Neural Basis for Priming of Pop-Out during Visual Search Revealed with fMRI

Árni Kristjánsson[1,2], Patrik Vuilleumier[3], Sophie Schwartz[3], Emiliano Macaluso[4] and Jon Driver[2]

[1]Department of Psychology, University of Iceland, [2]UCL Institute of Cognitive Neuroscience and Department of Psychology, University College London, [3]University Medical Centre, Geneva and [4]Fondazione Santa Lucia, Instituto di Ricovero e Cura a Carattere Scientifico

Maljkovic and Nakayama 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 functional magnetic resonance imaging (fMRI). We found that repeating either the location or the color of a singleton target led to repetition suppression of blood oxygen level–dependent (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, whereas 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.

Keywords: priming, repetition suppression attention, visul pop-out, fMRI

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., Biederman and Cooper 1991; Cooper and others 1992; Schacter and others 2004). More recently, neuroimaging studies have analogously investigated how various types of repetition might affect neural responses, often for visual objects (e.g., James and others 1999; Koutstaal and others 2001; Vuilleumier and others 2002; Winston and others 2004) but more generally for other types of repetition also. For visual objects, a typical finding has been that the blood oxygen level–dependent (BOLD) signal in ventral visual cortex can be reduced for repeated (or "primed") visual stimuli. Such functional magnetic resonance imaging (fMRI) effects are often referred to as BOLD repetition suppression or fMRI adaptation (e.g., see Buckner and others 1998; Grill-Spector and others 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 and Nakayama 1994, 1996; Hillstrom 2000; Goolsby and Suzuki 2001; Kristjánsson and others 2002; Kristjánsson 2006a; Olivers and Meeter 2006; Theeuwes and others 2006; see also Chun and Jiang 1998). For example, Maljkovic and Nakayama had their observers search for a uniquely colored diamond between 2 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 and others 2002; Wang and others 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., for reviews, see Nakayama and others 2004; Kristjánsson 2006b), relatively little is known as yet about their neural basis. In a recent neuropsychological study (Kristjánsson and others 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 2 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 and 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 pop-out 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 and Nakayama (1994) and equivalent to that in Kristjánsson and others (2005). The task was to search covertly (without shifting gaze from central fixation) for a briefly displayed, oddly colored (singleton) target diamond, between 2 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 (for review, see e.g., Grill-Spector and Malach 2001; Grill-Spector and others 2006) 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., George and others 1999; Henson and others 2000; Kourtzi and Kanwisher 2001; Vuilleumier and others 2003; Eger and others 2004). 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 and Buckner 1998; Grill-Spector and Malach 2001; Vuilleumier and others 2002; Henson and

others 2003] or for semantic processing [Buckner and others 2000; Wagner and others 2000; Naccache and Dehaene 2001; Simons and others 2003]). 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" (Mesulam 1999; Kastner and Ungerleider 2001; Corbetta and Shulman 2002; Yantis and 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 with various baseline conditions (for more subtle manipulations in response-conflict paradigms unlike the visual search task considered here, although see Jones and others 2002). 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 1) test for any reductions in BOLD signal when a target property was repeated to produce behavioral priming of pop-out; 2) examine whether such effects on particular neural populations might be specific to repeating target location, but not color, or vice versa; 3) test for any commonalities in the neural response to repetition of target location and (separate) repetition of target color; 4) identify any effects that depended specifically on repeating both target properties together at the same time; and finally 5) probe for any repetition effects that might be specific to one target hemifield versus another (as might in principle apply to contralateral visual cortex, e.g.).

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 and Nakayama 1994, 1996; Kristjánsson and Nakayama 2003; Nakayama and others 2004; Kristjánsson 2006b), then attention-related networks in parietal and frontal cortex (e.g., LaBar and others 1999; Hopfinger and others 2000; Awh and Jonides 2001; Culham and others 2001; Jovicich and others 2001; Corbetta and Shulman 2002; Yantis and Serences 2003) 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; for review, see Grill-Spector and others 2006).

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 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 and others 2003).
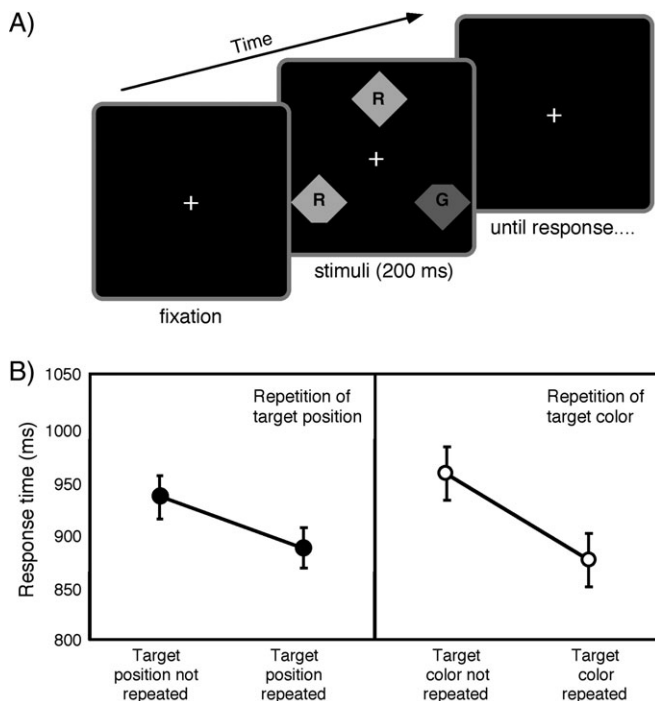
Figure 1. (A) Sample displays from the behavioral task. A central fixation cross was presented throughout. The brief search display contained 3 diamonds, 2 in 1 color and 1 in the other color, randomly chosen from red or green. The task was to judge whether the notch in the color singleton was at its 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 nonrepetition.

