Sources of Top–Down Control in Visual Search

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Abstract

■ Endogenous control of visual search can influence search guidance at the level of a supradimensional topographic saliency map [Wolfe, J. M. Guided Search 2.0: A revised model of visual search. *Psychonomic Bulletin & Review, 1,* 202–238, 1994], and modulate nonspatial mechanisms coding saliency in dimension-specific input modules [Müller, H. J., Reimann, B., & Krummenacher, J. Visual search for singleton feature targets across dimensions: Stimulus- and expectancy-driven effects in dimensional weighting. *Journal of Experimental Psychology: Human Perception and Performance, 29,* 1021–1035, 2003]. The current experiment used fMRI to dissociate these mechanisms in a singleton feature search task in which the likely target dimension (color or orientation) was semantically precued and target saliency in each dimension was varied parametrically. BOLD signal increases associated with increased demands for top–down guidance were observed within the fronto-parietal attention network and in the right anterior middle frontal gyrus. Decreasing requirements for top–down control led to BOLD signal increases in medial anterior prefrontal cortex, consistent with a gating mechanism in favor of stimulus-related processing [Burgess, P. W., Dumontheil, I., & Gilbert, S. J. The gateway hypothesis of rostral prefrontal cortex (area 10) function. *Trends in Cognitive Sciences, 11,* 290–298, 2007]. Another network of brain areas consisting of left lateral fronto-polar cortex, the left supramarginal gyrus, and the cerebellum, as well as a bilateral network consisting of the posterior orbital gyrus, the inferior frontal gyrus, and the pre-SMA were associated with top–down dimensional (re-) orienting. These data argue in favor of distinct endogenous control systems for visuospatial and dimension-based attentional processing. Finally, cue validity modulated saliency processing in the left temporo-parietal junction (TPJ), pointing to a crucial role of the left TPJ in integrating an endogenous dimension-based attention set with bottom–up saliency signals. ■

INTRODUCTION

Selective attention can be controlled by either salient stimulus properties or the observer's intentions. A highly salient stimulus, such as an abrupt luminance change, is hard to ignore, attracting focal attention in a seemingly automatic fashion (Theeuwes, 1991). This process is often referred to as "bottom–up" selection. The allocation of attention to such stimuli is assumed to be mediated by a topographic "overall-saliency" or "master" map of the visual field, the units of which integrate feature contrast signals generated in dimensionally organized input modules (for luminance, color, orientation, motion, etc.). Focal attention is allocated to that position in the field which achieves the highest overall saliency (Wolfe, 1994, 1998; Koch & Ullman, 1985). A singleton element that differs in one salient feature from homogeneous items in its surround (e.g., a single red element amongst many green elements) elicits a strong saliency signal at the level of the master map, with a high likelihood of attracting focal attention to its location. In contrast, if a singleton item generates only a weak feature contrast signal (e.g., a red element among many orange elements), the resulting distribution of saliency signals is relatively even, without any strong attractor for focal attention. In this situation, the guidance of focal attention may rely more on "top–down" control processes.

Top–down control can influence visual search via two different mechanisms: The first is the guidance of visuospatial scanning at the level of the overall saliency map, for example, by defining a scan path (e.g., from the left to the right and/or the top to the bottom of the display); the second involves selective weighting of dimension-specific features, or feature contrast, signals, thus conferring an advantage to stimuli sharing target features in the race to achieve saliency at the master map level. Visuospatial scanning has been reported to enhance activation within the so-called visuospatial attention network, which includes the frontal eye fields (FEFs) and superior parietal cortex as well as the intraparietal sulcus [IPS] (Donner et al., 2002; Weidner, Pollmann, Müller, & von Cramon, 2002; Corbetta, Shulman, Miezin, & Petersen, 1995). In contrast, lateral fronto-polar as well as medial prefrontal brain regions are involved in the selective weighting, or reweighting, of dimension-specific feature analyzer modules (Pollmann et al., 2007; Weidner et al., 2002; Pollmann, Weidner, Müller, & von Cramon, 2000).

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The aim of the present study was to investigate whether these two aspects of top–down control in visual search involve functionally separate or overlapping brain networks and how they interact with bottom–up generated saliency signals.

Observers performed a simple visual search task: They had to discern the presence, versus the absence, of a singleton feature ("pop-out") target. In order to manipulate the degree to which the search involved top–down guidance, the target's saliency was parametrically varied by modulating its feature difference relative to the distractors. The requirement for active search guidance was assumed to rise with decreasing target saliency, increasingly involving brain areas that had previously been associated with difficult visual searches and the control of visuospatial attention (Corbetta & Shulman, 2002).

