (Bartels & Zeki, 2000; Hadjikhani, 1998), which was affected here by color repetition regardless of the visual field where the targets were presented and repeated (see Fig. 4). Conversely, repetition of target location also produced some BOLD repetition-suppression effects that were stronger for location than for color repetitions. These location-specific effects depended on the current target hemifield in a strictly contralateral manner. For a LVF target, greater location- than color-repetition effects were found in right inferior parietal cortex, anterior IPS, and inferior frontal gyrus; whereas for a RVF target, this applied to left IPS and more medial left FEF. Thus, some contralaterality within attentional control-structures was revealed, but this only arose in the closely-matched, subtle comparison of location-repetition effects versus color-repetition effects (i.e., when directly testing for this interaction), for a target in a given hemifield.

Finally, we also tested for regions showing greater BOLD repetition-suppression effects when both location and color were repeated, relative to repetition of either feature alone. This affected control structures such as FEF and IPS, but the most distinctive (and overadditive) effect was in an anterior left fusiform gyrus region (anterior to the left temporal region influenced by color repetition per se). This anterior fusiform region showed repetition-suppression only when both target properties were repeated together, but no reliable effect for repetition of color alone or location alone. Moreover, the suppression produced here by repeating the same color at the same location was greater than the sum of repeating color alone and location alone. This effect of combined features may suggest a role of anterior fusiform cortex in encoding whole-object representations in which color and spatial layouts are bound together, with repetition effects arising here only when the global "Gestalt" or whole pattern of three colored shapes is presented again in the same configuration. Such representation of higher configural information in anterior fusiform cortex may be consistent with the role in coding for complex visual objects with multiple parts suggested by some other human imaging studies (Gauthier & Tarr, 2002; Fink et al. 2000) and by some neurophysiological recordings from IT cortex (Tanaka, Siato, Fukada & Moriya, 1991; Sigala & Logothetis, 2002; Baker, Behrmann & Olson, 2002). It might also explain some of the monkey lesion-data on disruption of priming effects.

Taken together, our results clearly demonstrate that combining repetition effects during visual search, with fMRI, can now be used to probe attentional control structures, as well as visual cortical regions. For attentional-control structures, we note that in the present paradigm, target repetition affected regions in both the 'superior' attentional control network posited by Corbetta & Shulman (2002), such as FEF and IPS; but also in the more 'inferior' network that those authors suggested, such as right inferior parietal cortex. Corbetta and Shulman (2002) proposed that the more superior regions are mainly involved in endogenous direction of spatial attention, whereas the more inferior regions might mediate 'exogenous' aspects of attentional capture (Folk & Remington, 1999; Kristjánsson, Mackeben & Nakayama, 2001; Kristjánsson & Nakayama, 2002; Nakayama & Mackeben, 1989; Yantis & Jonides, 1990). Both cortical regions were influenced by target repetition here, possibly since the targets had both endogenous (task-relevance) and exogenous (singleton) aspects. It might be worthwhile to try to tease these aspects apart, in future studies using further variations on the repetition approach to visual attention that is introduced here.

Color repetition and location repetition had common effects predominantly arising in bilateral IPS, but also in some anterior cingulate and frontal regions here, consistent with a general role in selective attention and covert search for these regions, not specific to only one target property. This contrasted with the left inferior temporal region affected only by color, and with other regions affected more by location repetition (as discussed above). The general question

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of whether attentional control operates in a similar or distinct manner for different visual properties (spatial vs nonspatial) has typically been considered in an all-or-none dichotomous manner within behavioural research to date (Treisman, 1988; Tsal & Lavie, 1988; 1993). Our fMRI results here suggest that in fact there are both some commonalities and some differences, specific to particular brain regions. The present finding that inferior right parietal cortex was mainly involved in location priming fits well with our recent work on priming of visual search in patients suffering from hemispatial neglect after lesions there, in whom we found that aspects of position priming could be disrupted but that color priming was fully preserved (Kristjánsson et al. 2005).