It still remains contentious whether or not some aspects of visual pop-out require any selective attention at all (e.g., see Nakayama and Silverman 1986; Treisman and Gormican 1988; Bravo and Nakayama 1992; Donner and others 2002). 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 and others (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 and others 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 and others 2002). Finally, because the singleton target in the present paradigm could appear in either the left or the 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 versus 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) between 2 other diamonds of a different color (see Fig. 1A) and to make a judgment on the target's shape. The 2 possible colors were green and red, so the oddly colored target could either be a red diamond among 2 green ones or a green diamond among 2 red ones. The target diamond in the LVF or RVF had a small notch cutoff 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 degree. Observers had to indicate as fast as they could, by pressing the appropriate key on a magnetic resonance–compatible button-box, whether the cutoff on just the "target" diamond was upper or lower. The size of the cutoff was 23 arc min. The target and distractors were all presented at equal distance from a central fixation cross (eccentricity 4 arc degree). The 3 possible diamond locations were at the top, right, and left at 0, 120, and 240 degrees, respectively, from vertical around an imaginary clock face (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 and others 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 Kristjánsson and others 2005).

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 2 lateral locations, both the left and the right items always had a notch cutoff. The actual position of the cutoff (i.e., at upper or lower part of diamond) was determined randomly and independently for these 2 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 and 5000 ms in steps of 90 ms (this step size corresponds 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 eye-tracker 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 degree 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 statistical parametric mapping (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 20–33 years (mean 27.6 years). The fMRI results for one subject were not included in the analyses because 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.

Magnetic Resonance Imaging Acquisition and Other Equipment
BOLD images were collected with echo planar imaging on a 1.5-T 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). Time repetition 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 min. A standard Siemens head coil was used for whole-brain acquisition. A further T_1-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 magnetic resonance imaging 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 60 Hz for 2 s on each trial.

Data Analysis
The 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 4 volumes from each of the 4 scanning sessions were discarded, whereas the remainder were used for our analysis of all 10 included participants. Individual events were modeled by a standard hemodynamic response function, including 8 experimental conditions (targets with repeated color but nonrepeated position, repeated position/nonrepeated color, repeated color/repeated position, or nonrepeated color/nonrepeated position; all separately for a target currently in the RVF or LVF) plus one regressor for all trials involving either incorrect responses (2.8% of trials) or eye movements (4.1% of trials). Finally, 6 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. SPMs of the *t*-statistic 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 <0.001, we occasionally selected a more liberal threshold of $P < 0.01$ (e.g., see Degonda and others 2005), specifying this below in each such case.

Additional confirmatory analyses of variance (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 less 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. 1*B*). The exceptional subject was excluded from the fMRI study because our goal was to investigate the neural correlates for priming of search, which was reliably observed in all other participants, and because the excluded participant was unusually slow and inaccurate. For the 10 remaining subjects, a repeated-measures ANOVA (on the effects of repeat versus nonrepeat of target location and orthogonally of target color) revealed strong facilitatory priming of reaction times for repeated target position ($F_{1,9} = 19.17$, $P < 0.001$) and repeated target color ($F_{1,9} = 24.68$, $P < 0.001$). Just as in the original studies of Maljkovic and Nakayama (1994, 1996), there was no interaction behaviorally between position and color repetition ($F_{1,9} = 0.979$, $P = 0.43$), which were thus additive in their effects (Sternberg 1969; for a recent discussion of this point, see also Kristjánsson 2006a). These behavioral "priming of pop-out" results confirm the findings from many previous, purely behavioral studies of priming in visual search (e.g., Maljkovic and Nakayama 1994, 1996; see Nakayama and others 2004), as expected, but as of now found during scanning.

The 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. 1*A*), 2 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 2 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 toward the target, as would be expected (e.g., see Driver and Frackowiak 2001; Kastner and Ungerleider 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, whereas 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 IPS bilaterally, as well as in bilateral FEF (for similar coordinates as those shown in Table 2, see Paus 1996), 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 Fig. 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 have long been implicated in control of spatial attention (e.g., see Mesulam 1999; Kastner and Ungerleider 2001; Corbetta and Shulman 2002; Giesbrecht and others 2003). Here, we found for the first time that several regions in this network can exhibit repetition-suppression effects during

Table 1

BOLD activations dependent on the hemifield of the current target, in random-effects analysis of $n = 10$

Target hemifield	Region	Coordinates			*t* value	*P* value
		x	*y*	*z*		
LVF > RVF	R visual cortex	29	−98	12	7.18	<0.001
	R superior occipital cortex	8	−90	26	9.21	<0.001
	R anterior inferior occipital cortex	38	−80	−10	9.97	<0.001
RVF > LVF	L visual cortex	−24	−100	12	5.27	<0.001
	L lateral occipital area/FG	−58	−60	6	5.74	<0.001

Note: *t* values and the associated *P* value from the SPM contrast described, with each voxel identified by the *x*, *y*, *z* coordinates in the Montreal Neurological Institute space, as well as the anatomical label. L, left; R, right.

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			t value	P value
		x	y	z		
Left hemisphere	L IPS	−30	−60	40	6.71	<0.001
	L FEFs	−32	−12	54	4.47	<0.001
	L middle frontal gyrus	−34	36	18	4.13	0.001
	L peristriate cortex	−8	−70	8	3.41	0.004
Right hemisphere	R FEFs	28	−8	56	4.61	<0.001
	R middle frontal gyrus	28	26	22	6.30	<0.001
	R inferior frontal gyrus	44	−18	−4	4.57	<0.001
	R anterior cingulate	2	22	36	6.70	<0.001
	R anterior parietal	34	−34	60	7.66	<0.001
	R inferior parietal	48	−42	40	5.24	<0.001
	R peristriate cortex	14	−68	20	5.66	<0.001
	R IPS	24	−66	48	3.87	0.001

Note: t values and the associated P value from the SPM contrast described, with each voxel identified by the x, y, z coordinates in the Montreal Neurological Institute space, as well as the anatomical label. L, left; R, right.

