

Neural Correlates of Attentional Capture in Visual Search

Jan de Fockert¹, Geraint Rees², Chris Frith², and Nilli Lavie²

Abstract

■ Much behavioral research has shown that the presence of a unique singleton distractor during a task of visual search will typically capture attention and thus disrupt target search. Here we examined the neural correlates of such attentional capture using functional magnetic resonance imaging in human subjects during performance of a visual search task. The presence (vs. absence) of a salient yet irrelevant color singleton distractor was associated with activity in the superior

parietal cortex and frontal cortex. These findings imply that the singleton distractor induced spatial shifts of attention despite its irrelevance, as predicted from an AC account. Moreover, behavioral interference by singleton distractors was strongly and negatively correlated with frontal activity. These findings provide direct evidence that the frontal cortex is involved in control of interference from irrelevant but attention-capturing distractors. ■

INTRODUCTION

Many studies have demonstrated that attention can be easily directed toward a subset of stimuli that are defined as goal relevant, as long as these stimuli are different from goal-irrelevant stimuli on the basis of a simple visual feature. For example, subjects can be very efficient in searching for targets with a curved feature among angular distractors (see Duncan & Humphreys, 1989; Treisman, 1988, for review).

However, although most of the distractor objects that carry an irrelevant feature (e.g., all angular stimuli in the example of focusing on targets with curved features) can be successfully ignored, an irrelevant distractor with a unique feature that makes it a singleton in the visual field (e.g., an irrelevant red distractor presented in an array of green objects) will typically distract attention from focusing entirely on relevant stimuli (see Yantis, 1996, 2000, for review). Such interruption of goal-driven attention can be found even when the distractor object forms a singleton on a dimension that is never relevant to the task (e.g., a color singleton will interfere with search on the basis of other features such as the shape search task described above), suggesting that the singleton distractor has captured attention, rather than that attention was voluntarily allocated to distractor processing (e.g., Theeuwes, 1996).

This phenomenon of attentional capture (AC) has stimulated much behavioral research (see Egeth & Yantis, 1997; Theeuwes, 1996; Yantis, 1996, 2000, for reviews). In the present article, we examine the neural correlates of AC. As behavioral research has demon-

strated that a salient, yet irrelevant, singleton distractor will nevertheless capture attention, we anticipated that neural systems known to be involved in the allocation of attention to goal-relevant stimuli may also be associated with AC by goal-irrelevant singleton distractors. Specifically, activity in the parietal cortex has been previously associated with the allocation of attention in a variety of tasks, including visual search (Corbetta, Shulman, Miezin, & Petersen, 1995) and spatial cueing (e.g., Hopfinger, Buonocore, & Mangun, 2000; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Rosen et al., 1999; Nobre et al., 1997; Corbetta, Miezin, Shulman, & Petersen, 1993; for reviews, see Corbetta & Shulman, 2002; Wojciulik & Kanwisher, 1999). We therefore expected that capture of attention by an irrelevant singleton distractor during visual search will also be associated with parietal activity. Moreover, capture of attention by a goal-irrelevant distractor should also impose a greater demand on top-down control mechanisms typically associated with the frontal lobe (for review, see Duncan & Owen, 2000; Miller, 2000), as these are needed in order to resolve the competition between the target and the irrelevant singleton distractor that has captured attention. We thus expected that AC by an irrelevant singleton will also implicate activity in frontal cortices associated with such top-down control.

Finally, as AC by singleton distractors produces clear interference effects with visual search performance, we sought to examine the relationship between the neural activity related to AC by such distractors and the extent to which they produce behavioral interference on visual search. Previous imaging studies have successfully identified neural correlates of attention and top-down control, but have not been able to specify the implications

¹Goldsmiths College, ²University College London

Figure 1. Example stimuli of each of the four experimental trial types. Participants were requested to make a speeded key-press response to the orientation of the line segment in the target circle. On color singleton present trials, one of the display items (the circle on target color singleton trials, and one of the diamonds on distractor color singleton trials) was presented in red. On color singleton absent trials, all display items were presented in green, and one of them (the circle on target singleton trials, and one of the diamonds on distractor singleton trials) was slightly reduced in size.

