Brain Structures Involved in Visual Search in the Presence and Absence of Color Singletons

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Abstract

■ It is still debated to what degree top–down and bottom–up driven attentional control processes are subserved by shared or by separate mechanisms. Interactions between these attentional control forms were investigated using a rapid event-related fMRI design, using an attentional search task. Following a prestimulus mask, target stimuli (consisting of a letter C or a mirror image of the C, enclosed in a diamond outline) were presented either at one unique location among three nontarget items (consisting of a random letter, enclosed in a circle outline; 50% probability), or at all four possible target locations (also 50% probability). On half the trials, irrelevant color singletons were presented, consisting of a color change of one of the four prestimulus masks, just prior to target appearance. Participants were required to search for a target letter inside the diamond and report its orientation. Results indicate that, in addition to a common network of parietal areas, medial frontal cortex is uniquely involved in top–down orienting, whereas bottom–up control is mainly subserved by a network of occipital and parietal areas. Additionally, we found that participants who were better able to suppress orienting to the color singleton showed middle frontal gyrus activation, and that the degree of top–down control correlated with insular activity. We conclude that, in addition to a common set of parietal areas, separate brain areas are involved in top–down and bottom–up driven attentional control, and that frontal areas play a role in the suppression of attentional capture by an irrelevant color singleton. ■

INTRODUCTION

From the overwhelming amount of information that reaches our senses at any moment, the human mind is capable of selecting and holding relevant information, and ignoring what is irrelevant. The selection process is accomplished through a mechanism that is known as attention. Many studies have demonstrated the existence of a fronto-parietal network of brain areas involved in attention (Grent-'T-Jong & Woldorff, 2007; Serences, Schwarzbach, Courtney, Golay, & Yantis, 2004; Woldorff et al., 2004; Liu, Slotnick, Serences, & Yantis, 2003; Hopfinger, Woldorff, Fletcher, & Mangun, 2001; LaBerge, 1995, 2001; Hopfinger, Buonocore, & Mangun, 2000; Brunia, 1999) that selectively modulates the sensitivity of neurons in perceptual brain areas, thereby favoring the processing of attended stimuli over unattended stimuli (Hillyard, Vogel, & Luck, 1998). The control network is believed to subserve the function of selecting and orienting attention to behaviorally relevant stimuli (Serences & Yantis, 2007; Woldorff et al., 2004; Yantis et al., 2002).

Attentional selection can be accomplished using one of two functionally different control mechanisms. Endogenous or top–down control refers to a voluntary mode of orienting that serves to keep attention directed at locations where behaviorally relevant stimuli are expected, regardless of the actual presence of stimuli (Posner, Snyder, & Davidson, 1980). Endogenous attention is said to be goal-directed when attentional priority is given to those events and objects that are in line with the current goals of the observer (Theeuwes, Atchley, & Kramer, 2000). In contrast, exogenous or bottom–up driven control refers to a presumably automatic mechanism in which salient stimuli capture attention (Theeuwes, 1991; Yantis & Jonides, 1984).

Behavioral studies investigating attention control typically utilize the well-known cueing paradigm developed by Posner (1980). In this paradigm, using a symbolic cue (typically an arrow), which predicts the location of the upcoming imperative stimulus, attention can be directed to a particular location in space in a top–down fashion. Likewise, attention can be shifted in a bottom–up driven fashion by using an abrupt onset cue that automatically triggers attention to move to the location of the cue. Studies using the cueing paradigm have shown that behavioral responses to stimuli presented at the cued location are typically faster and more accurate than those responses to stimuli presented at uncued locations (Posner, 1980). In this respect, however, a clear distinction exists between endogenous and exogenous forms of attentional orienting. When attention is under endogenous control, behavioral advantages can be found for prolonged periods.

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In contrast, when attention is exogenously pulled to a specific location, these behavioral advantages are only observed for a relatively short period (Posner, 1980). When the time between the exogenous cue and the imperative stimulus is short (i.e., around 50 msec), response times are typically shorter when the imperative stimulus is presented at the exogenous cue location, compared to when the imperative stimulus is presented at another location. This is referred to as attentional capture (Jonides & Irwin, 1981). When the interval between cue and imperative stimulus is longer, however, this initial facilitation is replaced by increased response times when the imperative stimulus is presented at the cue location, compared to when it is presented at other locations. This phenomenon is referred to as inhibition of return (Posner & Cohen, 1984), and it has been suggested that it serves a role in favoring novel items in visual scanning processes (e.g., Dorris, Klein, Everling, & Munoz, 2002; Fecteau, Bell, Dorris, & Munoz, 2005; Tipper, Weaver, & Watson, 1996; Klein & Kingstone, 1993).

Given the functional differences between top–down and bottom–up driven attentional control mechanisms, it is plausible to assume that different brain structures are responsible for specific control functions. Presumably, these specialized brain circuits operate in concert within a common network of fronto-parietal areas that subserve both top–down and bottom–up control. A considerable number of studies have reported that both top–down and bottom–up attentional control was subserved by the same network of brain areas (Peelen, Heslenfeld, & Theeuwes, 2004; Rosen et al., 1999; Kastner, De Weerd, Desimone, & Ungerleider, 1998; Mangun, Buonocore, Girelli, & Jha, 1998; Corbetta, Miezin, Shulman, & Petersen, 1993). Yet, another series of studies have reported considerable functional specialization of brain areas for top–down and bottom–up control of attention (Hahn, Ross, & Stein, 2006; Hopfinger & West, 2006; Grosbras, Laird, & Paus, 2005; Thomsen, Specht, Ersland, & Hugdahl, 2005; see also Corbetta & Shulman, 2002 for a review).

Although the cueing paradigm is an excellent tool to study the top–down and bottom–up driven processes of attention in isolation, its use in studying interactions between top–down and bottom–up driven processes is somewhat limited. One notable disadvantage of the cueing paradigm is that two different types of cues are used to modulate top–down versus bottom–up control of attention. Another drawback of the symbolic cueing paradigm lies in the different probabilities of valid versus invalid trials that are necessary to distinguish endogenous (top–down) from exogenous (bottom–up) orienting. According to the strict definition, attention is under top–down control when the symbolic cue has predictive value, whereas attention is considered to be under bottom–up control when the cueing effect is there even in the presence of a nonpredictive cue (Posner & Cohen, 1984). Adding to that, more recent work has found that cues that were heretofore considered endogenous may trigger—at least to a certain extent—an exogenous shift of attention (see, e.g., Ristic, Friesen, & Kingstone, 2002). Thus, studying the interactions between top–down and bottom–up driven control using a cueing task typically requires the combination of multiple cue types, making it hard to modulate these two forms of attention within one and the same framework.

A potentially better way to investigate the relation between top–down and bottom–up driven control is the attentional capture paradigm (Theeuwes, 1994). In this paradigm, participants search for a target location that is marked by a shape singleton, among many nontarget locations. The target locations, as well as the nontarget locations, are revealed by removing line elements from an initially uniform prestimulus mask (e.g., Figure 1), thereby preventing attentional capture by abrupt onsets in the display. Participants are therefore always required to exert strong top–down attentional control. The strength of this control can be manipulated by changing the number of nontarget items in the display and/or the similarity between target and distractor items. Bottom–up systems can be modulated independently by presenting a salient color singleton "distractor," at one of the nontarget locations that will capture attention. The degree of bottom–up capture can be manipulated by changing the saliency of the color singleton and by changing the interval between the appearance of the color singleton and the target stimulus. Some necessary physical differences exist between trial types (i.e., color/shape singletons). Brain responses to these pure physical difference are typically limited to striate and extrastriate areas (e.g., areas V1 and LOC for diamond shapes; Fang, Kersten, & Murray, 2008; and V1 and V4 for color signals; Wade, Augath, Logothetis, & Wandell, 2008), and are therefore unlikely to drive the attention effects of interest that we expected to find in frontal, parietal, and the remaining occipital areas. To summarize, the present design enabled us to independently manipulate top–down and bottom–up driven control within one and the same framework, whereas manipulating these processes independently using a cueing paradigm would have the disadvantage of requiring to separate frameworks.

So far, only a limited number of studies have attempted to use this paradigm to investigate brain activations linked to top–down and bottom–up control of visual attention, and in particular, the interactions between these two control processes (see Lavie & de Fockert, 2006; de Fockert, Rees, Frith, & Lavie, 2004 for notable exceptions).