priming of visual search by repeated target location. Besides IPS and FEF regions that are associated with top–down attention control (Kastner and 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 (x, y, $z = -44$, −52, 20; $t = 4.13$, $P < 0.002$), and for left inferior frontal gyrus (x, y, $z = -52$, 14, 8; $t = 6.82$; $P < 0.001$). 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 accordance with traditional suggestions (see Mesulam 1999; Driver and Vuilleumier 2001; Corbetta and Shulman 2002; Heilman and others 2002) that some regions involved in spatial attention in the left hemisphere may deal primarily with just the (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, $t = 5.24$, $P > 0.001$) and the RVF (50, −54, 46, $t = 3.46$, $P < 0.005$) 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 Fig. 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
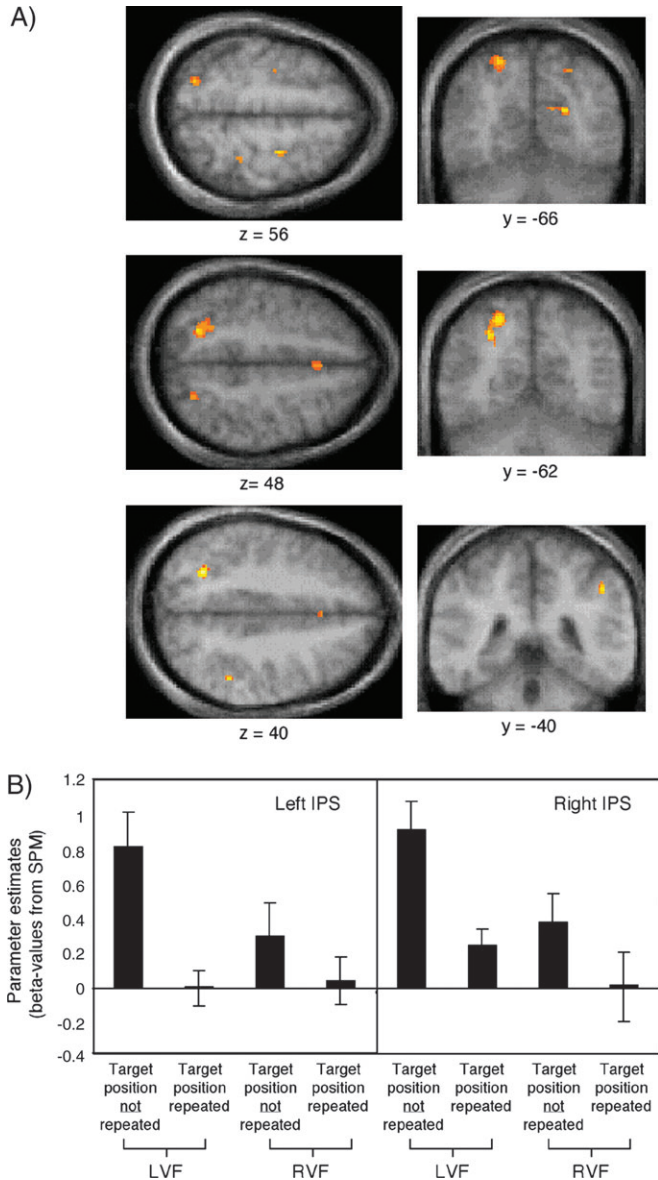

Figure 2. (*A*) Axial and coronal slices indicating regions showing repetition suppression (i.e., reduced BOLD signal) when target location was repeated. These SPMs are shown on the mean anatomical brain magnetic resonance imaging scan from our 10 participants, thresholded at $P < 0.005$ for display 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 ± standard error across all voxels significant at $P < 0.001$ within the group cluster; average peak in the Montreal Neurological Institute 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, for targets both in the LVF and in the RVF.

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 2 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 IPS 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 ACC and right middle frontal gyrus.

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			t value	P value
		x	y	z		
Left hemisphere	L IPS	−26	−62	48	5.71	<0.001
	L FEF	−34	6	52	6.99	<0.001
	L lateral occipital area	−36	−72	−6	7.24	<0.001
	L FG	−44	−56	−16	5.41	<0.001
Right hemisphere	R IPS	40	−48	58	7.97	<0.001
	R anterior cingulate	−2	−14	52	5.62	<0.001
	R middle frontal gyrus	32	40	26	5.53	<0.001
	R occipital cortex	12	−88	−8	4.64	0.001
	R FEF	32	−2	50	2.94	0.008

Note: t values and the associated P value from the SPM contrast described, with each voxel identified by the x, y, z coordinates in the Montreal Neurological Institute space, as well as the anatomical label. L, left; R, right.

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 (Fig. 3 and Table 3) appear to overlap with those exhibiting repetition effects for target "position" (see Fig. 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 (Fig. 2 and Table 2) did not show any reliable main effect of color repetition here (all $P > 0.01$ 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 2 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 and Zeki 2000; Hadjikhani and others 1998; but see also Wade and others 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 2 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 ($F_{1,9} = 93.5$, $P < 0.001$) but no other main effect and no interaction (i.e., including no interactions of color repetition with target visual field, or with location repetition [all these $F_{1,9} < 1.33$, $P > 0.22$]). 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
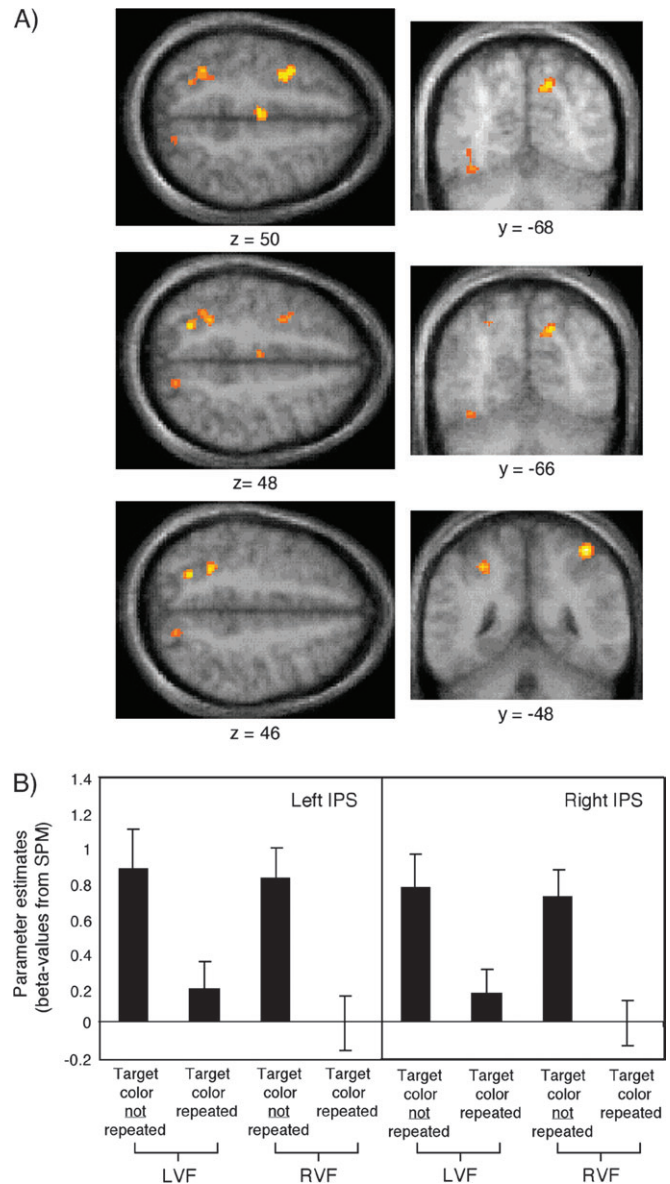