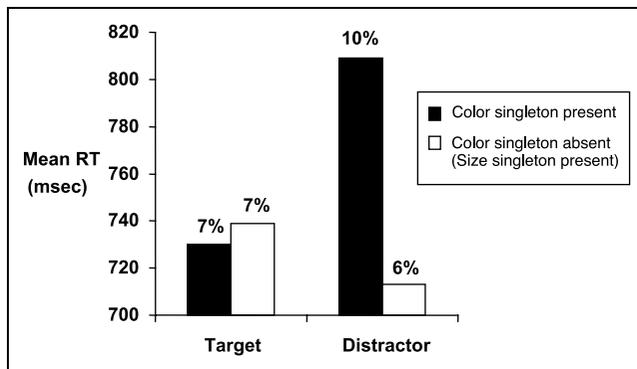
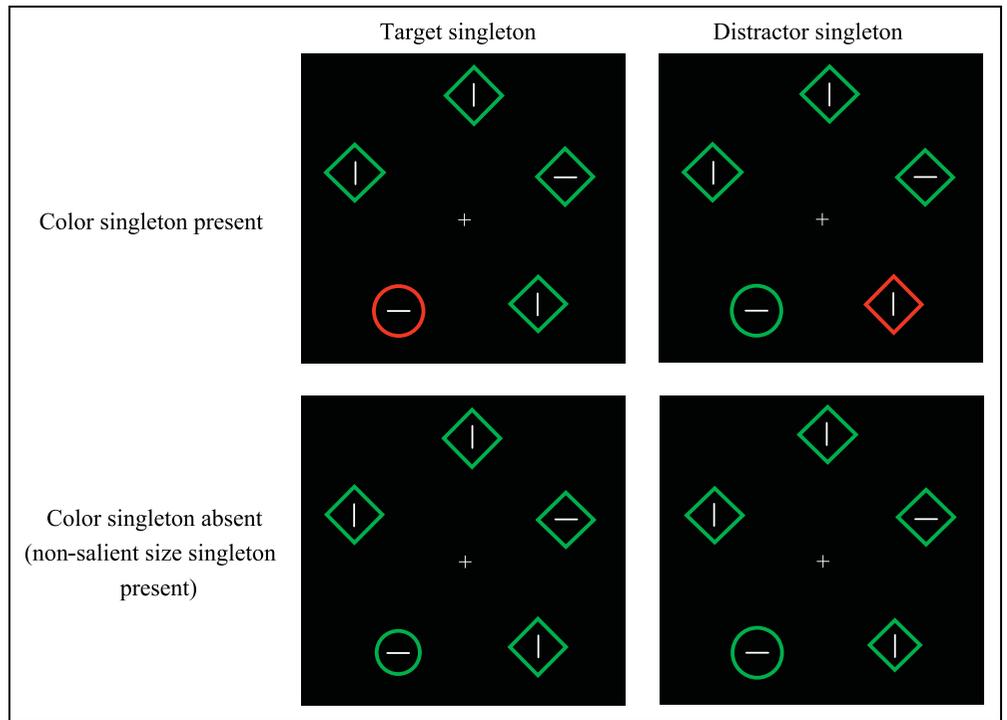
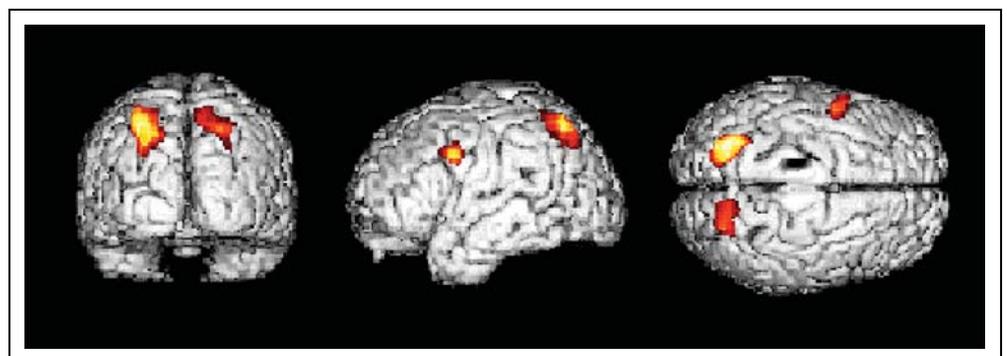


Figure 2. Behavioral performance during scanning. Bars represent mean RT and % error for targets and distractors, with a color singleton present or absent.

of this neural activity for the extent to which behavioral interference is found when attention is captured by goal-irrelevant distractors.

We measured brain activity using functional magnetic resonance imaging (fMRI) in humans during performance in a task of visual search for a unique shape target (circle) among distractors of a different shape (diamonds; see Figure 1). We assessed performance of this search for shape in the presence versus absence of a salient, yet irrelevant, color singleton distractor that is known to produce AC (Theeuwes, 1991, 1992). We also assessed performance of the shape search task in the presence (vs. absence) of a color singleton on the shape target. Thus, the effects of the presence (vs. absence) of a color singleton distractor could be contrasted with the effects of the presence (vs. absence) of a color singleton target.

Figure 3. Activity related to the presence (vs. absence) of a color singleton distractor. Shown are posterior (left panel), left lateral (middle panel), and dorsal (right panel) views of a T1-weighted anatomical template image in Talairach space (Talairach & Tournoux, 1988). For display purposes, activity is shown at $p < .001$, uncorrected, with an extent threshold of 200 voxels.



RESULTS

Behavioral Responses

Behavioral data were collected during the scanning sessions (see Figure 2). An ANOVA comparing target reaction times (RTs) showed that the presence (vs. absence) of a color singleton distractor produced significant interference [96 msec; $F(1,9) = 38.4, p < .001$]. This result is consistent with previous behavioral findings in similar visual search studies of AC (e.g., Theeuwes, 1991, 1992, 1994). When the shape singleton target was also presented in a unique color, there was a small and nonsignificant trend for facilitation (9 msec; $F < 1$).¹ Thus, participants were clearly able to select the target on the basis of its unique shape, gaining very little from presentation of the target in a unique color as well. Note that although salient singleton distractors have been consistently found to produce interference on performance of the feature search task used here, the effects of adding another singleton feature (e.g., a unique color) to the feature target (e.g., a unique shape) in this task have not been previously examined (facilitation effects have been previously found when a singleton feature has been added to more complex targets such as letters; see Yantis, 2000, for a review). For the present purpose, the finding that the RT interference was specific to the presence of a color singleton distractor [as also shown by the highly significant interaction, $F(1,9) = 21.8, p < .001$, between color singleton presence (present, absent) and singleton stimulus (target, distractor)] indicates that this interference was not simply due to the mere presence of an odd color in the array, but was associated with the presentation of a distractor, rather than a target, in a singleton color. Thus, despite efficient selection of the shape target, presentation of a color singleton distractor produced robust interference.