The aim of the present study was to investigate the degree to which brain areas involved in top–down and bottom–up attentional processes show interacting activations. In particular, we extend the attentional capture paradigm by contrasting a search with a no-search condition. In the search condition, the relevant target stimulus was present at only one of four possible locations (50% probability), whereas in the no-search condition, the target stimulus was presented redundantly at all four possi-

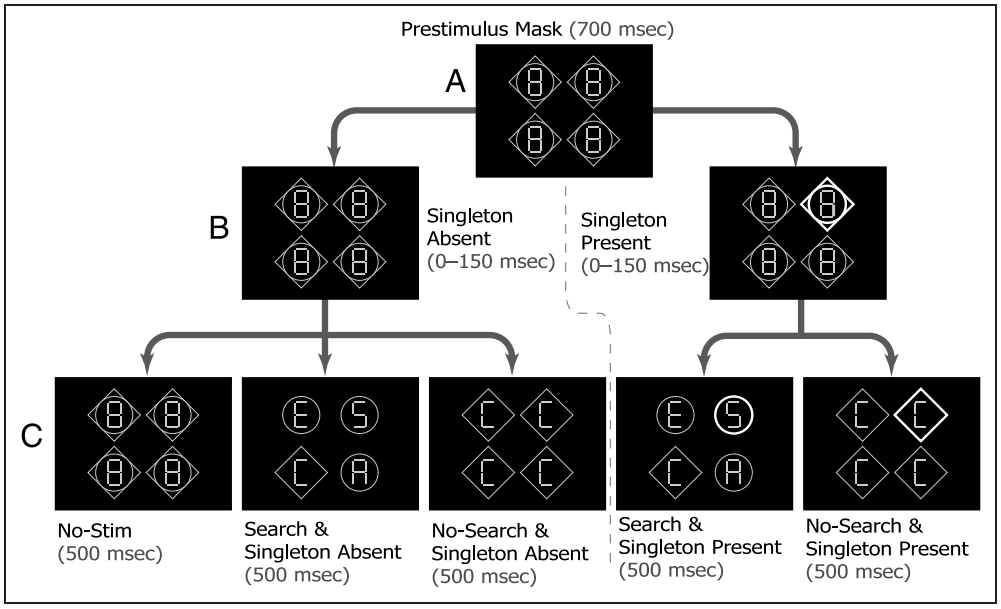

Figure 1. Outline of the present experiment. First, a prestimulus mask was presented for 700 msec. Second, in the singleton-present trials, one of the four display items changed color, whereas in the singleton-absent trials, the prestimulus mask remained unchanged. After a random delay of 0 to 150 msec (mean = 75 msec), the target display was presented. In the case of the search condition, this target display was composed of one target item (consisting of a regular or mirror image of the letter "C" enclosed by a diamond shape), among three distractors (consisting of a random letter enclosed by a circle). In the case of the no-search condition, this display consisted of four identical objects; each composed of the aforementioned letter "C," or mirror image thereof, enclosed by a diamond. Finally, no-stim trials consisted of an uninterrupted presentation of the prestimulus mask, and served to increase the randomness of the intertrial interval (see main text for details).

ble locations (also 50% probability). Contrasting these two conditions can therefore yield an estimate of brain activation related to the exertion of top–down attentional control. In addition, on half the trials, a color singleton was presented just prior to the onset of the target display. In the search condition, the color singleton did not coincide with the target location, and therefore, served as a distractor. In contrast, in the no-search condition, the color singleton could be present at any one of the four locations. Because the target stimulus could coincide with the target location in the no-search condition, the color singleton should actually serve the purpose of guiding attention to one of the locations. Thus, investigating differential brain activity elicited by color singletons in the search versus no-search conditions reveals the degree to which top–down and bottom–up driven processes interact.

Because the color singleton was presented in advance of the target stimulus, participants could not anticipate whether the color singleton would be irrelevant or not. Although participants were informed that the color singletons were irrelevant and should be ignored, the current design allowed for the possibility that (some) participants did not fully ignore the color singletons, as they would allow them to orient to a target location on half the trials. In order to investigate these possible differences, we conducted a detailed analysis of response times in the singleton present/search condition. More specifically, we computed response times for each relative position of the color singleton to the target stimulus, and related these effects to the behavioral patterns observed in the no-search conditions.

We expected that participants who were able to exert strong top–down attentional control would not only be faster overall but also be generally better able to suppress orienting toward the color singleton stimulus. In addition, we expected that participants who were able to exert strong top–down attentional control would show more activation in the fronto-parietal network than participants who were more easily captured by the color singleton.

METHODS

Participants

Sixteen volunteers (age = 18–32 years, mean = 22 years; 6 men) participated in the present study. The experiment was approved by the Research and Ethics Board of Queen's University, and adhered to the principles of the Declaration of Helsinki. All participants had normal or corrected-to-normal vision, were graduate or undergraduate students at Queen's University, and were recruited through local advertisements. No participant reported a history of mental or sustained physical illness. All participants gave informed consent prior to engaging in the experiment and received financial compensation.

Task and Stimuli

Participants were required to search for a shape singleton and make a speeded response regarding a letter that was presented inside this shape singleton (Figure 1). Each trial lasted 2 sec (coinciding with the repetition time of the

fMRI scanner), and consisted of the following sequence of events. At the start of the trial, a prestimulus display was presented in which four possible target locations were drawn (Figure 1A). At each of these four target locations, a figure was placed that consisted of a circle that was surrounded by a diamond. Inside the circle, a digital representation of the number 8 was drawn. After a delay of 700 msec, the outer lining (i.e., the circle/diamond combination) of one of the possible target locations could change color (either to red, green, or blue; Figure 1B). Then, after a random delay of 1 to 150 msec (in steps of 16.67 msec, coinciding with the refresh cycle of the projector), the search display was presented by removing parts of the outer lining, and line elements of the digital number 8. A random delay was chosen to allow the deconvolution of overlapping physiological signals for possible future event-related potential (ERP) usage of the same paradigm (cf. Woldorff, 1993). The target location was marked by a diamond outline (i.e., the circle was removed), whereas the other three locations were marked by a circle (i.e., the diamonds were removed). Coinciding with this change, the digital number 8 inside the target location was changed into a digital representation of the letter "C," or a mirror image of the letter "C" (Figure 1C). Likewise, the digital 8 at the other locations was changed into a digital representation of the letters "A," "E," "F," "G," "H," "I," "J," "L," "O," "P," "S," or "U." The target display was presented for 500 msec, after which it was again replaced by the mask (not shown in Figure 1). This mask remained on screen until the start of the next trial, which coincided with the start of the next scanning cycle (i.e., the total duration of one trial was exactly 2 sec). The participants' task was to indicate as fast as possible whether a regular "C" or a mirror-oriented "C" was presented inside the target location by pressing an fMRI-compatible response button with their right and left index fingers, respectively.

On half the trials, a color singleton was presented just prior to the presentation of the search display (e.g., see Figure 1B), whereas on the other half of the trials this was not the case. In addition, on half the trials, a unique target was presented among three distractors, whereas on the other half of the trials, the target stimulus was redundantly presented at all four locations. To summarize, four different trial types were present: (1) color singleton present, unique target location (25% probability); (2) color singleton present, redundant target location (25% probability); (3) color singleton absent, unique target location (25% probability); and (4) color singleton absent, redundant target location (also 25% probability).

A single block of trials contained 24 trials of each of the four types, totaling 96 trials. In addition, 48 "no-stim" trials of exactly the same duration as the regular trials were included in the design to relax the hemodynamic blood oxygen level dependent (BOLD) signal and to vary the onset of each trial according to a random exponential distribution that allowed us to estimate the BOLD response to each event of interest (Buckner et al., 1998; Burock, Buckner, Woldorff, Rosen, & Dale, 1998). All trial types were presented in a randomized first-order counterbalanced sequence, in which each trial type was preceded equally often by every trial type in the design.

Stimuli were masked at the end of the trial to increase stimulus difficulty. In addition, because we wanted to maximize the level of top–down control in the search condition, all target stimuli were defined by removing line elements from the initial prestimulus mask, thus ruling out any contributions from onset-related attentional capture in the search condition. To fully exclude the possibility that any stimulus onset-related activity affected the attentional control processes, we used a prestimulus mask that was identical to the poststimulus mask, leading to the start of each trial being indistinguishable from the end of the previous one. Because we anticipated that this procedure could result in a slightly higher level of a specific preparation in the singleton-present condition than in the singleton-absent condition, we carried out additional analyses of behavioral and fMRI data, as will be discussed below.