Figure 3. (*A*) Axial and coronal slices indicating regions showing repetition-suppression effects (reduced BOLD) as a function of repeated target color. The SPMs are shown on the mean anatomical brain magnetic resonance imaging scan from our 10 participants, thresholded at $P < 0.005$ for display purposes. (*B*) Parameter estimates of activity (beta values from the SPM analyses) averaged for the clusters in IPS of each hemisphere (average ± standard error across all voxels significant at $P < 0.001$ within the group cluster; average peak in the Montreal Neurological Institute 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, for targets both in the LVF and in the RVF.

suggested by comparing Figs 2 and 3 plus Tables 2 and 3). The random-effect analysis of location-repetition effects was used as an inclusive mask in SPM (mask threshold at $P < 0.01$), within which independent color-repetition effects were then assessed by a new random-effect group analysis at $P < 0.001$ (for such an analysis approach to conjunctions, see Friston and others 2005; Nichols and others 2005). 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
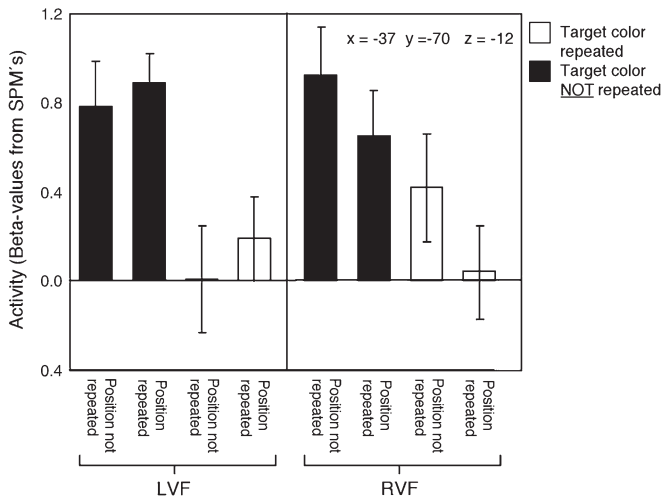
Figure 4. Activity plots for the left fusiform region (peak at –37, 70, –12) that showed BOLD repetition suppression for repeated target color, regardless of the current visual field of the target and regardless also of whether target location was repeated or not (average ± standard error across all voxels significant at *P* < 0.001 within the group cluster).
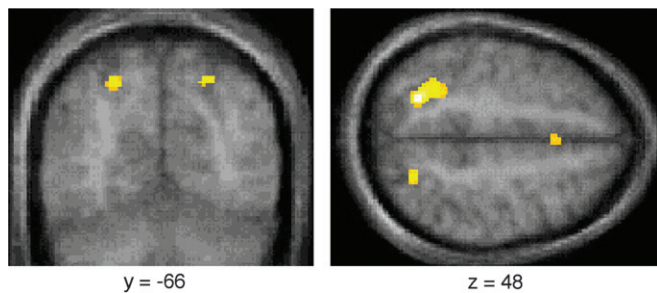

Figure 5. Areas in bilateral IPS and ACC showing common repetition-suppression effects for both color repetition and location repetition, as confirmed formally by combining these independent contrasts to test for overlap (see text).

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 Figs 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 Figs 3 and 4 and the separate analyses of these 2 orthogonal effects above), whereas by contrast the location-repetition but not the color-repetition effects affected inferior parietal cortex (see Fig. 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.

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			*t* value	*P* value
		x	*y*	*z*		
Left hemisphere	L IPS	−26	−62	48	5.71	<0.001
	L middle frontal gyrus	−36	30	22	3.22	0.005
Right hemisphere	R middle frontal gyrus	32	24	−16	4.95	<0.001
	R IPS	22	−66	48	2.86	0.009
	Anterior cingulate gyrus	0	14	46	3.96	<0.001

Note: *t* values and the associated *P* value from the SPM contrast described, with each voxel identified by the *x*, *y*, *z* coordinates in the Montreal Neurological Institute space, as well as the anatomical label. L, left; R, right.

These analyses confirmed that repetition decreases were indeed greater for color than location in left FG (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 ($x = –30$, $y = 6$, $z = 54$; $t = 3.5$, $P < 0.004$), right IPS ($x = 30$, $y = –58$, $z = 66$; $t = 5.11$, $P < 0.001$), and occipital cortex ($x = 24$, $y = –56$, $z = 30$; $t = 5.99$, $P < 0.001$).