Imaging Data

Brain activity time-locked to the individual trials was determined using an event-related analysis (see Methods) of the fMRI data. Figure 3 shows areas of activity associated with the presence (vs. absence) of color singleton distractors (see also Table 1 for stereotactic locations of the peak voxels in these areas of activation). As we anticipated, the presence (vs. absence) of a color singleton distractor was associated with bilateral activation of the superior parietal lobe (Brodmann's area [BA] 7), an area previously associated with voluntary allocation of attention in a variety of tasks (e.g., Kastner et al., 1999; Corbetta et al., 1993, 1995), but with involuntary allocation of attention (as in AC) only in spatial cueing tasks so far (Rosen et al. 1999; Nobre et al., 1997; Corbetta et al., 1993). Moreover, as can be seen in Figure 3, color singleton presence (vs. absence) was

also associated with activity in an area in the left lateral precentral gyrus (BA 6) of the frontal cortex (anterior, inferior, and lateral to the frontal eye fields; Paus, 1996). The finding that the presence of irrelevant singletons is associated with frontal activity is in line with our suggestion that target selection in the presence of a competing, attention-capturing singleton distractor would place a greater demand on top-down frontal control. No voxels showed significant activity (at $p < .05$ corrected for multiple comparisons) related to the presence (vs. absence) of a singleton color when it coincided with the shape target. This result is consistent with the lack of a significant behavioral effect in these conditions and clearly rules out the mere presence of a unique color in the array as a possible cause for the activity related to the presentation of a distractor in a unique color. Moreover, the parietal and frontal cortices also showed significant interactions, such that activity in the presence (vs. absence) of a color singleton distractor was greater than activity in the presence (vs. absence) of a color singleton target (left superior parietal cortex, $t = 4.2, p < .01$; right superior parietal cortex, $t = 3.73, p < .01$; left frontal cortex, $t = 4.4, p < .01$, using small volume correction). This result further confirmed that activity in the parietal and frontal cortices related to the presence (vs. absence) of a color singleton distractor could not be attributed to the mere presence of an odd color in the array.

To ensure that the interaction between singleton presence and singleton stimulus was consistent across participants, we extracted the neural signal (blood oxygenation level dependent [BOLD] signal, expressed as percent departure from a global mean of 100) for each of the three significant areas of activation in the comparison between presence and absence of a color singleton distractor (bilateral superior parietal cortex and left frontal area BA 6) for each subject, and entered these into an ANOVA with participants as the random factor. For all three areas of activity, there was a highly significant interaction, left superior parietal cortex, $F(1,9) = 21.84, p < .001$; right superior parietal cortex, $F(1,9) = 18.85, p < .01$; left frontal cortex, $F(1,9) = 19.68, p < .01$, between the presence of a color singleton (vs. absence) and the singleton stimulus (target vs. distractor). As can be seen in Figure 4, activity in these areas was greater in the color singleton distractor present conditions than in the color singleton distractor absent conditions, left superior parietal cortex, $t(9) = 3.6, p < .01$; right superior parietal cortex, $t(9) = 2.9, p < .02$; left frontal cortex, $t(9) = 2.8, p < .025$, all two-tailed, whereas there was no such difference for the presence (vs. absence) of a color singleton target (left superior parietal cortex, $t = .07, p = .95$; right superior parietal cortex, $t = .65, p = .53$; left frontal cortex, $t = 1.9, p = .092$, all two-tailed). These results confirm that the activity in the parietal and frontal cortices, which is specifically related to the presence of color singleton distractors rather than the

Table 1. Regions of Activation Related to the Presence (vs. Absence) of Color Singleton Distractors

	Talairach Coordinates			<i>t</i> Value	<i>p</i> Value (Corrected)
	<i>x</i>	<i>y</i>	<i>z</i>		
<i>Left</i>					
Superior parietal lobe (BA 7)	-24	-66	50	5.85	.001
Lateral precentral gyrus (BA 6)	-46	4	36	4.79	.018
<i>Right</i>					
Superior parietal lobe (BA 7)	26	-68	50	4.67	.030

Shown are voxels representing the peak activity in areas in which activity was greater than $p < .05$, corrected for multiple comparisons.

presence of color singletons per se, was consistent across participants.

These analyses included all (both correct and incorrect) trials. The activity revealed, however, could not have been due to processes occurring only on error trials for two reasons. First, the same contrast of activity in distractor present versus absent conditions, excluding trials on which an incorrect response was made, produced the same pattern of activity in the parietal and frontal cortices (as when error trials are included). Second, the areas revealed by a contrast of activity in error trials versus correct trials did not include any of the areas found in the comparison between distractor present and absent conditions. Thus, activity on error trials could not explain the results due to the presence (vs. absence) of the color singleton distractor.