Procedure

Participants visited the lab on 2 days. On Day 1, they completed one block of practice trials and completed an fMRI prescreening procedure. Participants were considered qualified for inclusion when the prescreening revealed no indications that would prevent them from entering the MRI facility and when they successfully completed at least one block of trials with an accuracy of 80% correct or higher, and a mean response time below 600 msec. These criteria were established on the basis of pilot studies that showed that participants who reached this level of performance during the training session would perform close to their optimum during the fMRI scanning session the following day. One participant failed to reach this criterion due to a problem with peripheral vision. One additional participant was not admitted to the experiment due to self-reported symptoms of claustrophobia. On the following day, participants returned to the lab for the real imaging experiment and fMRI data were collected.

Data collection was conducted in a 3-T Siemens Magnetom Trio, whole-body MRI scanner (Siemens Medical Systems, Erlangen, Germany). For each participant, structural images were collected using a T1-weighted sequence (repetition time [TR] = 1760 msec; echo time [TE] = 2.6 msec; flip angle = 9°), consisting of one hundred seventy-six 1-mm-thick slices of 480 by 512 pixels at a 0.5 mm × 0.5 mm in-slice resolution. The BOLD signal was measured using an EPI sequence (TR = 2000 msec; TE = 30 msec, flip angle = 77°), consisting of thirty-three 3.3-mm-thick slices of 384 by 384 pixels at a 3.3 × 3.3 mm resolution. Each participant completed at least 6 runs of the experimental task. During each 5-min run, 150 brain volumes were collected. The first two functional images of each run contained no trials and were discarded.

Stimulus presentation was controlled by a personal computer running the "E-Prime" software package (Psychology Software Tools, Pittsburgh, PA) and the Windows XP operating system. Visual stimuli were presented through an NEC LT256 DLP projector onto a screen at the back of the bore of the MRI scanner, which participants viewed through a mirror. Responses were collected using an fORP-optic button box, which was connected to the acquisition computer through a USB connection.

Data Analysis

Behavioral Data

Mean response times and accuracies were calculated for each participant and condition. These mean values were subjected to a within-subjects ANOVA, containing the factors search type (two levels: target present at one location or at all four locations) and color singleton (two levels: color singleton present or absent). Response times in excess of two times the standard deviation of the mean of each single subject were excluded from the analysis. Excluded trials comprised less than 5% of the total trials. Because we employed a rapid event-related fMRI design, excluding these trials from the fMRI analysis would compromise the estimation of the (overlapping) BOLD responses.[1] For this reason, these trials were not excluded from the fMRI analyses.

We analyzed each subject's response time pattern in the search/singleton-present condition on the basis of the relative location between target and distractor (see Figure 2). On the basis of these results, two groups of participants were identified, who responded differently to the distractor either orienting toward the color singleton (i.e., being distracted) or exerting a strong top–down control to orient away from it.

Imaging Data

Imaging data were preprocessed using the Brain Voyager QX software package (Brain Innovations BV, Maastricht, the Netherlands). The first two images of each run were discarded to avoid T1 saturation differences. Preprocessing of functional images consisted of slice scan time correction, temporal high-pass filtering (0.02 Hz), spatial smoothing (Gaussian kernel: 6 mm FWHM), and 3-D motion correction due to small head movements. Functional images were coregistered to the anatomical image using scanner-based position parameters and manual fine-tuning. The anatomical 3-D images were transformed into Talairach and Tournoux (1988) coordinates. The parameters for this transformation were then applied to the coregistered functional data.

A multirun/multisubject design matrix was created, which specified the start of each trial for each run and subject. This design matrix contained the four different trial types included in the experiment: (1) color singleton present, unique target location; (2) color singleton present, redundant target location; (3) color singleton absent, unique target location; and (4) color singleton absent, redundant target location. These event time series were convolved with a delayed γ function to model the hemodynamic response (Boynton, Engel, Glover, & Heeger, 1996). Voxel time series were *Z*-normalized and additional predictors accounting for baseline differences between runs were included in the design matrix.

Regions of interest (ROIs) were functionally defined using the BrainVoyager ANCOVA function. The search versus no-search contrast yielded brain areas that were primarily activated during visual search (see Figure 2). Likewise, a singleton-present versus singleton-absent condition yielded brain areas that were sensitive to the processing of the color singletons (see Figure 3). For both contrasts, active brain regions were defined as showing *F* values of 16 or greater, and being at least $3 \times 3 \times 3$ voxels in size (see Slagter et al., 2007; Weissman, Warner, & Woldorff, 2004 for comparable procedures). For each ROI, event-related averages, representing the BOLD response to each of the four stimulus type in these areas, were created. The peaks of these BOLD responses were then submitted to a within-subject ANOVA with the factors search type and singleton presence to determine possible interactions between visual search and color singleton processing.

Finally, in a second analysis, participants were subdivided into "opposite-slow" responders and "opposite-fast" responders, on the basis of their response time to targets opposite the color singleton location in the search/singleton-present condition. Brain activation evoked by the color singleton stimulus was analyzed and compared between these two groups.

RESULTS

Behavioral Data

Overall Response Times

Figure 4A illustrates the mean response times. A highly significant main effect of the factor search type indicated that participants responded significantly slower in the search condition than in the no-search condition [$F(1, 15) = 150, p < .0001$]. A main effect of color singleton [$F(1, 15) = 3.80, p = .07$] was just short of significance. The interaction between search type and color singleton was not significant [$F(1, 15) < 1$].

Overall Accuracy

Response accuracy followed the overall pattern of response time (Figure 4B). A highly significant main effect of the factor search type indicated that subjects were less accurate in the search condition than in the no-search condition [$F(1, 15) = 174, p < .0001$]. Neither main effect of color singleton [$F(1, 15) = 2.78, p = .11$] nor interactions