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 ($x = 64$, $y = –52$, $z = 22$; $t = 5.49$, $P < 0.001$), right anterior IPS ($x = 34$, $y = –36$, $z = 44$; $t = 4.92$, $P < 0.001$), and right inferior frontal gyrus ($x = 40$, $y = 34$, $z = –2$; $t = 5.49$, $P < 0.001$). For RVF targets, greater position than color effects were found in contralateral left posterior IPS ($x = –28$, $y = –70$, $z = 32$; $t = 4.65$, $P < 0.001$) and left FEF ($x = –20$, $y = –8$, $z = 50$; $t = 5.49$, $P < 0.001$), 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 Fig. 1*B*) 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 frontoparietal 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; that is, less attention demand when appropriate allocation of attention was already primed, thus requiring the same attractor state for the attention network (for discussion, see Serences and Yantis 2006) 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 color was repeated. Such

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			t value	P value
		x	y	z		
Left hemisphere	L FEFs	−40	−12	46	5.48	<0.001
	L superior frontal gyrus	−12	8	58	5.97	<0.001
	L anterior FG	−48	−36	−20	4.20	0.001
	L IPS	−20	−54	50	4.18	0.002
Right hemisphere	R IPS	30	−42	60	4.35	0.001
	R FEFs	32	−4	30	4.92	0.001
	R superior frontal gyrus	10	8	62	5.36	<0.001

Note: *t* values and the associated *P* value from the SPM contrast described, with each voxel identified by the *x*, *y*, *z* coordinates in the Montreal Neurological Institute space, as well as the anatomical label. L, left; R, right.

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 the left FG (anterior to the region shown in Figs 3 and 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 superadditive effect, at $P < 0.00001$. This anterior fusiform region might therefore be involved in processing conjoined object features or the display Gestalt, that is color combined along with location for all 3 stimuli. Other regions such as IPS and FEF did not show a similarly superadditive 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 2 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 Maccotta and Buckner 2004; Wig and others 2005). For each participant, we computed the benefits in median reaction times (RT) 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 repeat 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 nonrepeat and repeat trials, for IPS and FEF clusters (at $P < 0.001$) 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 preselected 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, $r_9 = 0.58$, $P = 0.039$) and to some extent for color repetition ($r_9 = 0.54$, $P = 0.052$). Some trend for a brain–behavior correlation was also found for location repetition in right IPS ($r_9 = 0.53$, $P = 0.057$). The other 2 regions considered showed no reliable correlations or substantial trends (left FEF: $r = 0.26$ for location; $r = 0.04$ for color, $P > 0.26$; left IPS: $r = 0.35$ for both location and color, $P = 0.158$). The right FEF correlations are striking, given that this region was not preselected 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 (for review, see Henson and Rugg 2003; Grill-Spector and others 2006). 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 and others 2005). It is worthwhile to note, however, that Turk-Browne and others (2006) found that behavioral 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 1*B*) and that these 2 effects were additive, as
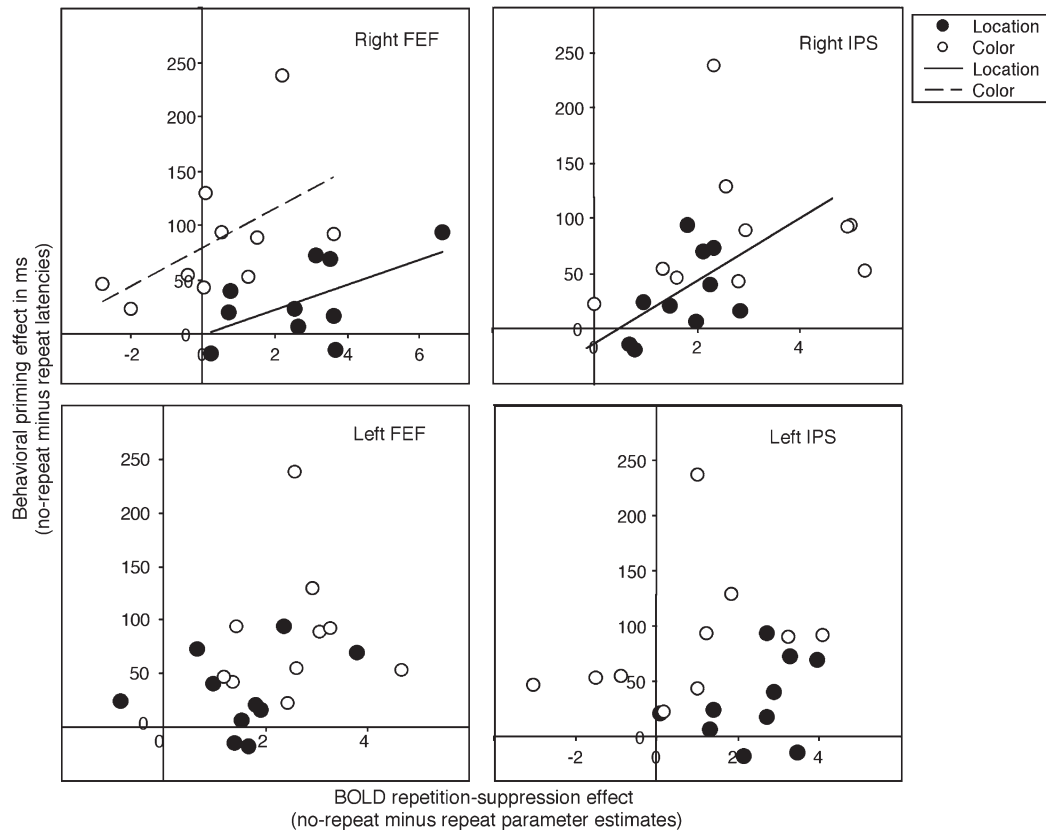
Figure 6. Scatter plots of any relation between priming-related decreases in visual search RTs (nonrepeat minus repeat trials, behavioral difference shown along *y* axis) and the BOLD repetition-suppression effects (again nonrepeat minus repeat trials) in individual participants, for left or right IPS and FEF clusters that showed overall repetition effects for location and color, respectively (cf., 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).