In order to investigate the relationship between behavioral interference by singleton distractors and the accompanying pattern of neural activity, we performed

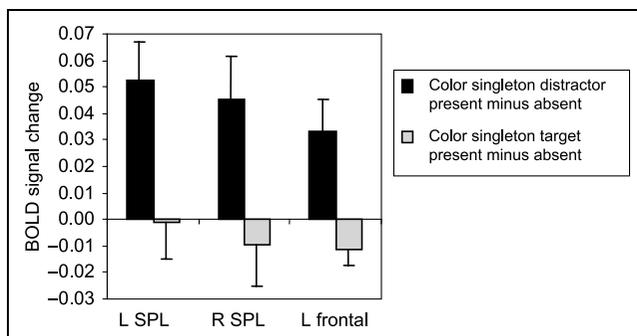


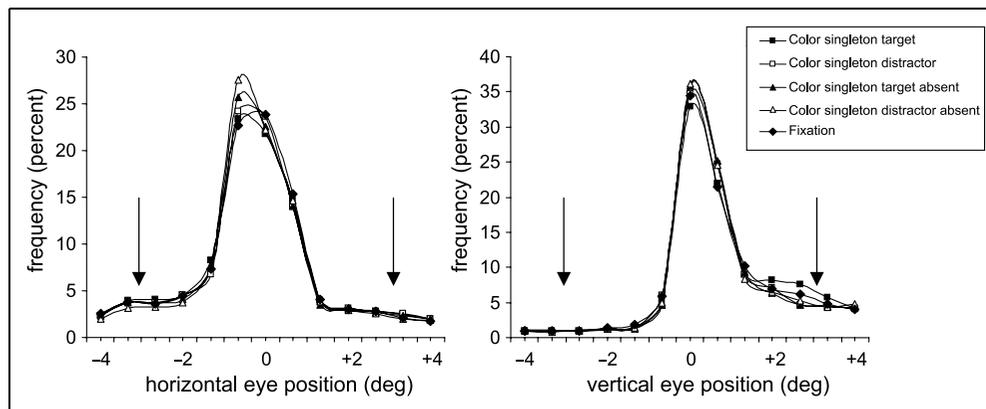
Figure 4. Activity associated with the interaction between color singleton presence (present, absent) and singleton stimulus (distractor, target). Bars represent BOLD signal change, averaged across voxels in each cluster and across participants. Shown is the difference in mean activity between color singleton present versus absent, plotted separately for left superior parietal cortex (L SPL), right superior parietal cortex (R SPL), and left lateral precentral gyrus, and for distractor and target singletons. Error bars represent interparticipant standard error.

a correlational analysis between the RT data and the fMRI signal. First, to control for between-subject differences in the overall fMRI signal and in the overall RT, we derived an index of interference by representing the interference effect (color distractor present minus color distractor absent) per participant as a proportion of their average fMRI signal and average RT in the distractor color singleton present and absent trials. We then computed Pearson's correlation coefficient between RTs and the fMRI signal in each of the three areas of significant activity. No significant correlation was found in the two clusters of activation in the bilateral superior parietal cortex ($R = .247, p = .49$ and $R = -.103, p = .78$ for the left and right superior parietal cortex, respectively). However, there was a significant negative correlation between activity in the left frontal cortex and the magnitude of the interference effect in RT, $R = -.712, p = .021$ (two-tailed). The sign of this correlation is important, as it indicates that greater activity in the frontal cortex (when a color distractor was present vs. absent) is associated with smaller interference effects by the irrelevant distractors. Further analysis confirmed that greater interference effects on RTs were not significantly correlated with greater overall variance in RTs (assessed by the magnitude of standard deviation from mean RT per subject, $R = .46, p = .18$). Thus, the negative correlation between the interference effects on RT and activity in the frontal cortex cannot be attributed to greater RT variability in subjects with greater interference effects (compared to those with smaller behavioral interference).

Eye Position Data

Subjects were requested to maintain fixation at the center of the display. During scanning, eye position was monitored continually to ensure that participants indeed succeeded to maintain fixation throughout the experimental sessions. Figure 5 presents the frequency of the vertical and horizontal eye positions across all subjects, plotted as a function of trial type. Eye position

Figure 5. Frequency plot of vertical and horizontal eye position. Data are shown for each trial type, averaged across subjects. Arrows indicate eccentricity of the visual array. In both the vertical and the horizontal eye position data, there was no difference between trial types, both in terms of individual subjects' mean eye position, and their standard deviations (all $F < 1$).



was consistently maintained within two degrees of fixation, less than the eccentricity of the search array (which subtended 3.1° from fixation to the center of each display item). Moreover, there were no significant differences between any of the conditions (including fixation, as well as the presence vs. absence of a color singleton distractor), both in terms of individual subjects' mean eye position, and their standard deviations (all $F < 1$), in either vertical or horizontal eye position. Thus, none of the activations resulting from the comparisons of the experimental conditions could be explained in terms of eye movements (or, conversely, inhibition of eye movements), as such accounts would predict a change in the mean or the variance (or both) of the eye positions between the experimental conditions.

DISCUSSION

The present results show that the neural correlates of AC by an irrelevant color singleton in visual search are the bilateral superior parietal cortex and left lateral precentral gyrus in the frontal lobe. Moreover, our results also show a strong negative correlation between the strength of the neural signal in the frontal cortex and the magnitude of singleton distractor interference effects on behavior. These findings are in line with our expectation that an irrelevant singleton will capture attention and thus compete with the goal-relevant target for selection, as we discuss below.