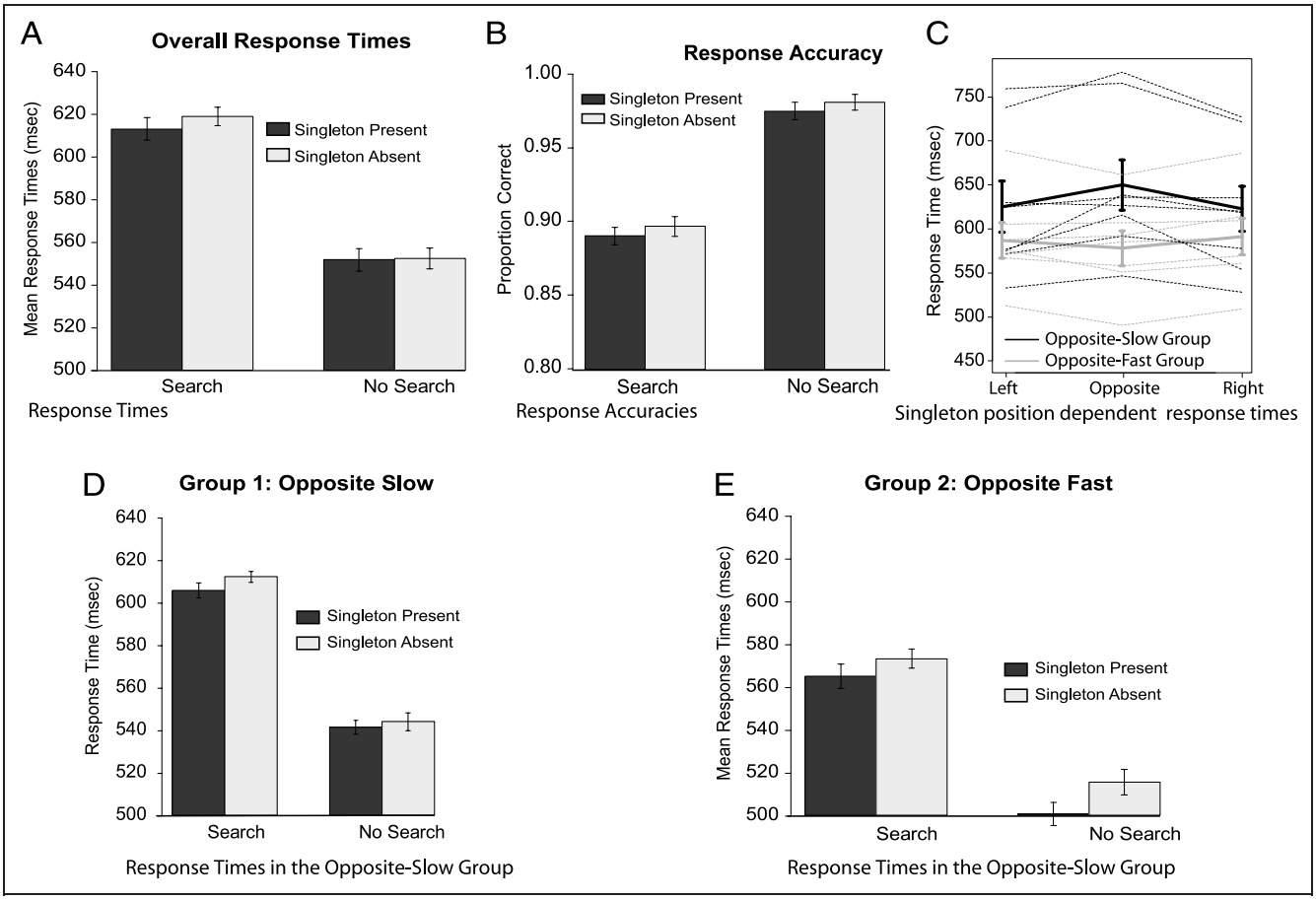

Figure 2. Behavioral data. (A) Overall response times. Response times in the search condition were significantly longer than those in the no-search condition. (B) Overall accuracy. Response accuracy was significantly higher in the no-search condition than in the search condition. (C). Response times in the singleton-present/search condition, plotted as function of the relative position of the color singleton to the target. For about half the participants, responses were significantly slower when the target was presented to the location opposite to that of the distractor (opposite-slow group; black lines). For approximately the other half of the participants, responses were actually faster when the target was presented opposite to the distractor location (opposite-fast group; red lines. For each group, the single-subject response patterns are superimposed using dashed lines.). (D) Response times of the opposite-slow group. Note that in the no-search condition the response times to singleton-present and singleton-absent trials are similar. (E). Response time of the opposite-fast group. Notice that in contrast to the opposite-slow group, responses in the no-search condition are significantly faster here when a color singleton is present than when a color singleton is not present.

between search type and color singleton were found [$F(1, 15) = 2.18, p = .16$].

Position Effects of the Color Singleton

The above-described near-significant response time effect of color singleton indicated that the color signal possibly served an additional role as a warning signal, which led to the tendency for participants to respond faster on singleton-present trials. To separate attentional orienting effects from such a general alerting effect, response times of the singleton-present/search trials (which were the only trial types where the color singleton could serve a role as distractor) were subjected to a further analysis. Response times were calculated according to position of the color singleton, relative to the position of the target. Although no overall effect of position was found, analysis of each single participant's data revealed the following pattern (Figure 4C): When the color singletons were presented at orthogonal positions, relative to the target, response times were about equal. When the color singletons were presented at the opposite position, relative to the target, however, two clearly distinctive patterns could be observed. Half the participants ($n = 8$) showed a clear increase in response time (opposite-slow), whereas the approximate other half ($n = 7$) showed the opposite pattern (i.e., showing a decrease in response time when the color singleton was presented at the opposite position: opposite-fast). These patterns were mainly identified on the basis of the criterion that the mean response time to the target opposite of the color singleton should either be the fastest or the slowest of the three mean responses. That is, when the response times to a target that was opposite to that of the color singleton were relatively fast, compared to the response times that were adjacent to the target location, this was taken as strong top–down

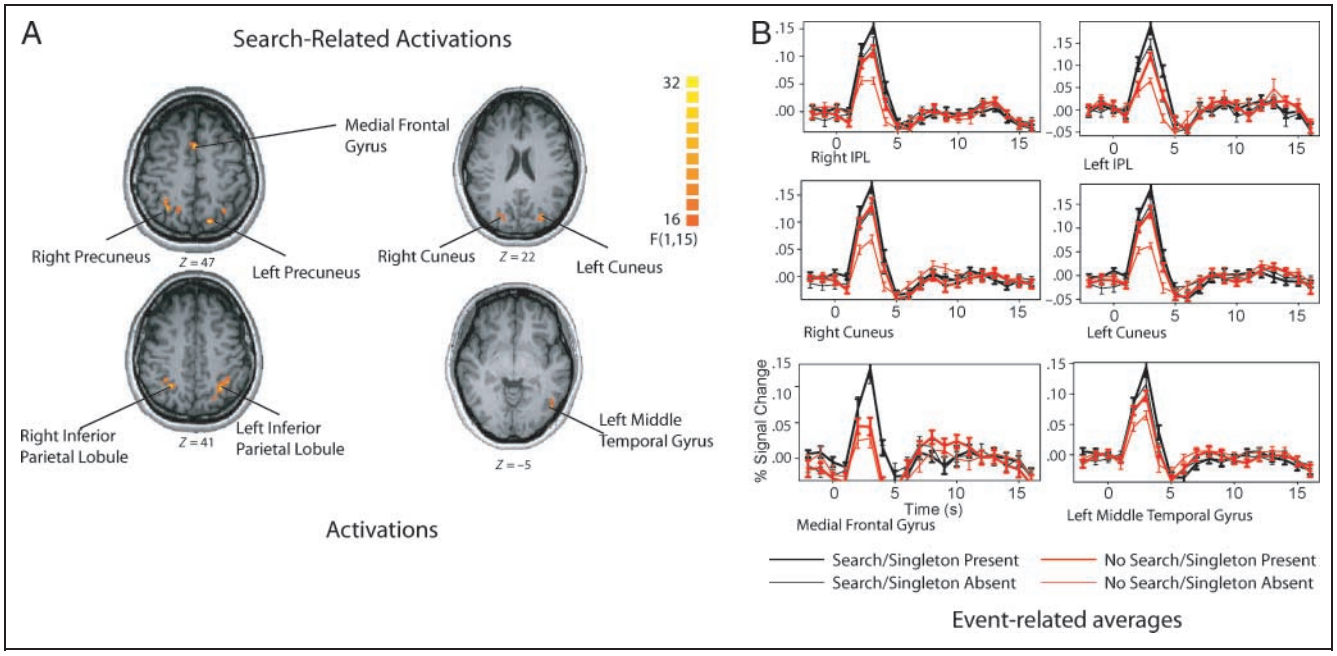

Figure 3. Overview of brain areas that were more active in the search condition than in the no-search condition. (A) Brain areas showing significant activation. (B) Time courses of BOLD response in key areas activated by the top–down control. The activated areas are mainly located in frontal and parietal cortex.

control. In contrast, when the response time to the target location opposite that of the color singleton was relatively slow, this was considered to be weak top–down control. For one participant, this pattern could not be observed. As a secondary criterion, response times to the target at left and right adjacent location should be approximately equal. Although Figure 4 suggests that the opposite-fast responders were faster overall than the opposite-slow responders, we could find no firm statistical evidence for this observation [$F(1, 13) = 2.13, p = .16$].

Imaging Data

Visual Search Effects

Figure 2A summarizes the brain areas that were more active in the search condition than in the no-search condition. As can be seen, search was reflected in a significant increase in activation in the medial frontal gyrus, and several posterior areas including the left and right precuneus, the left inferior parietal lobule, the left middle temporal gyrus, and the right cuneus (see Table 1 for a summary). The BOLD responses observed in these ROIs are plotted in Figure 2B. In addition to the significant main effects of the factor search type [$F(1, 15) > 24.1$, $p < .005$ for all ROIs], which merely confirm the significance of our initial whole-brain analyses, we also found significant effects of singleton presence in six ROIs. More specifically, we found that the BOLD response in the left and right inferior parietal lobule, the left and right cuneus, the right precuneus, and the left medial temporal gyrus was significantly larger in response to singleton-present trials than to singleton-absent trials [for all tests; $F(1, 15) > 10.5, p < .01$; see Figure 2B]. Finally, we found a significant interaction between search type and singleton presence for the left cuneus ROI [$F(1, 15) = 5.93$, $p < .05$]. Although Figure 2B suggests the presence of a similar interaction for the right cuneus, no firm statistical evidence for this observation could be found [$F(1, 15) = 1.72, p < .2$]. The areas that are relatively active in the search condition show close correspondence to similar areas that have been found using symbolic cueing tasks (e.g., Woldorff et al., 2004). We therefore conclude that these areas are, indeed, a reflection of a fronto-parietal network involved in attentional control.

Color Singleton Effects

The presentation of the color singleton activated a number of predominantly occipital and parietal areas, including the left middle occipital gyrus, the left lingual gyrus, the right superior parietal lobule, the bilateral precuneus, the bilateral cuneus, and the bilateral fusiform gyrus. In addition, two small areas inside the cerebellum were found active (see Table 2). Confirming these areas, the peak of the BOLD response in each ROI was larger on singleton-present trials than on singleton-absent trials [$F(1, 15) > 31.1, p < .0001$ for all ROIs]. In addition, in three ROIs we found larger BOLD signals in response to search trials than to no-search trials [for all tests; $F(1, 15) > 12.5, p < .005$]. Finally, in the right precuneus, we found a near-significant interaction between search type and singleton presence [$F(1, 15) = 4.14, p < .05$].