In conclusion, the present results uncover fMRI correlates for the 'priming' of pop-out in human visual search, by repeating target location and/or color in the unpredictable trial sequence. Here we found BOLD repetition-suppression effects that affected components of the attention network, in parietal and frontal cortex, for the first time. These may arise because the attention network settles more readily into an 'attractor-state' (Serences & Yantis, 2006) when the same attention state is required, than when a different target location and/or color must be selected. Repetition fMRI paradigms have already been used with considerable success to study neural representations of objects in the ventral visual stream (see e.g. Malach et al. 1995; Grill-Spector et al. 1998; Kourtzi & Kanwisher, 2001; Eger et al. 2004; Vuilleumier et al. 2005). Our study now indicates that an analogous approach may prove fruitful for studying the neural basis of attentional control and visual search.

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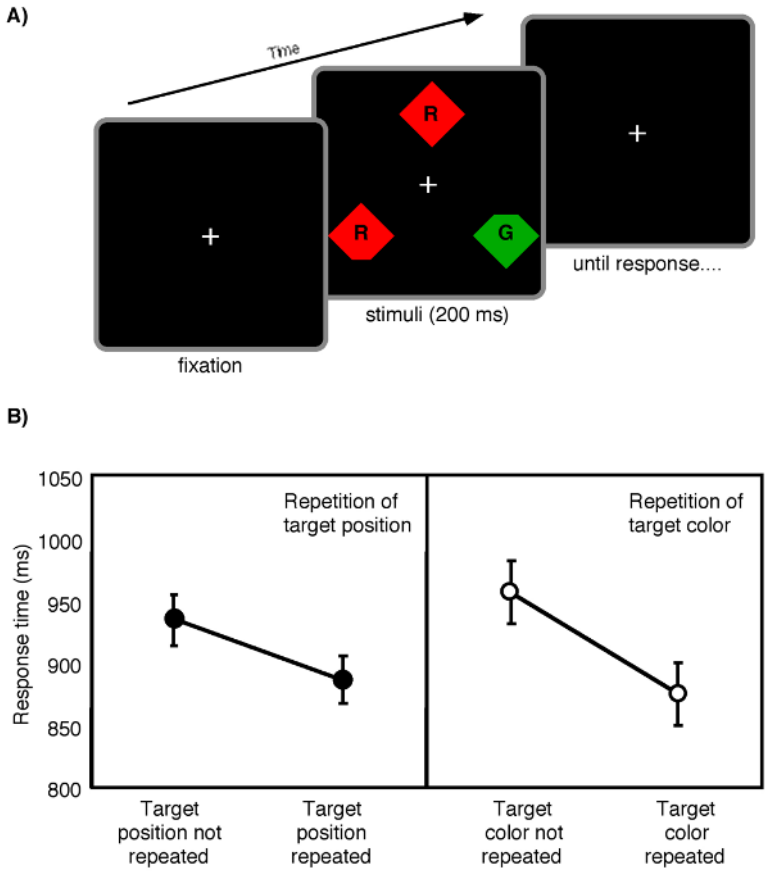


**Fig. 1.**

(A) Sample displays from the behavioral task. A central fixation cross was presented throughout. The brief search display contained 3 diamonds, two in one color, one in the other color, randomly chosen from red or green. The task was to judge whether the notch in the color singleton was at its top corner (as shown for the red singleton at bottom-left) or its bottom (equally likely). (B) Average reaction times as a function of repetition or target location (left graph) or of target color (right graph), for 10 of the 11 subjects tested (see main text). Error bars show the standard error of the mean of the *difference* between repetition of location or color and non-repetition