The Role of the Superior Parietal Cortex in AC

Activity in the superior parietal cortex has been typically associated with spatial shifts of attention (see Corbetta & Shulman, 2002, for a review, but see Hopfinger et al., 2000, for an exception, emphasizing the involvement of inferior parietal cortex in spatial attention shifts). The finding that superior parietal cortex activity is associated with the presence of an irrelevant singleton distractor in visual search suggests that spatial attention was allocated to the singleton distractor, consistent with an AC ac-

count of the behavioral effects. Specifically, many previous behavioral studies have shown that capture of attention by an irrelevant singleton involves spatial shifts of attention to the singleton position (e.g., Yantis & Jonides, 1990; see Yantis, 2000, for a review).²

More recently, Theeuwes, Kramer, Hahn, and Irwin (1998) have found that AC by a singleton distractor not only involves covert shifts of attention, but can also involve triggering an eye movement to the location of the singleton distractor. The superior parietal cortex has been associated with both covert shifts of attention (that do not involve eye movements) and overt shifts of attention (that do involve eye movements; Corbetta, 1998; Corbetta et al., 1998). In the present study, we focused on the potential effects of singleton distractors on covert attention, and therefore requested subjects to maintain fixation at the center of the display, while monitoring their eye position during scanning. The eye position data confirmed that the presence (vs. absence) of a color singleton distractor did not result in any change in the number or variance of eye movements. Activity related to the presence of a color singleton distractor in our study therefore cannot be attributed to eye movements. Instead, it suggests that such distractors triggered involuntary covert shifts of spatial attention.

It is perhaps worth noting that although serial spatial shifts of attention may not be required for the search process in this feature-search task (Treisman, 1988), shifts of focused attention to the target position are required for the orientation discrimination aspect of this task (in order to discriminate the orientation of the small line [0.5° of visual angle] within the target shape, among the competing orientations in the nontarget shapes). Thus, in the absence of a singleton distractor, although the target will initially pop out, focused attention will be shifted to it in order to perform the orientation discrimination task. When the singleton distractor is present, however, it will pop out more readily than the target (due to its greater salience; see Theeuwes, 1992), and thus may be wrongly selected for a spatial shift of attention. Thus, the presence of a singleton distractor should involve an extra shift of spatial attention (as

attention has to be shifted once more from the distractor to the target).

Finally, by contrast with the strong negative correlation between the signal in the frontal cortex and the magnitude of behavioral interference, there was no significant correlation between activity in the superior parietal cortex and behavioral interference. This contrast between the superior parietal cortex and frontal cortex with respect to correlations with distractor interference may indicate that these structures serve different functions in AC. The activity in the superior parietal cortex may reflect shifts of attention towards the irrelevant distractor that occur in a bottom-up, stimulus-driven manner due to the distractor being more visually salient than the target (as in the case of the color singleton here; see Theeuwes, 1996). As such, attention may always be captured by the more salient distractor (with very little variation in the extent of attentional shifts and the strength of the associated signal in the superior parietal cortex, thus precluding any correlation with behavioral interference effects). The magnitude of the interference effects on behavior may in turn be determined by the extent to which the frontal cortex exerts top-down control in order to resolve the competition between the target and the irrelevant distractor (that has nevertheless captured spatial attention) as we describe below.

The Role of the Frontal Cortex in AC

AC by a goal-irrelevant distractor should lead to a competition for selection (for further processing and action) between the irrelevant distractor and the relevant target. Top-down control functions that are known to be mediated by the frontal cortex are needed to resolve such competition. Indeed, the activity we found in the left lateral precentral gyrus of the frontal lobe has been previously associated with competition induced by stimuli that are incongruent (vs. neutral or congruent) with the current response in Stroop-like tasks (e.g., color-word Stroop, counting Stroop, flanker task; Hazeltine, Bunge, Scanlon, & Gabrieli, 2003; Schumacher & D'Esposito, 2002; Ruff, Woodward, Laurens, & Liddle, 2001; Zysset, Müller, Lohmann, & Von Cramon, 2001; Bush et al., 1998). Stroop-like studies typically also implicate the anterior cingulate and the prefrontal cortex in congruency effects (see Bush, Luu, & Posner, 2000, for a review). The partial overlap between the current activity and the pattern of activity in Stroop-like studies, however, may not be surprising given that the competition between target and singleton distractor in the AC paradigm does not depend on manipulations of response congruency between the two. Rather, in the typical visual search paradigm of AC, the distractor stimulus is not directly associated with any response.³

Thus, whereas Stroop-like tasks mainly involve competition between incongruent responses, the competition between the color singleton distractor and target in

our task may have occurred at a different level, for example, between the distractor and target features (e.g., conflicting locations, colors). Alternatively, each of the target and singleton distractor objects as a whole may compete for selection for action, as would be stipulated on a framework of competitive interactions (Desimone & Duncan, 1995). Indeed, activity in BA 6 has often been implicated in attentional selection for action, such as when response selection is contingent upon a visual or auditory cue, by contrast with a fixed sequence of responses (e.g., Van Oostende, Van Hecke, Snaert, Nuttin, & Marchal, 1997; Deiber et al., 1991).

Furthermore, our finding of a substantial negative correlation between the magnitude of the neural signal in the left lateral frontal cortex and the level of interference produced by the irrelevant singleton distractors, so that greater activity in the left lateral frontal cortex is associated with reduced interference from irrelevant distractors, strongly suggests a role for this area in control of interference from irrelevant distractors.

This finding supports previous suggestions that the frontal cortex plays an important role in control of attention. Such suggestions were made on the basis of various methods of investigation. Neuropsychological studies (e.g., Shallice & Burgess, 1991) have found that patients with damage to the frontal lobes show impairments in maintaining focused attention. However, such patients show a large repertoire of behavioral deficits (e.g., in memory and action, in addition to tasks of focused attention), and lesions typically cover a wide area of the frontal cortex. It is thus hard to infer a specific role for particular regions of the frontal cortex in controlling for distractor interference from the variety of symptoms following such extensive lesions. In contrast, our study suggests a specific role for a highly localized region of the frontal cortex in preventing interference from irrelevant distractors.