It should be noted that one of the areas activated by the color singletons; the right superior parietal lobule, is

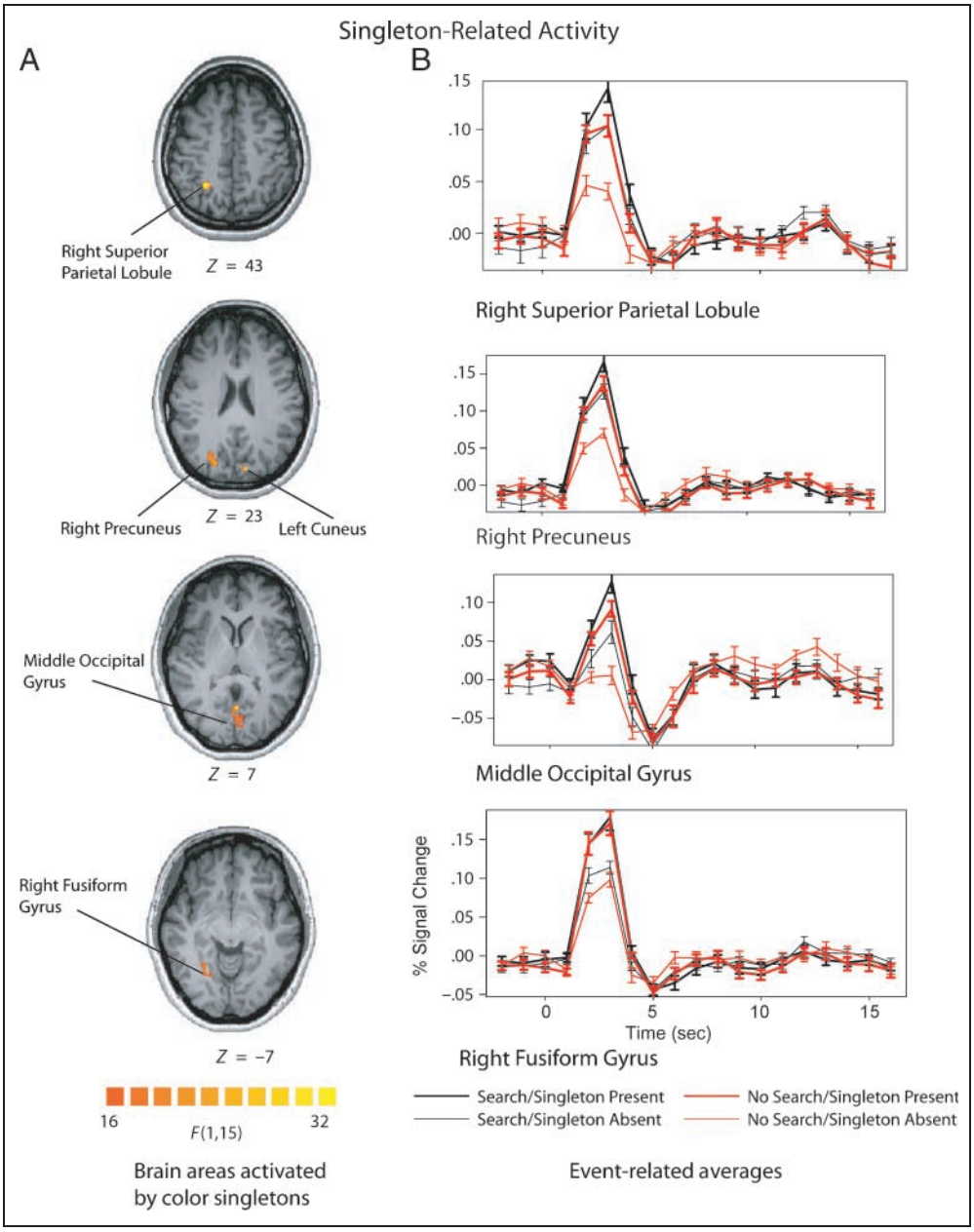

Figure 4. Brain areas activated by the color singleton. (A) Brain areas showing significant singleton related activation. (B) Time courses of the BOLD response in key areas activated by the singleton. Notice that in contrast to the search related activations (see Figure 2), the color singleton activated predominantly areas in parietal and occipital brain regions.

located adjacent to one area that was activated in the search condition. In addition, the left precuneus was activated both by the color singletons and by the search conditions. The other areas activated by the color singletons show no correspondence, however, with the areas activated by the search conditions. In addition, no frontal activation was observed in response to the color singleton. Thus, we conclude that, in addition to some overlapping areas, top–down and bottom–up driven processes are at least, in part, subserved by different brain mechanisms.

Response Time Based Differences in Singleton Processing

In order to further delineate the brain activity evoked by the color singletons, we analyzed the color singleton data separately for those participants who tended to orient away from the color singleton and those who oriented toward the color singleton. We hypothesized that those participants who oriented away (i.e., the opposite-fast group) from the singleton were capable of exerting a strong top–down control that prevented them from orienting to the singleton. For this reason, we expected to find brain areas involved in top–down attentional control to be activated in this particular group of participants, whereas we did not expect this to be the case in the group of participants who oriented toward the distractor location (i.e., the opposite-slow group).

To test whether these behavioral differences would be related to differences in brain activity, two additional analyses were carried out. Firstly, the strength of each participant's top–down control ability was correlated with the

Table 1. Overview of Brain Areas Activated by Search

	Talairach Coordinates			*Statistics*	
Area	*x*	*y*	*z*	*F*	*p*
Right insula	30	14	13	45.2	<.00007
Right precuneus	25	−54	47	18.1	<.0008
Right cuneus	18	−83	20	23.1	<.0003
Right medial frontal gyrus	2	10	46	34.9	<.00003
Left precuneus	−15	−69	47	33.4	<.00003
Left inferior parietal lobule	−31	−55	41	50.3	<.00001
Left precuneus	−26	−76	22	40.3	<.00002
Left cerebellum culmen	−28	−56	−23	39.9	<.00002
Left middle temporal gyrus	−46	−60	0	34.2	<.00002

search-related BOLD signal increase in each ROI. In this analysis, the strength of top–down control was defined as the difference between the mean response time to the opposite target location and the mean response times to the adjacent target locations in the search/singleton-present condition (see Behavioral Data above). This analysis revealed that activity in the right insula correlated significantly with the behaviorally observed strength of attentional control ($r = .59$, $p < .008^2$; see Figure 5A).

Secondly, an additional analysis was carried out that tested whether the effects of search type and singleton presence differed between the opposite-slow and opposite-fast groups. This was done by conducting a whole-brain analysis using the BrainVoyager ANCOVA function, using an analysis consisting of the aforementioned within-subjects factors search type (search vs. no search) and singleton presence (present vs. absent), and the additional between-subject factor group (opposite-slow vs. opposite-fast).

From these analyses, it was found that the left precentral gyrus showed an interaction between singleton presence and group (see Figure 5B). A follow-up analysis revealed that this area was, indeed, significantly more activated by color singletons in the opposite-slow group, but not in the opposite-fast group.

Table 2. Areas Activated by the Color Singleton

	Talairach Coordinates			*Statistics*	
Area	*x*	*y*	*z*	*F*	*p*
Right precuneus	24	−73	23	50.8	<.00003
Right superior parietal lobule	27	−51	43	42.0	<.00001
Right fusiform gyrus	26	−56	−7	34.3	<.0003
Right precuneus	21	−59	47	27.9	<.00009
Right cerebellum culmen	15	−42	−11	33.2	<.00004
Right cuneus	11	−79	10	32.1	<.00005
Right cerebellum	9	−72	−29	40.2	<.00002
Left lingual gyrus	0	−74	4	39.6	<.00002
Left cuneus	−6	−82	21	34.6	<.00003
Left precuneus	−23	−69	39	27.3	<.0001
Left middle occipital gyrus	−28	−82	3	35.7	<.0003
Left cerebellum declive	−31	−63	−12	36.6	<.0003
Left fusiform gyrus	−25	−49	−9	26.7	<.0002

DISCUSSION

Here we investigated the interactions between top–down and bottom–up driven attentional control. This was done by comparing search and no-search conditions using a rapid event-related design. Results indicate that in addition to a possible common network in parietal areas, additional brain areas are uniquely involved in either top–down or bottom–up driven control of attention. Both the search versus no-search contrast and singleton-present versus singleton-absent contrasts activated regions in parietal brain areas. In addition, top–down control-related activity (i.e., the search vs. no-search contrast) included medial frontal regions that were not activated by the color singletons, whereas bottom–up driven activations were largely confined to the occipital and parietal areas. We thus conclude that separate mechanisms are involved in top–down and bottom–up driven attentional control.