In order to examine the other mechanism of endogenous control, that is, the top–down weighting of feature contrast signals, observers were presented with semantic precues that indicated the likely dimension of an upcoming target. This permitted the observers to set themselves for—that is, to top–down weight—the indicated dimension prior to the presentation of the target display, thereby expediting the emergence of a target saliency signal at the master map level. The requirement to reconfigure the dimension-based attention set (following a change in the target-defining dimension on the current relative to the preceding trial) has previously been demonstrated to activate lateral and, respectively, medial prefrontal cortex (Pollmann et al., 2000, 2007; Pollmann, Weidner, Müller, & von Cramon, 2006; Weidner et al., 2002). Detecting a target following an invalid semantic cue was therefore expected to also activate these areas, in addition to activation in brain areas associated with cognitive control such as the posterior end of the inferior frontal gyrus (Brass, Derrfuss, Forstmann, & von Cramon, 2005; Derrfuss, Brass, Neumann, & von Cramon, 2005).

METHODS

Participants

Thirteen observers participated in a single fMRI session (4 women, 9 men; age range = 19–34 years, mean age = 24 years). They were all right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). All subjects gave informed consent prior to the experiment in accordance with the Declaration of Helsinki.

Stimuli

Visual stimuli were presented using a Silent Vision fiber-optic system (Avotec Inc., FL, USA). Stimulus displays consisted of 64 colored bars, arranged in a grid-like pattern (Figure 1). Stimulus color (either green or red) and orientation (either steep or shallow) were variable across trials but identical for all bars presented within a trial

display (except for the target, which was different in either color or orientation).

Target saliency values were determined individually for each observer prior to scanning (while already placed in the scanner). The reaction times (RTs) taken to detect a given target were used as an indicator of the target's saliency. The saliency of orientation and color targets was adjusted in a three-step procedure: First, RTs were averaged across 15 trials in which the observer had to detect a maximally salient odd-one-out luminance stimulus. This time was then taken as a baseline to set the maximum and minimum saliency levels of the orientation and color targets: Maximum saliency was determined to result in RTs that were 30 msec slower compared to the luminance baseline, and minimum saliency was determined to yield RTs 90 msec slower. In order to find the saliency levels matching these criteria, the feature difference between the target and the distractors was varied systematically in an "adaptive modified binary search (MOBS)" procedure (Tyrrell & Owens, 1988). This procedure iteratively adjusted the lower and upper bounds of range of saliencies so as to converge on the saliencies generating RTs within ±6 msec of the desired RTs (30 and 90 msec slower, respectively, than the baseline RT). Bounded by the values determined in this way, a monotonic set of 10 equidistant saliency levels was generated (step size equal to the difference between minimum and maximum saliency divided by nine).

This procedure was performed separately for color and orientation targets (Figure 1A), with order counterbalanced across observers (7 subjects starting with color target and 6 subjects starting with orientation targets). There is evidence that orientation saliency is coded in separate channels, coding for left–right differences and differences related to the "steepness" (steep vs. shallow) of the stimuli (Wolfe, 1994). In the present experiment, variations were made in terms of stimulus steepness, that is, targets and distractors were always tilted in the same direction (left or right), but differed in steepness. The various saliency levels thus determined were then introduced as stimulus parameters into the main experiment. Targets were expected to be attracting focal attention and to be detected faster with increasing bottom–up saliency.

Task and Design

The main experiment consisted of 470 trials. Following the symbolic dimension precueing procedure developed by Müller, Reimann, and Krummenacher (2003), a trial began with the presentation of a cue word in the center of the display for 527 msec, which indicated the most likely dimension of the upcoming target, specifically: the German words for color ("Farbe") and, respectively, orientation ("Orientierung") (Figure 1B). These precues correctly indicated the target-defining dimension in 70% of all (target-present) trials (i.e., 70% were valid- and 30% invalid-cue trials). Following a cue–target interval