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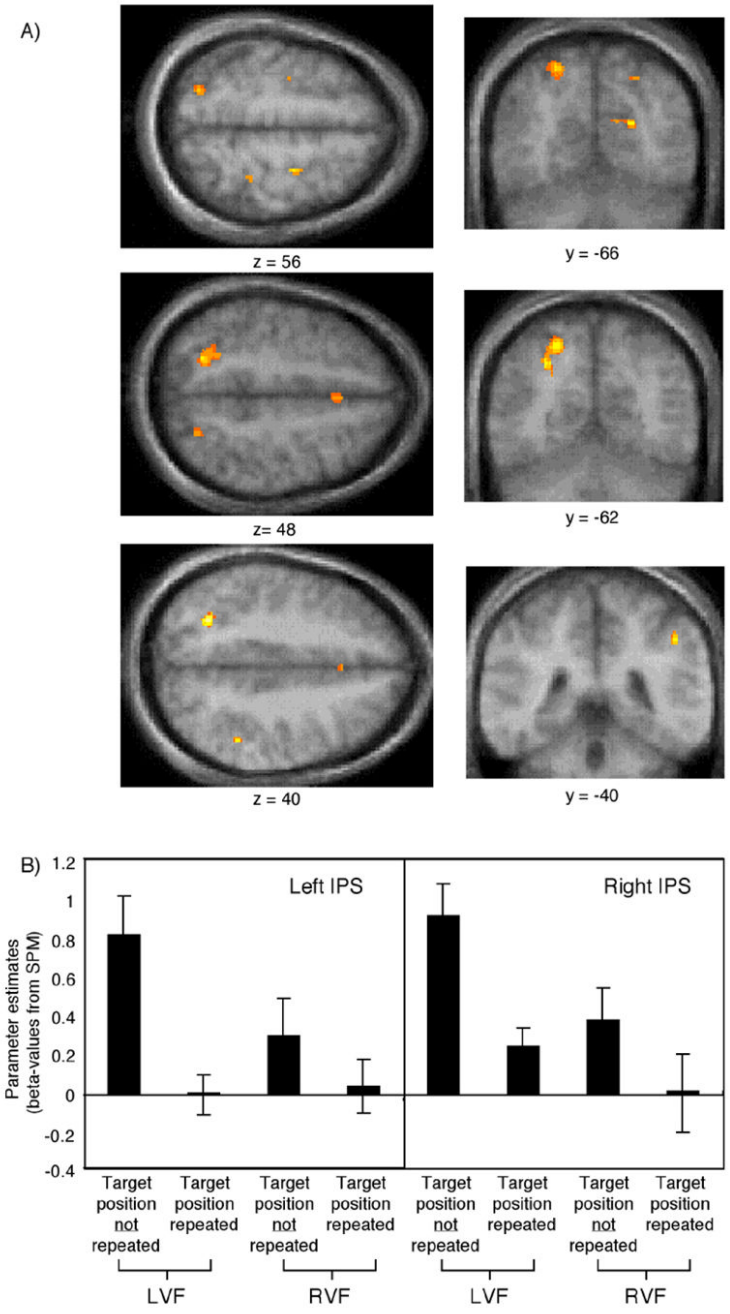


**Fig. 2.**

A) Axial and coronal slices indicating regions showing 'repetition-suppression' (i.e. reduced BOLD signal) when target location was repeated. These SPMs are shown on the mean anatomical brain MRI scan from our 10 participants, thresholded at $p < .005$ for display purposes. Panel B shows the mean parameter estimates of activation (beta values) from the SPM analyses for the clusters in IPS of each hemisphere (average ± SE across all voxels significant at $p < .001$ within the group cluster; average peak in MNI coordinates, left = −3 −60 40, and right = 24 −66 48 ). Note that the IPS in each hemisphere showed a reduced response when target location was repeated, both for targets in the LVF and in the RVF.