One novel finding of this study is that participants who oriented away from the color singleton stimulus in the search condition were also benefiting more from the color singleton in the no-search condition, compared to participants who tended to orient toward the color singleton. Interestingly, this difference in top–down control ability was related to brain activity in two areas. Activity in the right insula correlated significantly with the strength of top–down control that we observed at the behavioral level. In addition, activity in the left precentral gyrus was present only in participants with a relatively weak top–down control.

Brain Activity Related to Top–Down and Bottom–Up Control

The current study shows that top–down and bottom–up attentional control is subserved—at least in part—by different brain areas. These results are in line with several other studies that have reported a dissociation between top–down and bottom–up control mechanisms of atten-

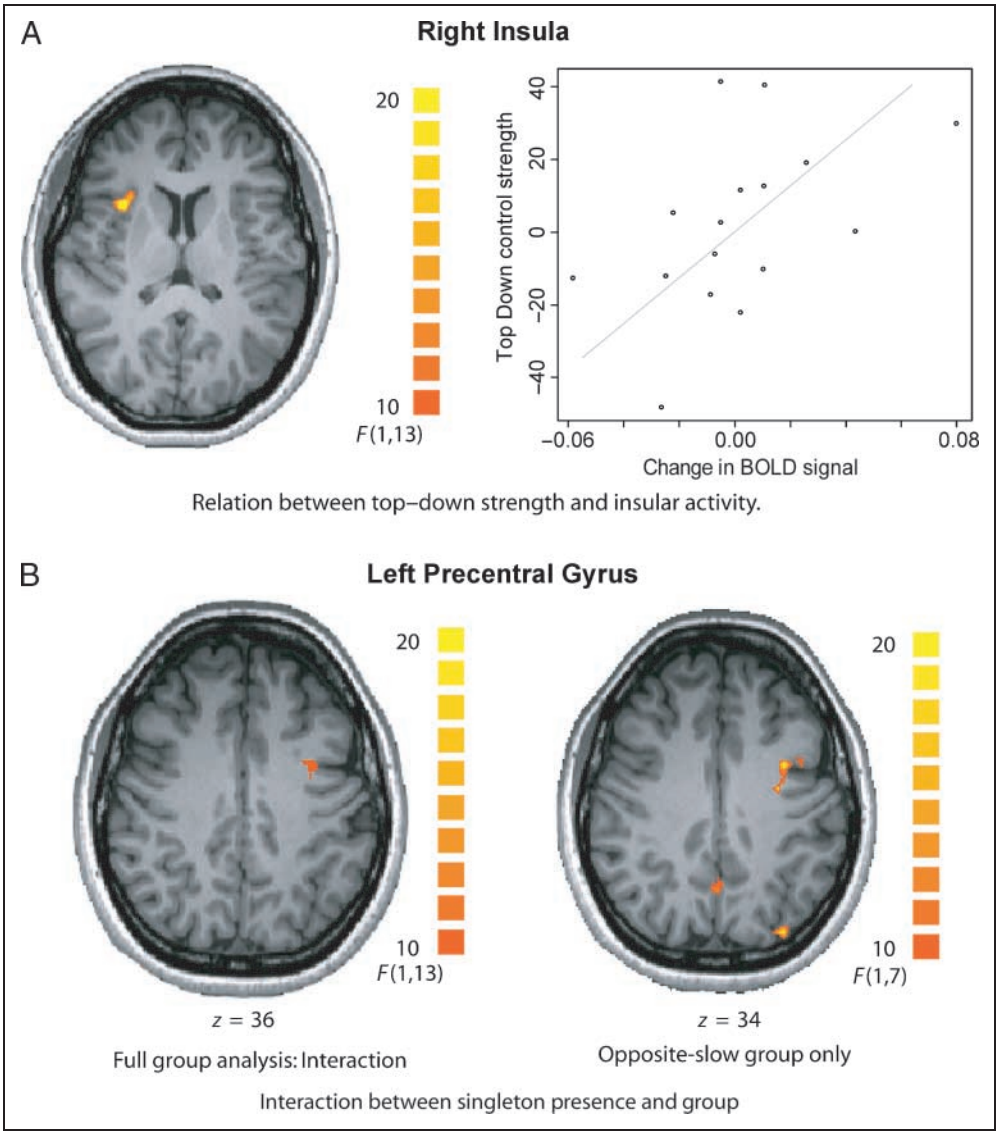

Figure 5. Relation between brain activity and attentional control. (A) Correlation between the strength of attentional control and activation in the right insula. Top–down control strength is defined as the response time difference between responses to targets presented opposite to a color singleton and responses to targets that were presented at locations adjacent to the color singleton. (B) Interaction between group and singleton presence. Left: One area in the left precentral gyrus yielded a significant interaction between singleton presence and group, suggesting that this area was more strongly activated by color singletons in the opposite-slow group than in the opposite-fast group. Right: A post hoc analysis confirmed that this area was indeed significantly activated in the opposite-slow group alone (right), but not in the opposite-fast group (data not shown here).

tion (e.g., Hahn et al., 2006; Hopfinger & West, 2006; Grosbras et al., 2005; Thomsen et al., 2005). For instance, Grosbras et al. (2005) reported a meta-analysis of 15 fMRI and PET studies on top–down and bottom–up driven shifts of attention. This meta-analysis revealed activations in the right inferior frontal gyrus, the left dorsolateral prefrontal cortex, and the superior parietal lobule for top–down controlled shifts of attention. In contrast, bottom–up driven attentional orienting activated right ventral precentral cortex, left fusiform gyrus, bilateral insula, putamen, and one location in the cerebellum. Likewise, on the basis of ERP data, Hopfinger and West (2006) concluded that different but interacting functional networks are involved in top–down and bottom–up control of attentional orienting. These authors reported that exogenous attention modulated the amplitude of the later phase of the early latency (~100 msec after stimulus onset) extrastriate P1 component. Endogenous attention affected the much later (>300 msec after stimulus onset) occurring P3 component, with an intermediate stage in between these early and late stages where bottom–up and top–down control appeared to interact.

It is interesting to note that despite these findings, other studies have reported that both endogenous and exogenous forms of orienting are subserved by a common network of brain areas (Peelen et al., 2004; Rosen et al., 1999; Kastner et al., 1998; Mangun et al., 1998; Corbetta et al., 1993). For instance, using PET, Corbetta et al. (1993) reported greater activation of superior parietal and superior frontal areas, both in conditions where attention was shifted actively (i.e., in a top–down controlled fashion) as well as in conditions in which attention was oriented passively (i.e., in a bottom–up driven fashion). More recently, Peelen et al. (2004) reported similar findings in a study employing fMRI. These authors reported that both endogenous and exogenous cues elicited comparable levels of activation in a number of cortical areas that included the supplementary motor area, anterior cingulate cortex, right inferior frontal gyrus, bilateral premotor area, precuneus, temporal parietal junction, and cuneus.

One considerable difference between the abovementioned studies is that those studies reporting commonality are mainly block-designed PET of fMRI studies, whereas studies reporting differences between brain areas involved in exogenous and endogenous attentional orienting are mainly event-related designs, either using fMRI or ERPs. It seems, therefore, that block design fMRI or PET is more sensitive to brain activity that is commonly activated by both top–down and bottom–up control processes, whereas (rapid) event-related fMRI designs are more sensitive to brain areas selectively activated by either top–down or bottom–up driven control.

One potential limitation of the present study is that some physical differences exist between our trial types. One could argue that these differences could—at least in part—contribute to the observed effects. For instance, one could argue that bottom–up factors, such as local feature contrast between the target and the nontarget stimuli in the search condition could have contributed to our top–down results. We deem this to be unlikely, however, because Theeuwes (1992) has shown that color singletons are easily capable of capturing attention, whereas shape singletons are not. This conclusion is further underscored by our response time effects, which show that the responses to search trials took considerably longer than responses to the no-search trials. If local features contrasts were to exert a strong bottom–up driven influence, no such response time differences would have been expected. It remains an interesting challenge for future studies to delineate between search and no-search conditions by using stimuli that are less characterized by physical differences.