previously reported by Maljkovic and Nakayama in purely behavioral work (1996; see also discussion in Nakayama and others 2004; Kristjánsson 2006a). Within psychology, such additivity has often been used to argue that the 2 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 Mesulam 1999; Corbetta and Shulman 2002; Serences and Yantis 2006; for effects of trial history in the context of response-conflict tasks rather than visual search, see also Jones and others 2002). 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 and others 1995; Grill-Spector and others 1998; Kourtzi and Kanwisher 2001; Eger and others 2004; Vuilleumier and others 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., LaBar and others 1999; Hopfinger and others 2000; Awh and Jonides 2001; Culham and others 2001; Jovicich and others 2001, Kastner and Ungerleider 2001; Corbetta and Shulman 2002; Yantis and Serences 2003). Thus, our study demonstrates for the first time that the repetition-suppression methodology (Grill-Spector and Malach 2001; Grill-Spector and others 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. 2*A*) 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). Although the repetition effects in FEF during search found in humans here appear broadly consistent with previous findings from single-cell neurophysiology in monkeys (Bichot and 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 and others 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 frontoparietal areas are well known to play a role in attention (Mesulam 1999; Kastner and Ungerleider 2001; Corbetta and Shulman 2002; Yantis and 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 with 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 with 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 behavioral literature, processing of pop-out stimuli was traditionally thought to be strictly preattentive (e.g., Treisman and Gelade 1980), rather than to involve attentional mechanisms as indicated here. More recent behavioral work had suggested possible attentional involvement in pop-out (see, e.g., discussion in Nakayama and Joseph 1998), though some controversies still exist concerning this (e.g., Donner and others 2002). 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 (Malach and others 1995; Tong and others 1998) 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 and others 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 Wiggs and Martin 1998; Grill-Spector and others 2006).

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 and 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 (because both aspects were found by Bichot and Schall at the single-unit level) rather than the fatigue/habituation possibility that Grill-Spector and others (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 Fig. 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 long-standing 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., Mesulam 1999; Corbetta and Shulman 2002; Heilman and others 2002). 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 not only 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 not only 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 and Shulman 2002; Donner and others 2002; Nobre and others 2003) that appear to be implicated in priming of selective attention regardless of the particular feature (color or location here) that was repeated.

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 (Hadjikhani and others 1998; Bartels and Zeki 2000), 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 over additive) effect was in an anterior left FG 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 3 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 (Fink and others 2000; Gauthier and Tarr 2002) and by some neurophysiological recordings from inferotemporal cortex (Tanaka and others 1991; Baker and others 2002; Sigala and Logothetis 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 not only in both the "superior" attentional control network posited by Corbetta and 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 (Nakayama and Mackeben 1989; Yantis and Jonides 1990; Folk and Remington 1999; Kristjánsson and others 2001; Kristjánsson and Nakayama 2002). Both cortical regions were influenced by target repetition here, possibly because 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 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 behavioral research to date (Treisman 1988; Tsal and 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 and others 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 and 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 and others 1995; Grill-Spector and others 1998; Kourtzi and Kanwisher 2001; Eger and others 2004; Vuilleumier and others 2005). Our study now indicates that an analogous approach may prove fruitful for studying the neural basis of attentional control and visual search.

Notes

Address correspondence to Árni Kristjánsson, Department of Psychology, University of Iceland, Oddi v. Sturlugötu 101 Reykjavík, Iceland. Email: ak@hi.is.

References

Awh E, Jonides J. 2001. Overlapping mechanisms of attention and spatial working memory. Trends Cogn Sci 5:119-126.

Baker CI, Behrmann M, Olson CR. 2002. Impact of learning on representation of parts and wholes in monkey inferotemporal cortex. Nat Neurosci 5:1210-1216.

Bartels A, Zeki S. 2000. The architecture of the colour centre in the human visual brain: new results and a review. Eur J Neurosci 12:172-193.

Bichot NP, Schall JD. 1999. Effects of similarity and history on neural mechanisms of visual selection. Nat Neurosci 2:549-554.

Bichot NP, Schall JD. 2002. Priming in macaque frontal cortex during popout visual search: feature-based facilitation and location-based inhibition of return. J Neurosci 22:4675-4685.

Biederman I, Cooper EE. 1991. Priming contour-deleted images: evidence for intermediate representations in visual object recognition. Cognit Psychol 23:393-419.

Bravo MJ, Nakayama K. 1992. The role of attention in different visual-search tasks. Percept Psychophys 51:465-472.

Buckner RL, Goodman J, Burock M, Rotte M, Koutstaal W, Schacter DL, Rosen B, Dale AM. 1998. Functional-anatomic correlates of object priming in humans revealed by rapid presentation recognition event related fMRI. Neuron 20:285-296.

Buckner RL, Koutstaal W, Schacter DL, Rosen BR. 2000. Functional MRI evidence for a role of frontal and inferior temporal cortex in amodal components of priming. Brain 123(Pt 3):620-640.

Chun MM, Jiang Y. 1998. Contextual cueing: implicit learning and memory of visual context guides spatial attention. Cognit Psychol 36:28-71.

Cooper LA, Schacter DL, Ballesteros S, Moore C. 1992. Priming and recognition of transformed three-dimensional objects: effects of size and reflection. J Exp Psychol Learn Mem Cogn 18:43-57.

Corbetta M, Shulman GL. 2002. Control of goal-directed and stimulus-driven attention in the brain. Nat Rev Neurosci 3:201-215.

Culham JC, Cavanagh P, Kanwisher NG. 2001. Attention response functions: characterizing brain areas using fMRI activation during parametric variations of attentional load. Neuron 32:737-745.

Degonda N, Mondadori CR, Bosshardt S, Schmidt CF, Boesiger P, Nitsch RM, Hock C, Henke K. 2005. Implicit associative learning engages the hippocampus and interacts with explicit associative learning. Neuron 46:505-520.

Donner TH, Kettermann A, Diesch E, Ostendorf F, Viillringer A, Brandt SA. 2002. Visual feature and conjunction searches of equal difficulty engage only partially overlapping frontoparietal networks. Neuroimage 15:16-25.

Driver J, Frackowiak RS. 2001. Neurobiological measures of human selective attention. Neuropsychologia 39:1257-1262.

Driver J, Vuilleumier P. 2001. Perceptual awareness and its loss in unilateral neglect and extinction. Cognition 79:39-88.

Eger E, Henson RN, Driver J, Dolan RJ. 2004. BOLD repetition decreases in object-responsive ventral visual areas depend on spatial attention. J Neurophysiol 92:1241-1247.

Fink GR, Marshall JC, Weiss PH, Shah NJ, Toni I, Halligan PW, Zilles K. 2000. 'Where' depends on 'what': a differential functional anatomy for position discrimination in one- versus two-dimensions. Neuropsychologia 38:1741-1748.