Single-unit electrophysiology (e.g., Miller, 2000) has been able to identify a specific role for neurons in particular regions of the frontal cortex during tasks of selective attention in nonhuman primates. Neuroimaging research (e.g., Miller & Cohen, 2001) has also implicated certain regions of the frontal lobes in a range of cognitive control functions. However, none of these studies has specifically related activity in the human frontal cortex to the extent to which irrelevant distractors produce interference effects on behavior. Thus, our findings provide the first direct evidence that activity in the frontal cortex is strongly related to control of interference from salient but irrelevant distractors.

There are at least two possible accounts of how the frontal cortex may exert top-down control of visual processing in accordance with goal relevance, so that interference from irrelevant distractors is minimized. It has been recently suggested that top-down control of selective attention by the frontal cortex involves active maintenance of priorities between goal-relevant and

goal-irrelevant stimuli throughout task performance (De Fockert, Rees, Frith, & Lavie, 2001; Lavie, 2000). A weaker signal in frontal areas that serve to actively maintain such priorities should lead to greater interference from irrelevant distractors. Indeed, De Fockert et al. (2001) found a significant increase in distractor interference effects and in distractor-related neural responses when such frontal control was unavailable for visual selective attention (by loading working memory during performance of the selective attention task). Importantly, the frontal areas involved in such control in De Fockert et al.'s (2001) study included the frontal area implicated in control against singleton distractor interference in the present study.

Alternatively, top-down control by the frontal cortex may serve to directly inhibit the distractor stimuli or their responses. As mentioned above, the present area of frontal activity has previously also been associated with response competition effects in Stroop-like studies, and in attentional selection of responses (which may well involve inhibition of the unselected response or object). Although the present task was not designed to test these two specific alternatives, our results clearly demonstrate the involvement of the frontal cortex in control of interference from an irrelevant distractor. Finding the specific mechanisms by which such control is obtained is an important area for further investigation.

METHODS

Subjects

Ten young adults (2 men; mean age, 22.4 years; range, 19–32 years) with normal vision and normal color vision gave informed consent and participated in the study. The study was approved by the ethics committee of the National Hospital for Neurology and Neurosurgery.

Stimuli

The visual search displays consisted of five shapes that were equally spaced in a circular arrangement with a radius of 3.1° from a central fixation point (+) to the center of each shape. On each trial, four of the shapes were nontarget diamonds (size 1.5° diagonally). The target shape was always a circle (diameter 1.5°). In the center of each shape was a line segment (length 0.5°), randomly chosen to have either a horizontal or a vertical orientation. These line segments were always presented in white and the stimuli were presented on a black background.

To produce an orthogonal design (required for examining the interaction effect) we assigned color singleton absent trials to a distractor condition or a target condition by presenting either one of the distractors or the target with a nonsalient size singleton, to produce color singleton distractor absent or color singleton target

absent conditions, respectively. Thus, on half of the experimental trials, one of the distractors was presented with a singleton feature (25% of the trials in red color, 25% with a reduced size subtending 1.2° diagonally). On the other half of the trials, the target was presented with an additional singleton (25% of the trials in red color, 25% with a reduced size subtending 1.2° in diameter). In a behavioral pilot experiment, we established that these size singleton distractors indeed do not produce any interference effects on RTs or errors. Trials were randomly intermixed within experimental sessions to prevent observers from adopting different task strategies based on whether color singletons coincided with targets or distractors.

Procedure

Stimuli were projected onto a screen approximately 300 mm from the participant's eyes and viewed by a mirror mounted on the head coil. Each experimental trial consisted of presentation of the visual search display for 500 msec, followed by a 1600-msec response interval. Participants were required to make a speeded response to the orientation (horizontal or vertical) of the line segment in the target circle by pressing one of two response keys on a keypad they held in their right hand. One fifth of all trials were null events, on which only the fixation point was presented for the duration of a trial. Each participant completed two blocks of 240 trials, chosen at random from the five trial categories, while being scanned. Prior to the scanning sessions, participants completed a practice block consisting of 20 trials.

Eye Position Monitoring

During scanning, eye position was continually sampled at 60 Hz using long-range infrared video-oculography (ASL 504LRO Eye Tracking System, Massachusetts). Eye position data from seven runs (out of the total of 20) was discarded due to problems with data logging or data conversion. Horizontal and vertical eye position from the remaining 13 runs were determined for each trial type separately and combined to produce frequency histograms (Figure 5). Data were collapsed in bins of 0.25° of visual angle.

fMRI Imaging Parameters

A 2T Siemens VISION system was used to acquire both T1 anatomical volume images and T2*-weighted echoplanar (EPI) images with BOLD contrast. Each echoplanar image comprised thirty-two 2.4-mm axial slices taken every 3.6 mm, positioned to cover the frontal, parietal, and posterior temporal cortex. Data were acquired during two runs, consisting of 216 volumes each, of which the first six volumes per run were discarded to allow for T1 equilibration effects. Volumes were ac-

quired continuously with an effective repetition time (TR) of 2.4 sec/volume.

fMRI Preprocessing and Analysis

Statistical parametric mapping (SPM99, Wellcome Department of Imaging Neuroscience, University College London) was used for temporal and spatial data preprocessing and data analysis. Data were time-corrected for slice acquisition times (using the middle slice as a reference). All volumes were then realigned to the first volume, and normalized to a standard EPI template volume (based on the MNI reference brain, Cocosco, Kollokian, Kwan, & Evans, 1997) in the space of Talairach and Tournoux (1988). These EPI volumes were then smoothed with an isotropic 10-mm FWHM Gaussian kernel.