Finally, it could be argued that the aforementioned response time differences between search and no-search conditions could be driven by processes other than a top–down control process, for instance, processes related to the cognitive appraisal of differences in difficulty between conditions. Even though this is feasible, it should be noted that the brain areas that we identified as being involved in top–down attentional control are consistent with earlier findings identifying similar areas as being involved in top–down attentional control (e.g., Mao, Zhou, Zhou, & Han, 2007; Rinne et al., 2007 for medial frontal gyrus and Hopfinger et al., 2000, for insular activity). Yet, we cannot exclude the possibility that the activation in these areas reflect a more generic cognitive control process that is involved in attentional control rather than being a pure attention-only process. For instance, Garavan, Ross, Murphy, Roche, and Stein (2002) found increased activation in the medial frontal gyrus as well as in the insula, using a stop-signal paradigm, and suggested that these areas, among others, are part of a cognitive control network that is involved in response inhibition. Given that in the present experiment participants were required to respond on each and every trial, we consider it unlikely that response inhibition plays a role of importance here. We therefore conclude that these areas are more strongly activated due to a greater need for selectivity, that is, for a control process that is related to attention.

Secondly, given that response times are larger in the search condition than in the no-search condition, it could be argued that the increased BOLD responses observed in these conditions are not reflecting additional brain activity due to increased attentional or more generic cognitive control processes, but are merely a reflection of the prolonged duration of the same processes in the search conditions. For instance, in the ERP literature, it is well known that the amplitude of the P300 component correlates with the response latency (e.g., Talsma, Mulckhuyse, Slagter, & Theeuwes, 2007; Talsma, Wijers, Klaver, & Mulder, 2001). It is also known from the ERP literature, however, that the amplitude of these components decreases with increasing response time, due to the fact that the average brain activity is smeared out across a larger range of response times, observed on the constituting trials.

In the present experiment, we consider a similar effect driving our results as unlikely for two reasons. First, the low temporal resolution of the fMRI BOLD responses makes it unlikely to be sensitive to duration changes in the order of 100 msec or less (as is the case in the present study). Second, if the BOLD effect would have been affected by such a smearing process, then we would have expected its amplitude to be lower in the search conditions, compared to the no-search condition, whereas we actually observed the opposite.

Differential Roles of the Color Singleton

One interesting, and somewhat unexpected, result from our study is that participants showed somewhat different responses to the color singleton in the search condition. Whereas about half the participants tended to orient toward the color singleton, as shown by a increase in response time when the target object was presented opposite of the color singleton location, about the other half appeared to orient away from the singleton, as shown by a decrease in response time when the target object was presented opposite that of the color singleton.

A possible explanation for this phenomenon is that there are individual differences in the time course of attentional orienting. In the current paradigm, the location of the color singleton would never be behaviorally relevant as a possible target location, and participants knew this in advance. Unlike more traditional cueing paradigms, participants could therefore prepare to inhibit attending to the location where the color singleton was presented. This interpretation is in line with the observation that participants who oriented away from the color singleton location were also more benefiting from the singleton in the no-search condition. Presumably, these subjects were capable of rapidly exerting inhibition at the location of the color singleton (see Theeuwes & Chen, 2005). Because these participants orient away from the singleton location, they engage their attention on the opposite location in advance, and are thus relatively fast at identifying the target at that location. This interpretation would also be consistent with the observation that the participants who oriented away from the color singleton were also the ones who tended to have faster overall response times than those participants who oriented toward the color singleton.

A relatively strong ability to suppress the position of the color singleton would be in line with our functional imaging results. The fMRI data show a decrease in posterior activation related to color singleton processing, combined with an increase in anterior activation in those participants who oriented away from the singleton location, compared to subjects who showed capture by the singletons. Interestingly, these areas most strongly activated by participants who oriented away from the color singleton correspond closely to brain areas that have been found active in top–down attentional control. For instance, Hopfinger et al. (2000) report increased activation in the middle frontal gyrus and the insula as being related to the voluntary orienting of attention. The insular activity observed by Hopfinger et al. was interpreted as an inhibitory filtering of information. Such an interpretation would be consistent with a stronger ability to inhibit irrelevant color singletons in the present study.

Likewise, increased activity in the precentral gyrus was reported by Thomsen et al. (2005). These authors presented endogenous and exogenous cues simultaneously. The endogenous and exogenous cues could be congruent or incongruent. During a block of trials, participants were instructed that either the endogenous or exogenous cues were relevant. In conditions where the endogenous cue was relevant and valid, but paired with an exogenous cue that was irrelevant and invalid, top–down attentional control mechanisms needed to overrule the bottom–up driven orienting process. In this condition, increased activity was found in the precentral gyrus, suggesting that this area plays an important role in increasing top–down controlled attentional demands.

Top–down attentional control processes were modulated by contrasting the search and no-search conditions. Increased activation in the medial frontal gyrus is consistent with earlier reports showing that this area is involved in top–down control of attention (Mao et al., 2007; Rinne et al., 2007). Interestingly, this medial frontal activation seemed to be unique for top–down attention. Additional activation related to top–down control included the left and right precuneus, the left inferior parietal lobule, left middle temporal gyrus, and the right cuneus. It should be noted that many of these areas were also activated by the color singleton, suggesting that these areas are part of a common attentional control network that is shared between top–down and bottom–up driven control (cf. Mangun et al., 1998).

Summary and Conclusions

The present study investigated the interactions between top–down and bottom–up driven attentional control. This was done by presenting a target stimulus at either one of four possible locations, or presenting this target redundantly at all four location. Prior to the presentation of the target, a color singleton could be presented just prior to the presentation of the target. Results indicate that the search condition activated the medial frontal gyrus more than the no-search condition. This activation was unique to the top–down control processes. Additional activations in parietal and occipital areas were also found in relation to the presence of a color singleton stimulus.

One novel finding is that participants who could efficiently inhibit orienting to the color singleton were also showing additional activation in the left insula and precentral gyrus, and less activation in posterior brain areas. We conclude that these frontal areas are involved in suppressing distractor locations. Finally, we conclude that although top–down and bottom–up driven attentional control mech-

anisms share a common network of brain areas, other brain areas are uniquely involved in either top–down or bottom–up driven control.

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Notes

1. For the analysis of response times, it was deemed necessary to exclude slow responses, because these outliers typically have a strong impact on response time estimates. The criterion of excluding response times in excess of twice the standard deviation of the mean is a common practice. Although it would have been desirable to also exclude these trials from the fMRI analysis, this exclusion led to several problems. Due to the rapid stimulus presentation protocol employed in the present experiment, the estimation of the BOLD responses elicited on each trial has to take into account the average activity of all trial types that are both preceding and succeeding the currently estimated BOLD response. Given that all trials were presented in a counterbalanced fashion, this preceding and succeeding activity was, on average, equal for each trial type, and therefore, not affecting the BOLD estimation process. Omitting these error trials, however, would lead to a significant skewing of the BOLD response estimation procedure due to the fact that overlapping activity on some trials would selectively not be modeled, whereas on other trials it would be. Additional analyses, in which the error trials were modeled as a separate event led to unstable estimates, due to the fact that not enough error trials were available for a reliable estimate.
2. Considering that the activations in nine ROIs were tested for significance, a Bonferroni correction of this effect yields a conservatively adjusted p value of .065.

REFERENCES

Boynton, G. M., Engel, S. A., Glover, G. H., & Heeger, D. J. (1996). Linear systems analysis of functional magnetic resonance imaging in human V1. *Journal of Neuroscience, 16,* 4207–4221.

Brunia, C. H. M. (1999). Neural aspects of anticipatory behavior. *Acta Psychologica, 101,* 213–242.

Buckner, R. L., Goodman, J., Burock, M., Rotte, M., Koutstaal, W., Schacter, D., et al. (1998). Functional–anatomic correlates of object priming in humans revealed by rapid presentation event-related fMRI. *Neuron, 20,* 285–296.

Burock, M. A., Buckner, R. L., Woldorff, M. G., Rosen, B. R., & Dale, A. M. (1998). Randomized event-related experimental designs allow for extremely rapid presentation rates using functional MRI. *NeuroReport, 9,* 3735–3739.

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.

de Fockert, J., Rees, G., Frith, C., & Lavie, N. (2004). Neural correlates of attentional capture in visual search. *Journal of Cognitive Neuroscience, 16,* 751–759.

Dorris, M. C., Klein, R. M., Everling, S., & Munoz, D. P. (2002). Contributions of the Primate Superior colliculus to Inhibition of Return. *Journal of Cognitive Neuroscience, 14,* 1256–1263.