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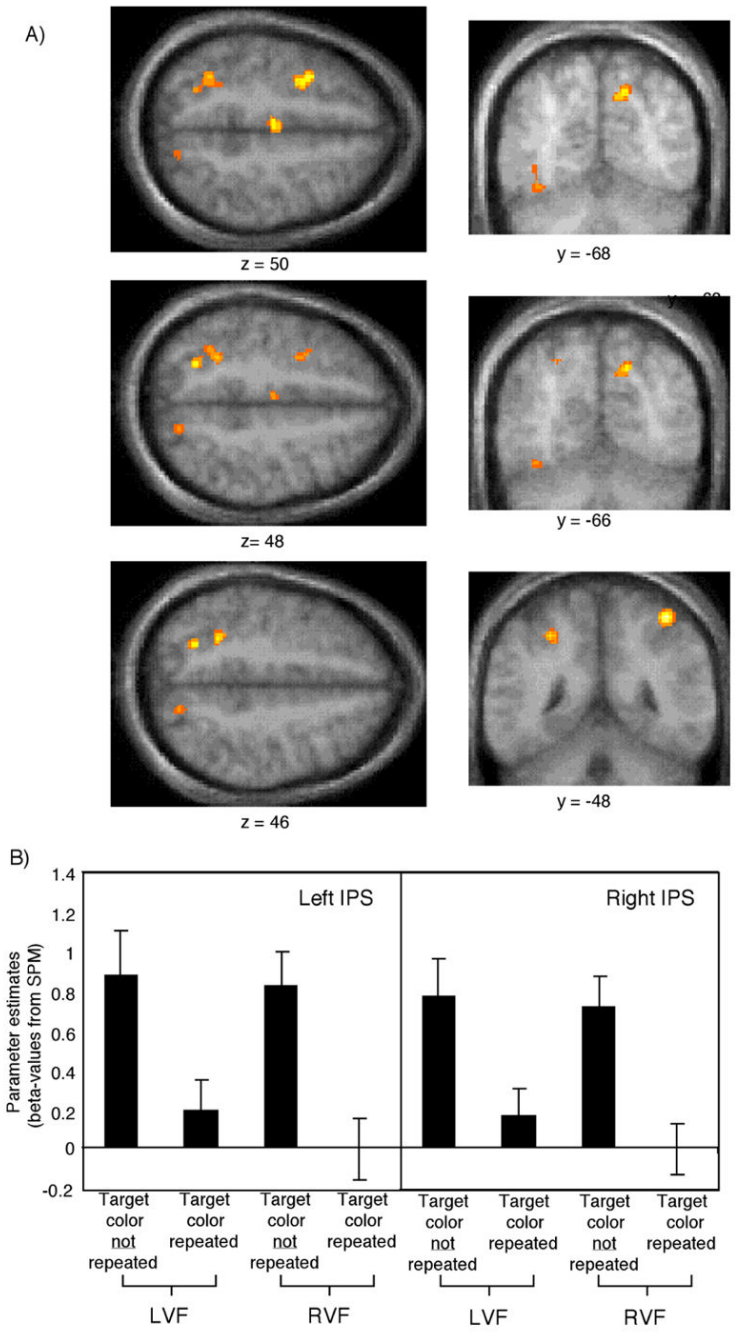


**Fig. 3.**

(A) Axial and coronal slices indicating regions showing repetition-suppression effects (reduced BOLD) as a function of repeated target color. The SPMs are shown on the mean anatomical brain MRI scan from our 10 participants, thresholded at $p < .005$ for display purposes. B) Parameter estimates of activity (beta values from the SPM analyses) averaged for the clusters in IPS of each hemisphere (average ± SE across all voxels significant at $p < .001$ within the group cluster; average peak in MNI coordinates, left= −26 −62 48, and right = 40 −48 58). Note that the IPS in each hemisphere showed a reduced response when color was repeated, both for targets in the LVF and in the RVF.

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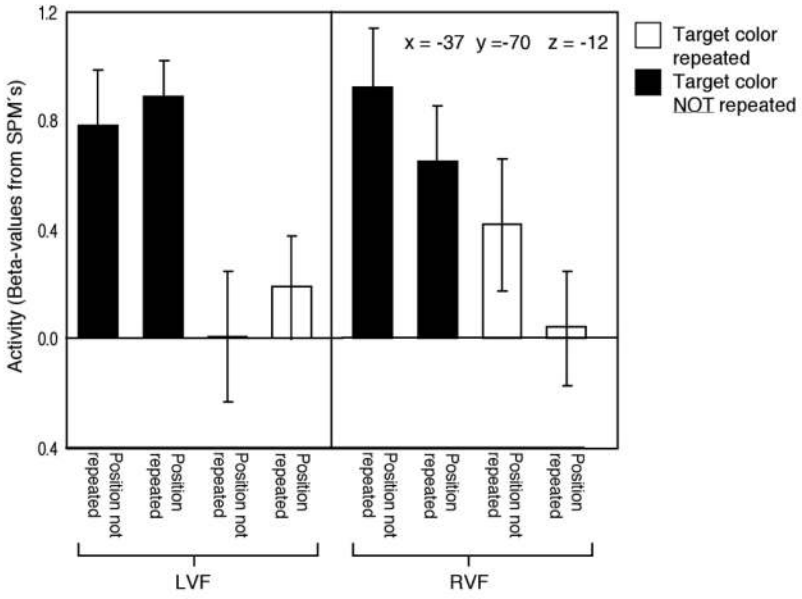


**Fig. 4.**

Activity plots for the left fusiform region (peak at −37, 70, −12) that showed BOLD repetition-suppression for repeated target color, regardless of the current visual field of the target, and regardless also of whether target location was repeated or not (average ± SE across all voxels significant at p <.001 within the group cluster).