The fMRI data were initially analyzed using an event-related design, using a fixed effect model. Voxels that were activated during the experimental conditions were identified with a statistical model containing regressors that represented the transient responses produced by the individual trials in each condition. The event-related changes in evoked activity were modeled by convolving an empirically derived hemodynamic impulse response function with trains of unitary events that were aligned on the trial onsets. Each component of the model served as a regressor in a multiple regression analysis. In addition, high-pass filtering removed participant-specific low-frequency drifts in signal, and global changes in activity were removed by proportional scaling. Linear contrasts between the different regressors representing the experimental conditions allowed determination of activated areas by creating a spatially distributed map of the t statistic. All statistical results are based on a single-voxel t threshold of 3.10 (corresponding to $p < .001$, uncorrected for multiple comparisons). Resultant regions of activation were characterized in terms of their peak heights. In assessing statistical significance, we made a correction (based on the theory of random Gaussian fields) for multiple comparisons across the whole brain volume examined and report only regions of activation above a threshold corresponding to $p < .05$, corrected for the volume examined. For the interaction contrast, we used a small-volume correction with spheres of 10-mm radius around the peak voxels in the areas of significant activity related to the simple main effect (presence vs. absence of color singleton distractors).

For the ANOVA with subjects as the random factor, the BOLD signal (expressed as percent departure from a global mean of 100) was extracted for all voxels contained within the three clusters of significant activation (at $t > 4.54$, corresponding to $p < .05$, corrected for multiple comparisons) during interference by distractor singletons (bilateral superior parietal cortex and left lateral precentral gyrus). Next, for each participant, the BOLD signal was averaged across all voxels in each

separate cluster as a function of the experimental factors. These averages were entered into ANOVAs with color singleton presence (present, absent) and singleton stimulus (target, distractor) as within-subjects factors, and participants as the random factor.

Acknowledgments

This work was supported by a Medical Research Council grant (N. L.) and The Wellcome Trust (G. R., C. F.).

Reprint requests should be sent to Jan de Fockert, Department of Psychology, Goldsmiths College, New Cross, London SE14 6NW, UK, or via e-mail: j.de-fockert@gold.ac.uk.

The data reported in this experiment have been deposited in the fMRI Data Center (<http://www.fmridc.org>). The accession number is 2-2003-114FY.

Notes

1. As can be seen in Figure 2, the nonsalient size singleton produced a small (26 msec) but significant interference effect, $F(1,9) = 5.7, p = .04$, when it was presented as a target (vs. a distractor). As the size singleton was created by reducing the size of the outline circle or diamond, this interference may be due to some lateral masking effects of the closer contours of the outline and the small bar in it. Alternatively, it may be a result of the low probability (25%) of targets with a reduced size. This effect, however, does not bear on any of the important results regarding the effects of the presence of a color singleton distractor (because the interaction was largely driven by the difference [of 79 msec] between the two color singleton conditions, $F(1,9) = 22, p < .001$, for the difference).
2. Although it has been shown that attentional set can under some conditions eliminate spatial cueing effects (e.g., Folk, Remington, & Johnston, 1992), this has only been shown in tasks that are very different from the task used in the present study (e.g., the singleton is presented before the search array and thus does not directly compete with the target).
3. Congruency effects from the singleton have been found when letters were inserted within the shapes in Theeuwes's (1996) AC in visual search paradigm. However, the potential effects of orientation congruency for the bars typically presented within the shapes in Theeuwes's task (Figure 1) have not as yet been established.

REFERENCES

- Bush, G., Luu, P., & Posner, M. I. (2000). Cognitive and emotional influences in anterior cingulate cortex. *Trends in Cognitive Sciences*, 4, 215–222.
- Bush, G., Whalen, P. J., Rosen, B. R., Jenike, M. A., McInerney, S. C., & Rauch, S. L. (1998). The counting Stroop: An interference task specialized for functional neuroimaging—Validation study with functional MRI. *Human Brain Mapping*, 6, 270–282.
- Cocosco, C. A., Kollokian, V., Kwan, R. K.-S., & Evans, A. C. (1997). BrainWeb: Online interface to a 3D MRI simulated brain database. *Neuroimage*, 5 (Part 2/4), S425.
- Corbetta, M. (1998). Fronto-parietal cortical networks for directing attention and the eye to visual locations: Identical, independent, or overlapping neural functions? *Proceedings of the National Academy of Sciences, U.S.A.*, 95, 831–838.
- Corbetta, M., Akbudak, E., Conturo, T. E., Drury, H. A.,