Fang, F., Kersten, D., & Murray, S. (2008). Perceptual grouping and inverse fMRI activity patterns in human visual cortex. *Journal of Vision, 8,* 2–9.

Fecteau, J. H., Bell, A. H., Dorris, M. C., & Munoz, D. P. (2005). Neurophysiological correlates of the reflexive orienting of spatial attention. In L. Itti, G. Rees, & J. Tsotsos (Eds.), *Neurobiology of attention*. Amsterdam: Elsevier.

Garavan, H., Ross, T. J., Murphy, K., Roche, R. A. P., & Stein, E. A. (2002). Dissociable executive functions in the dynamic control of behavior: Inhibition, error detection, and correction. *Neuroimage, 17,* 1820–1829.

Grent-'T-Jong, T., & Woldorff, M. G. (2007). Timing and sequence of brain activity in top–down control of visual–spatial attention. *PLoS Biology, 5,* 114–126.

Grosbras, M. N., Laird, A. R., & Paus, T. (2005). Cortical regions involved in eye movements, shifts of attention, and gaze perception. *Human Brain Mapping, 25,* 140–154.

Hahn, B., Ross, T. J., & Stein, E. A. (2006). Neuroanatomical dissociation between bottom–up and top–down processes of visuospatial selective attention. *Neuroimage, 32,* 842–853.

Hillyard, S. A., Vogel, E. K., & Luck, S. J. (1998). Sensory gain control (amplification) as a mechanism of selective attention: Electrophysiological and neuroimaging evidence. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences, 353,* 1257–1270.

Hopfinger, J. B., Buonocore, M. H., & Mangun, G. R. (2000). The neural mechanisms of top–down attentional control. *Nature Neuroscience, 3,* 284–291.

Hopfinger, J. B., & West, V. M. (2006). Interactions between endogenous and exogenous attention on cortical visual processing. *Neuroimage, 31,* 774–789.

Hopfinger, J. B., Woldorff, M. G., Fletcher, E. M., & Mangun, G. R. (2001). Dissociating top–down attentional control from selective perception and action. *Neuropsychologia, 39,* 1277–1291.

Jonides, J., & Irwin, D. E. (1981). Capturing attention. *Cognition, 10,* 145–150.

Kastner, S., De Weerd, P., Desimone, R., & Ungerleider, L. C. (1998). Mechanisms of directed attention in the human extrastriate cortex as revealed by functional MRI. *Science, 282,* 108–111.

Klein, R., & Kingstone, A. (1993). Why do visual offsets reduce saccadic latencies. *Behavioral and Brain Sciences, 16,* 583–584.

LaBerge, D. (1995). *Attentional processing: The brain's art of mindfulness*. Cambridge, MA: Harvard University Press.

LaBerge, D. (2001). Attention, consciousness, and electrical wave activity within the cortical column. *International Journal of Psychophysiology, 43,* 5–24.

Lavie, N., & de Fockert, J. (2006). Frontal control of attentional capture in visual search. *Visual Cognition, 14,* 863–876.

Liu, T. S., Slotnick, S. D., Serences, J. T., & Yantis, S. (2003). Cortical mechanisms of feature-based attentional control. *Cerebral Cortex, 13,* 1334–1343.

Mangun, G. R., Buonocore, M. H., Girelli, M., & Jha, A. P. (1998). ERP and fMRI measures of visual spatial selective attention. *Human Brain Mapping, 6,* 383–389.

Mao, L. H., Zhou, B., Zhou, W., & Han, S. H. (2007). Neural correlates of covert orienting of visual spatial attention along vertical and horizontal dimensions. *Brain Research, 1136,* 142–153.

Peelen, M. V., Heslenfeld, D. J., & Theeuwes, J. (2004). Endogenous and exogenous attention shifts are mediated by the same large-scale neural network. *Neuroimage, 22,* 822–830.
Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology, 32,* 3–25.
Posner, M. I., & Cohen, Y. P. C. (1984). Components of visual orienting. In H. Bouma & D. Bouwhuis (Eds.), *Attention and performance X* (pp. 531–556). London: Erlbaum.
Posner, M. I., Snyder, C. R. R., & Davidson, B. J. (1980). Attention and the detection of signals. *Journal of Experimental Psychology: General, 109,* 160–174.
Rinne, T., Kirjavainen, S., Salonen, O., Degerman, A., Kang, X. J., Woods, D. L., et al. (2007). Distributed cortical networks for focused auditory attention and distraction. *Neuroscience Letters, 416,* 247–251.
Ristic, J., Friesen, C. K., & Kingstone, A. (2002). Are eyes special? It depends on how you look at it. *Psychonomic Bulletin & Review, 9,* 507–513.
Rosen, A. C., Rao, S. M., Caffarra, P., Scaglioni, A., Bobholz, J. A., Woodley, S. J., et al. (1999). Neural basis of endogenous and exogenous spatial orienting: A functional MRI study. *Journal of Cognitive Neuroscience, 11,* 135–152.
Serences, J. T., Schwarzbach, J., Courtney, S. M., Golay, X., & Yantis, S. (2004). Control of object-based attention in human cortex. *Cerebral Cortex, 14,* 1346–1357.
Serences, J. T., & Yantis, S. (2007). Spatially selective representations of voluntary and stimulus-driven attentional priority in human occipital, parietal, and frontal cortex. *Cerebral Cortex, 17,* 284–293.
Slagter, H. A., Giesbrecht, B., Kok, A., Weissman, D. H., Kenemans, J. L., Woldorff, M. G., et al. (2007). fMRI evidence for both generalized and specialized components of attentional control. *Brain Research, 1177,* 90–102.
Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. New York: Thieme.
Talsma, D., Mulckhuyse, M., Slagter, H. A., & Theeuwes, J. (2007). Faster, more intense! The relation between electrophysiological reflections of attentional orienting, sensory gain control, and speed of responding. *Brain Research, 1178,* 92–105.
Talsma, D., Wijers, A. A., Klaver, P., & Mulder, G. (2001). Working memory processes show different degrees of lateralization: Evidence from event-related potentials. *Psychophysiology, 38,* 425–439.
Theeuwes, J. (1991). Exogenous and endogenous control of attention—The effect of visual onsets and offsets. *Perception & Psychophysics, 49,* 83–90.
Theeuwes, J. (1992). Perceptual selectivity for color and form. *Perception & 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., Atchley, P., & Kramer, A. F. (2000). On the time course of top–down and bottom–up control of visual attention. In S. Monsell & J. Driver (Eds.), *Attention and performance XVIII* (pp. 105–124). Cambridge, MA: MIT Press.
Theeuwes, J., & Chen, C. Y. D. (2005). Attentional capture and inhibition (of return): the effect on perceptual sensitivity. *Perception & Psychophysics, 67,* 1305–1312.
Thomsen, T., Specht, K., Ersland, L., & Hugdahl, K. (2005). Processing of conflicting cues in an attention-shift paradigm studied with fMRI. *Neuroscience Letters, 380,* 138–142.
Tipper, S. P., Weaver, B., & Watson, F. L. (1996). Inhibition of return to successively cued spatial locations: Commentary on Pratt and Abrams (1995). *Journal of Experimental Psychology: Human Perception and Performance, 22,* 1289–1293.
Wade, A., Augath, M., Logothetis, N., & Wandell, B. (2008). fMRI measurements of color in macaque and human. *Journal of Vision, 8,* 1–19.
Weissman, D. H., Warner, L. M., & Woldorff, M. G. (2004). The neural mechanisms for minimizing cross-modal distraction. *Journal of Neuroscience, 24,* 10941–10949.
Woldorff, M. G. (1993). Distortion of ERP averages due to overlap from temporally adjacent ERPs—Analysis and correction. *Psychophysiology, 30,* 98–119.
Woldorff, M. G., Hazlett, C. J., Fichtenholtz, H. M., Weissman, D. H., Dale, A. M., & Song, A. W. (2004). Functional parcellation of attentional control regions of the brain. *Journal of Cognitive Neuroscience, 16,* 149–165.
Yantis, S., & Jonides, J. (1984). Abrupt visual onsets and selective attention—Evidence from visual-search. *Journal of Experimental Psychology: Human Perception and Performance, 10,* 601–621.
Yantis, S., Schwarzbach, J., Serences, J. T., Carlson, R. L., Steinmetz, M. A., Pekar, J. J., et al. (2002). Transient neural activity in human parietal cortex during spatial attention shifts. *Nature Neuroscience, 5,* 995–1002.