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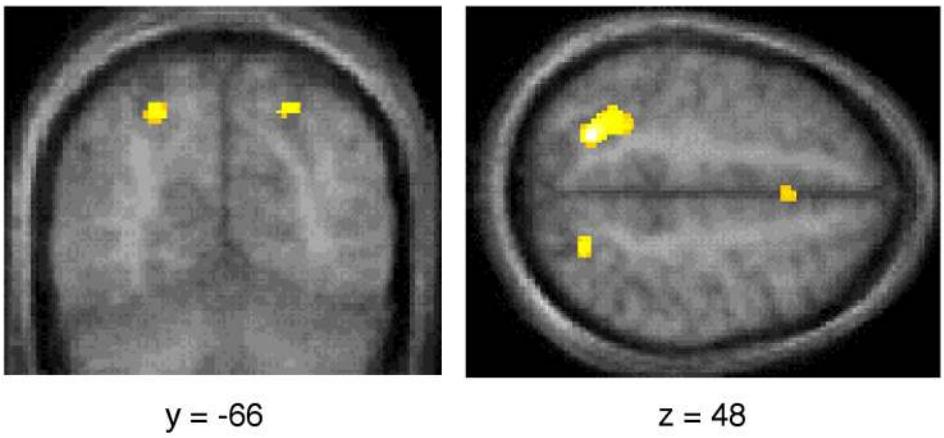


**Fig. 5.**

Areas in bilateral IPS and ACC showing common repetition-suppression effects for both color-repetition and location-repetition, as confirmed formally by combining these independent contrasts to test for overlap (see text).

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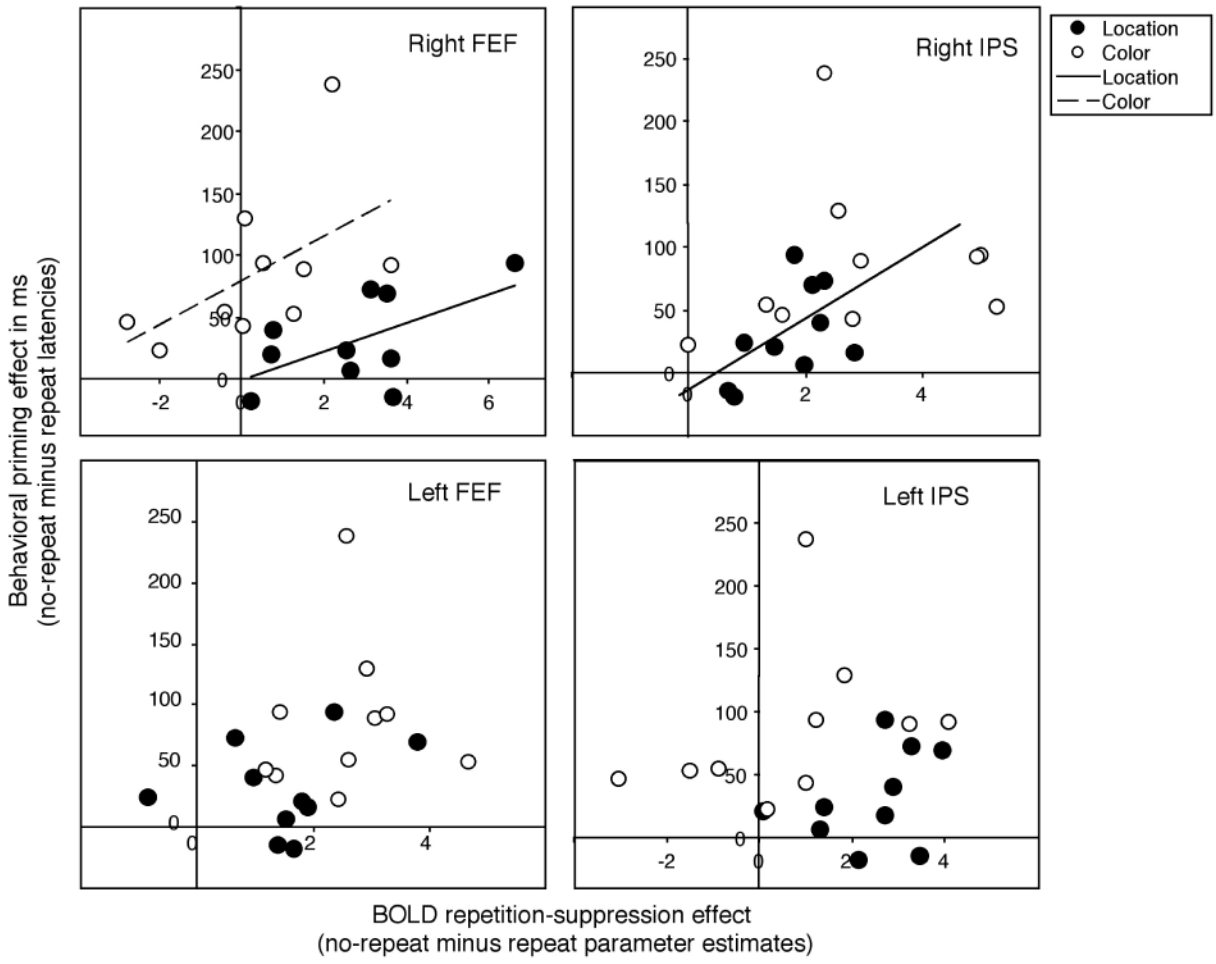