Folk CL, Remington R. 1999. Can new objects override attentional control settings? Percept Psychophys 61:727-739.

Friston KJ, Penny WD, Glaser DE. 2005. Conjunction revisited. Neuroimage 25:661-667.

Gauthier I, Tarr MJ. 2002. Unraveling mechanisms for expert object recognition: bridging brain activity and behavior. J Exp Psychol Hum Percept Perform 28:431-446.

Geng JJ, Eger E, Ruff CC, Kristjánsson A, Rotshtein P, Driver J. Forthcoming. Attentional selection from competing stimuli in opposite visual fields: control processes and effects on visual activations revealed with fMRI. J Neurophysiol.

George N, Dolan RJ, Fink GR, Baylis GC, Russell C, Driver J. 1999. Contrast polarity and face recognition in the human fusiform gyrus. Nat Neurosci 2:574-580.

Giesbrecht B, Woldorff MG, Song AW, Mangun GR. 2003. Neural mechanisms of top-down control during spatial and feature attention. Neuroimage 19:496-512.

Goolsby BA, Suzuki S. 2001. Understanding priming of color-singleton search: roles of attention at encoding and "retrieval". Percept Psychophys 63:929-944.

Grill-Spector K, Henson R, Martin A. 2006. Repetition and the brain: neural models of stimulus-specific effects. Trends Cogn Sci 10:14-23.

Grill-Spector K, Kushnir T, Edelman S, Itzchak Y, Malach R. 1998. Cue-invariant activation in object-related areas of the human occipital lobe. Neuron 21:191-202.

Grill-Spector K, Malach R. 2001. fMR-adaptation: a tool for studying the functional properties of human cortical neurons. Acta Psychol 107:293-321.

Hadjikhani N, Liu AK, Dale AM, Cavanagh P, Tootell RB. 1998. Retinotopy and colour sensitivity in human visual cortical area V8. Nat Neurosci 1:235-241.

Heilman KM, Watson RT, Valenstein E. 2002. Spatial neglect. In: Karnath H, Milner D, Vallar G, editors. The cognitive and neural bases of spatial neglect. New York, NY: Oxford University Press. p 3-30.

Henson R, Shallice T, Dolan R. 2000. Neuroimaging evidence for dissociable forms of repetition priming. Science 287:1269-1272.

Henson RN, Goshen-Gottstein Y, Ganel T, Otten LJ, Quayle A, Rugg MD. 2003. Electrophysiological and haemodynamic correlates of face perception, recognition and priming. Cereb Cortex 13:793-805.

Henson RN, Rugg MD. 2003. Neural response suppression, haemodynamic repetition effects, and behavioural priming. Neuropsychologia 41:263-270.

Hillstrom AP. 2000. Repetition effects in visual search. Percept Psychophys 62:800-817.

Hopfinger JB, Buonocore MH, Mangun GR. 2000. The neural mechanisms of top-down attentional control. Nat Neurosci 3:284-291.

James TW, Humphrey GK, Gati JS, Menon RS, Goodale MA. 1999. Repetition priming and the time course of object recognition: an fMRI study. Neuroreport 10:1019-1023.

Jones AD, Cho RY, Nystrom LE, Cohen JD, Braver TS. 2002. A computational model of anterior cingulate function in speeded response tasks: effects of frequency, sequence, and conflict. Cogn Affect Behav Neurosci 2:300-317.

Jovicich J, Peters RJ, Koch C, Braun J, Chang L, Ernst T. 2001. Brain areas specific for attentional load in a motion-tracking task. J Cogn Neurosci 15:1048-1058.

Kastner S, Ungerleider LG. 2001. The neural basis of biased competition in human visual cortex. Neuropsychologia 39:1263-1276.

Kourtzi Z, Kanwisher N. 2001. Representation of perceived object shape by the human lateral occipital complex. Science 293:1506-1509.

Koutstaal W, Wagner AD, Rotte M, Maril A, Buckner RL, Schacter DL. 2001. Perceptual specificity in visual object priming: functional magnetic resonance imaging evidence for a laterality difference in fusiform cortex. Neuropsychologia 39:184-199.

Kristjánsson Á. 2006a. Simultaneous priming along multiple dimensions in visual search task. Vision Res 46:2554-2570.

Kristjánsson Á. 2006b. Rapid learning in attention shifts—a review. Vis Cogn 13:324-362.

Kristjánsson Á, Mackeben M, Nakayama K. 2001. Rapid, object based learning in the deployment of transient attention. Perception 30:1375-1387.

Kristjánsson Á, Nakayama K. 2002. The attentional blink in space and time. Vision Res 42:2039-2050.

Kristjánsson Á, Nakayama K. 2003. A primitive memory system for the deployment of transient attention. Percept Psychophys 65:711-724.

Kristjánsson Á, Vuilleumier P, Malhotra P, Husain M, Driver J. 2005. Priming of color and position during visual search in unilateral spatial neglect. J Cogn Neurosci 17:859-873.

Kristjánsson Á, Wang D, Nakayama K. 2002. The role of priming in conjunctive visual search. Cognition 85:37-52.

LaBar KS, Gitelman DR, Parrish TB, Mesulam M. 1999. Neuroanatomic overlap of working memory and spatial attention networks: a functional MRI comparison within subjects. Neuroimage 10:695-704.

Maccotta L, Buckner RL. 2004. Evidence for neural effects of repetition that directly correlate with behavioral priming. J Cogn Neurosci 16:1625-1632.

Malach R, Reppas JB, Benson RR, Kwong KK, Jiang H, Kennedy WA, Ledden PJ, Brady TJ, Rosen BR, Tootell RB. 1995. Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. Proc Natl Acad Sci USA 92:8135-8139.

Maljkovic V, Nakayama K. 1994. Priming of pop-out: I. Role of features. Mem Cogn 22:657-672.

Maljkovic V, Nakayama K. 1996. Priming of pop-out: II. Role of position. Percept Psychophys 58:977-991.

Mesulam MM. 1999. Spatial attention and neglect: parietal, frontal and cingulate contributions to the mental representation and attentional

targeting of salient extrapersonal events. Philos Trans R Soc Lond B Biol Sci 354:1325-1346.