- Linenweber, M., Ollinger, J. M., Petersen, S. E., Raichle, M. E., Van Essen, D. C., Snyder, A. Z., & Shulman, G. L. (1998). A common network of functional areas for attention and eye movements. *Neuron*, *21*, 761–773.
- Corbetta, M., Miezin, F. M., Shulman, G. L., & Petersen, S. E. (1993). A PET study of visuospatial attention. *Journal of Neuroscience*, *13*, 1202–1226.
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*, 201–215.
- Corbetta, M., Shulman, G. L., Miezin, F. M., & Petersen, S. E. (1995). Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. *Science*, *270*, 802–805.
- De Fockert, J. W., Rees, G., Frith, C. D., & Lavie, N. (2001). The role of working memory in visual selective attention. *Science*, *291*, 1803–1806.
- Deiber, M. P., Passingham, R. E., Colebatch, J. G., Friston, K. J., Nixon, P. D., & Frackowiak, R. S. (1991). Cortical areas and the selection of movement: A study with positron emission tomography. *Experimental Brain Research*, *84*, 393–402.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, *18*, 193–222.
- Duncan, J., & Humphreys, G. (1989). Visual search and stimulus similarity. *Psychological Review*, *96*, 433–458.
- Duncan, J., & Owen, A. M. (2000). Common regions of the human frontal lobe recruited by diverse cognitive demands. *Trends in Neurosciences*, *23*, 475–483.
- Egeth, H. E., & Yantis, S. (1997). Visual attention: Control, representation, and time course. *Annual Review of Psychology*, *48*, 269–297.
- Folk, C. L., Remington, R. W., & Johnston, J. C. (1992). Involuntary covert orienting is contingent on attentional control settings. *Journal of Experimental Psychology: Human Perception and Performance*, *18*, 1030–1044.
- Hazeltine, E., Bunge, S. A., Scanlon, M. D., & Gabrieli, J. D. E. (2003). Material-dependent and material-independent selection processes in the frontal and parietal lobes: An event-related fMRI investigation of response competition. *Neuropsychologia*, *41*, 1208–1217.
- Hopfinger, J. B., Buonocore, M. H., & Mangun, G. R. (2000). The neural mechanisms of top-down attentional control. *Nature Neuroscience*, *3*, 284–291.
- Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron*, *22*, 751–761.
- Lavie, N. (2000). Selective attention and cognitive control: Dissociating attentional functions through different types of load. In S. Monsell & J. Driver (Eds.), *Attention and performance XVIII*, (pp. 175–194). Cambridge: MIT Press.
- Miller, E. K. (2000). The prefrontal cortex and cognitive control. *Nature Reviews Neuroscience*, *1*, 59–65.
- Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience*, *24*, 167–202.
- Nobre, A. C., Sebestyen, G. N., Gitelman, D. R., Mesulam, M. M., Frackowiak, R. S. J., & Frith, C. D. (1997). Functional localization of the system for visuospatial attention using positron emission tomography. *Brain*, *120*, 515–533.
- Paus, T. (1996). Location and function of the human frontal eye-field: A selective review. *Neuropsychologia*, *34*, 475–483.
- Rosen, A. C., Rao, S. M., Caffarra, P., Scaglioni, A., Bobholz, J. A., Woodley, S. J., Hammel, T. A., Cunningham, J. M., Prieto, T. E., & Binder, J. R. (1999). Neural basis of endogenous and exogenous spatial orienting: A functional MRI study. *Journal of Cognitive Neuroscience*, *11*, 135–152.
- Ruff, C. C., Woodward, T. S., Laurens, K. R., & Liddle, P. F. (2001). The role of the anterior cingulate cortex in conflict processing: Evidence from reverse Stroop interference. *Neuroimage*, *14*, 1150–1158.
- Schumacher, E. H., & D'Esposito, M. (2002). Neural implementation of response selection in humans as revealed by localized effects of stimulus-response compatibility on brain activation. *Human Brain Mapping*, *17*, 193–201.
- Shallice, T., & Burgess, P. W. (1991). Higher-order cognitive impairments and frontal lobe lesions in man. In H. S. Levin, H. M. Eisenberg, & A. L. Benson (Eds.), *Frontal lobe function and injury*. Oxford: Oxford University Press.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. New York: Thieme Medical.
- Theeuwes, J. (1991). Cross-dimensional perceptual selectivity. *Perception and Psychophysics*, *50*, 184–193.
- Theeuwes, J. (1992). Perceptual selectivity for color and form. *Perception and Psychophysics*, *51*, 599–606.
- Theeuwes, J. (1994). Stimulus-driven capture and attentional set: Selective search for color and visual abrupt onsets. *Journal of Experimental Psychology: Human Perception and Performance*, *20*, 799–806.
- Theeuwes, J. (1996). Perceptual selectivity for color and form: On the nature of the interference effect. In A. Kramer, M. Coles, & G. Logan (Eds.), *Converging operations in the study of selective visual attention* (pp. 297–314). Washington, DC: American Psychological Association.
- Theeuwes, J., Kramer, A. F., Hahn, S., & Irwin, D. E. (1998). Our eyes do not always go where we want them to go: Capture of the eyes by new objects. *Psychological Science*, *9*, 379–385.
- Treisman, A. (1988). Features and objects: The Fourteenth Bartlett Memorial Lecture. *Quarterly Journal of Experimental Psychology A*, *40*, 201–237.
- Van Oostende, S., Van Hecke, P., Snaert, S., Nuttin, B., & Marchal, G. (1997) fMRI studies of the supplementary motor area and the premotor cortex. *Neuroimage*, *6*, 181–190.
- Wojciulik, E., & Kanwisher, N. (1999). The generality of parietal involvement in visual attention. *Neuron*, *23*, 747–764.
- Yantis, S. (1996) Attentional capture in vision. In A. Kramer, M. Coles, & G. Logan (Eds.), *Converging operations in the study of selective visual attention* (pp. 45–76). Washington, DC: American Psychological Association.
- Yantis, S. (2000) Control of visual attention. In S. Monsell & J. Driver (Eds.), *Control of cognitive processes: Attention and performance XVIII*. (pp. 71–208). Cambridge: MIT Press.
- Yantis, S., & Jonides, J. (1990) Abrupt visual onsets and selective attention: Voluntary versus automatic allocation. *Journal of Experimental Psychology: Human Perception and Performance*, *16*, 121–134.
- Zysset, S., Muller, K., Lohmann, G., & von Cramon, D. Y. (2001). Color–word matching Stroop task: Separating interference and response conflict. *Neuroimage*, *13*, 29–36.