**Fig. 6.**

Scatter-plots of any relation between priming-related decreases in visual search RTs (nonrepeat minus repeat trials, behavioral difference shown along Y-axis) and the BOLD repetition-suppression effects (again non-repeat minus repeat trials) in individual participants, for left or right IPS and FEF clusters that showed overall repetition effects for location and color, respectively (c.f. Tables 2 and 3). Note that these regions were not selected for showing a brain-behavior correlation, but rather the correlation was assessed for those regions that showed overall BOLD repetition-suppression in the whole-brain group analysis. The right FEF region (bottom-right graph) showed the most reliable brain-behavior correlation for location-repetition, and to some extent for color-repetition also. The right IPS showed a weaker correlation for location-repetition. No other significant correlations were found for the 4 regions considered; see main text. The lines show significant correlations in the figures (see also text).

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**Table 1**

BOLD activations dependent on the hemifield of the current target, in random-effects analysis of n=10 (RVF: Right Visual Field; LVF: Left Visual Field).

| Target hemifield | Region | Coordinates X | y | Z | t-value | p-value |
|---|---|---|---|---|---|---|
| LVF > RVF | R Visual cortex | 29 | −98 | 12 | 7.18 | <.001 |
| | R Superior occipital cortex | 8 | −90 | 26 | 9.21 | <.001 |
| | R Anterior inferior occ. Cortex | 38 | −80 | −10 | 9.97 | <.001 |
| RVF > LVF | L Visual Cortex | −24 | −100 | 12 | 5.27 | <.001 |
| | L Lateral occipital area /Fusiform gyrus | −58 | −60 | 6 | 5.74 | <.001 |

t-values and the associated p-value from the SPM contrast described, with each voxel identified by the x, y, z coordinates in MNI space, as well as the anatomical label.

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**Table 2**

BOLD repetition-decreases due to repetition of target position between successive trials, regardless of target hemifield, from a random-effects analysis (n=10).