Naccache L, Dehaene S. 2001. The priming method: imaging unconscious repetition priming reveals an abstract representation of number in the parietal lobes. Cereb Cortex 11:966-974.

Nakayama K, Mackeben M. 1989. Sustained and transient components of visual attention. Vision Research 29:1631-1647.

Nakayama K, Joseph JS. 1998. Attention, pattern recognition and pop-out in visual search. In: Parasuraman R, editor. The attentive brain. Cambridge, MA: MIT Press. p 279-298.

Nakayama K, Maljkovic V, Kristjánsson Á. 2004. Short term memory for the rapid deployment of visual attention. In: Gazzaniga M, editor. The cognitive neurosciences. 3rd ed. Cambridge, MA: MIT Press. p 397-408.

Nakayama K, Silverman GH. 1986. Serial and parallel processing of visual feature conjunctions. Nature 320:264-265.

Nichols T, Brett M, Andersson J, Wager T, Poline JB. 2005. Valid conjunction inference with the minimum statistic. Neuroimage 25:653-660.

Nobre AC, Coull JT, Walsh V, Frith CD. 2003. Brain activations during visual search: contributions of search efficiency versus feature binding. Neuroimage 18:91-103.

Olivers CNS, Meeter M. 2006. On the dissociation between compound and present/absent tasks in visual search: intertrial priming is ambiguity-driven. Vis Cogn 13:1-28.

Paus T. 1996. Location and function of the human frontal eye-field: a selective review. Neuropsychologia 34:475-483.

Pollmann S, Weidner R, Muller HJ, von Cramon DY. 2000. A fronto-posterior network involved in visual dimension changes. J Cogn Neurosci 12:480-494.

Schacter DL, Buckner RL. 1998. Priming and the brain. Neuron 20:185-195.

Schacter DL, Dobbins IG, Schnyer DM. 2004. Specificity of priming: a cognitive neuroscience perspective. Nat Rev Neurosci 5:853-862.

Serences JT, Yantis S. 2006. Selective visual attention and perceptual coherence. Trends Cogn Sci 10:38-45.

Sigala N, Logothetis NK. 2002. Visual categorization shapes feature selectivity in the primate temporal cortex. Nature 415:318-320.

Simons JS, Koutstaal W, Prince S, Wagner AD, Schacter DL. 2003. Neural mechanisms of visual object priming: evidence for perceptual and semantic distinctions in fusiform cortex. Neuroimage 19:613-626.

Sternberg S. 1969. The discovery of processing stages: extensions of Donders' method. Acta Psychol 30:276-315.

Tanaka K, Saito H, Fukada Y, Moriya M. 1991. Coding visual images of objects in temporal cortex of the macaque monkey. J Neurophysiol 66:170-189.

Theeuwes J, Riemann B, Mortier K. 2006. Visual search for feature singletons: no top-down modulation, only intertrial priming. Vis Cogn 14:466-489.

Tong F, Nakayama K, Vaughan JT, Kanwisher N. 1998. Binocular rivalry and visual awareness in human extrastriate cortex. Neuron 21:753-759.

Treisman AM. 1988. Features and objects: the fourteenth Bartlett memorial lecture. Q J Exp Psychol A Hum Exp Psychol 40A:201-237.

Treisman AM, Gelade G. 1980. A feature integration theory of attention. Cognit Psychol 12:97-136.

Treisman AM, Gormican S. 1988. Feature analysis in early vision: evidence from search asymmetries. Psychol Rev 95:15-48.

Tsal Y, Lavie N. 1988. Attending to color and shape: the special role of location in selective visual processing. Percept Psychophys 44:15-21.

Tsal Y, Lavie N. 1993. Location dominance in attending to color and shape. J Exp Psychol Hum Percept Perform 19:131-139.

Turk-Browne NB, Yi DJ, Chun MM. 2006. Linking implicit and explicit memory: common encoding factors and shared representations. Neuron 49:917-927.

Vuilleumier P, Armony JL, Driver J, Dolan RJ. 2003. Distinct spatial frequency sensitivities for processing faces and emotional expressions. Nat Neurosci 6:624-631.

Vuilleumier P, Henson RN, Driver J, Dolan RJ. 2002. Multiple levels of visual object constancy revealed by event-related fMRI of repetition priming. Nat Neurosci 5:491-499.

Vuilleumier P, Schwartz S, Duhoux S, Dolan RJ, Driver J. 2005. Selective attention modulates neural substrates of repetition priming and "implicit" visual memory: suppressions and enhancements revealed by fMRI. J Cogn Neurosci 17:1245-1260.

Wade AR, Brewer AA, Rieger JW, Wandell BA. 2002. Functional measurements of human ventral occipital cortex: retinotopy and colour. Philos Trans R Soc Lond B Biol Sci 357:963-973.

Wagner AD, Koutstaal W, Maril A, Schacter DL, Buckner RL. 2000. Task-specific repetition priming in left inferior prefrontal cortex. Cereb Cortex 10:1176-1184.

Walsh V, le Mare C, Blaimire A, Cowey A. 2000. Normal discrimination performance is accompanied by priming deficits in monkeys with V4 or TEO lesions. Neuroreport 11:1459-1462.

Wang D, Kristjánsson Á, Nakayama K. 2005. Efficient visual search without top-down or bottom-up guidance. Percept Psychophys 67:239-253.

Wig GS, Grafton ST, Demos KE, Kelley WM. 2005. Reductions in neural activity underlie behavioral components of repetition priming. Nat Neurosci 8:1228-1233.

Wiggs CL, Martin A. 1998. Properties and mechanisms of perceptual priming. Curr Opin Neurobiol 8:227-233.

Winston JS, Henson RN, Fine-Goulden MR, Dolan RJ. 2004. fMRI-adaptation reveals dissociable neural representations of identity and expression in face perception. J Neurophysiol 92:1830-1839.

Yantis S, Jonides J. 1990. Abrupt visual onsets and selective attention: voluntary versus automatic allocation. J Exp Psychol Hum Percept Perform 16:121-134.

Yantis S, Serences JT. 2003. Cortical mechanisms of space-based and object-based attentional control. Curr Opin Neurobiol 13:187-193.