| | Region | Coordinates X | Y | Z | t-value | p-value |
|---|---|---|---|---|---|---|
| Left hemisphere | L Intraparietal Sulcus | −30 | −60 | 40 | 6.71 | <.001 |
| | L Frontal Eye Fields | −32 | −12 | 54 | 4.47 | <.001 |
| | L middle Frontal Gyrus | −34 | 36 | 18 | 4.13 | .001 |
| | L Peristriate Cortex | −8 | −70 | 8 | 3.41 | .004 |
| Right hemisphere | R Frontal Eye Fields | 28 | −8 | 56 | 4.61 | <.001 |
| | R middle Frontal Gyrus | 28 | 26 | 22 | 6.30 | <.001 |
| | R inferior Frontal Gyrus | 44 | −18 | −4 | 4.57 | <.001 |
| | R Anterior Cingulate | 2 | 22 | 36 | 6.70 | <.001 |
| | R Anterior Parietal | 34 | −34 | 60 | 7.66 | <.001 |
| | R Inferior Parietal | 48 | −42 | 40 | 5.24 | <.001 |
| | R Peristriate Cortex | 14 | −68 | 20 | 5.66 | <.001 |
| | R Intraparietal Sulcus | 24 | −66 | 48 | 3.87 | .001 |

t-values and the associated p-value from the SPM contrast described, with each voxel identified by the x, y, z coordinates in MNI space, as well as the anatomical label.

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**Table 3**

BOLD repetition-decreases due to repetition of target color between successive trials, regardless of target hemifield, in random-effects analysis (n=10).

| | Region | Coordinates X | Y | z | t- value | p-value |
|---|---|---|---|---|---|---|
| Left hemisphere | L Intraparietal Sulcus | −26 | −62 | 48 | 5.71 | <.001 |
| | L Frontal Eye Field | −34 | 6 | 52 | 6.99 | <.001 |
| | L Lateral Occipital Area | −36 | −72 | −6 | 7.24 | <.001 |
| | L Fusiform Gyrus | −44 | −56 | −16 | 5.41 | <.001 |
| Right hemisphere | R Intraparietal Sulcus | 40 | −48 | 58 | 7.97 | <.001 |
| | R Anterior Cingulate | −2 | −14 | 52 | 5.62 | <.001 |
| | R Middle Frontal Gyrus | 32 | 40 | 26 | 5.53 | <.001 |
| | R Occipital Cortex | 12 | −88 | −8 | 4.64 | .001 |
| | R Frontal Eye Field | 32 | −2 | 50 | 2.94 | .008 |

t-values and the associated p-value from the SPM contrast described, with each voxel identified by the x, y, z coordinates in MNI space, as well as the anatomical label.

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**Table 4**

Regions showing common BOLD repetition-suppression effects for both location and color repetition, when using the former contrast as an inclusive mask for the latter in SPM (see main text).

| | Region | Coordinates X | Y | z | t-value | p-value |
|---|---|---|---|---|---|---|
| Left hemisphere | L Intraparietal Sulcus | −26 | −62 | 48 | 5.71 | <.001 |
| | L Middle Frontal Gyrus | −36 | 30 | 22 | 3.22 | .005 |
| Right hemisphere | R Middle Frontal Gyrus | 32 | 24 | −16 | 4.95 | <.001 |
| | R Intraparietal Sulcus | 22 | −66 | 48 | 2.86 | .009 |
| | Anterior Cingulate Gyrus | 0 | 14 | 46 | 3.96 | <.001 |

t-values and the associated p-value from the SPM contrast described, with each voxel identified by the x, y, z coordinates in MNI space, as well as the anatomical label.

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**Table 5**

Repetition suppression that was significantly greater for repetitions of both target color and position than for repetition of only one feature.

| | Region | Coordinates x | Y | z | t-value | p-value |
|---|---|---|---|---|---|---|
| Left hemisphere | L Frontal Eye Fields | −40 | −12 | 46 | 5.48 | <.001 |
| | L Superior Frontal Gyrus | −12 | 8 | 58 | 5.97 | <.001 |
| | L Anterior Fusiform Gyrus | −48 | −36 | −20 | 4.20 | .001 |
| | L Intraparietal Sulcus | −20 | −54 | 50 | 4.18 | .002 |
| Right hemisphere | R Intraparietal Sulcus | 30 | −42 | 60 | 4.35 | .001 |
| | R Frontal Eye Fields | 32 | −4 | 30 | 4.92 | .001 |
| | R Superior Frontal Gyrus | 10 | 8 | 62 | 5.36 | <.001 |

t-values and the associated p-value from the SPM contrast described, with each voxel identified by the x, y, z coordinates in MNI space, as well as the anatomical label.

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