Figure 1. Example displays used in the experiment, illustrating the different experimental variations. (A) Saliency of a singleton item was parametrically varied across trials. Ten different saliency levels per stimulus dimension were used in the experiment, five of which are depicted here. (B) Example trial sequences for the different experimental conditions. A semantic cue was presented prior to the presentation of the search display. In 70% of all target-present trials, the cue validly indicated the upcoming target-defining dimension (left); accordingly, on the remaining trials, the cues were invalid (right). (Note that the illustrated number of elements per display is different from that used in the experiment, where all displays consisted of 64 elements.)
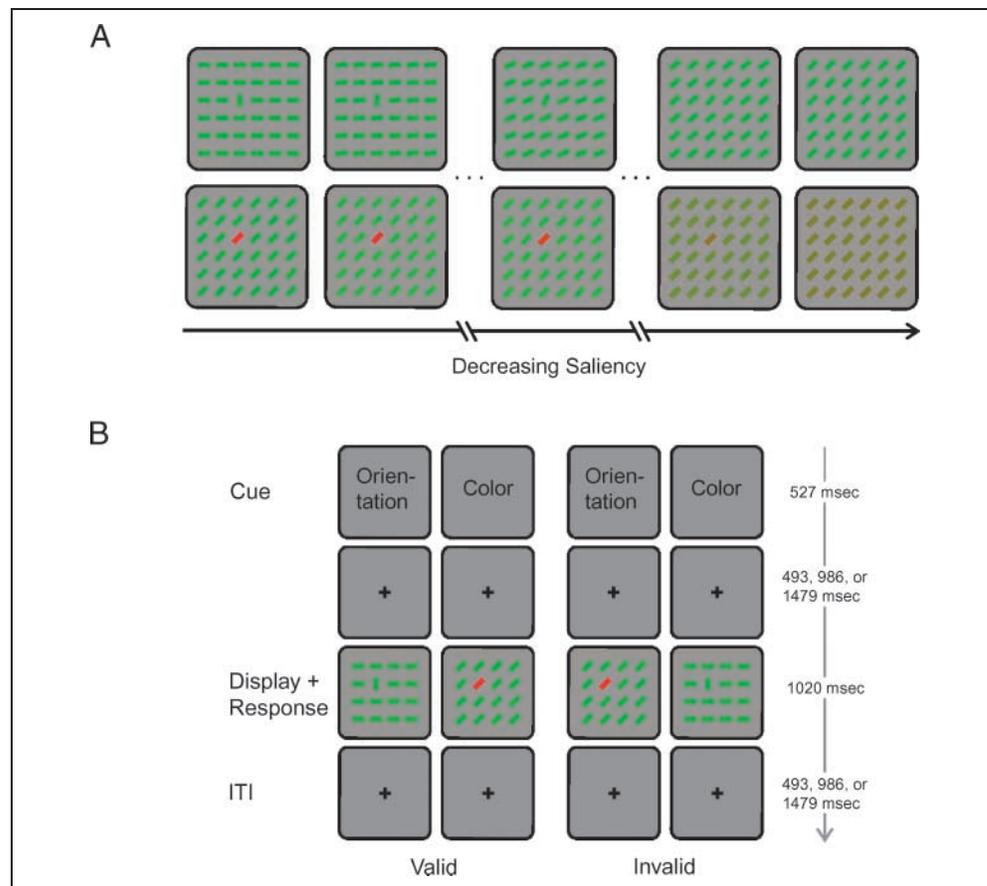
(CTI) of 493, 986, or 1479 msec, the visual search array was presented for 1020 msec. In 60% of the trials, the search array contained a target, and 50% of the targets were color-defined and 50% orientation-defined. The observer's task was to simply indicate the presence (right button press) versus the absence (left button press) of a target (i.e., a target-present response was to be made irrespective of the target's identity). After the off-set of the search array, there was an interval of 493, 986, or 1479 msec. Ninety of the total of 470 trials were replaced by null events, in which case no stimuli (neither cue nor search array) were presented and no response had to be made. Observers were expected to top–down increase the weight for the indicated dimension (and decrease that for the alternative dimension) in response to the precue, thereby facilitating the detection of a target in the likely dimension (see Müller et al., 2003).

fMRI Measurement

Functional images were acquired by means of a 1.5-Tesla SONATA MRI system (Siemens, Erlangen, Germany), using a T2*-weighted echo-planar imaging (EPI) sequence (TR = 3.02 sec, TE = 66 msec). Five hundred fifty-eight volumes were obtained, each consisting of 30 axial slices, allowing for whole-brain coverage. Slice thickness was 4 mm and interslice distance was 0.4 mm, with a 20-cm FOV, a 64×64 image matrix, and a voxel size of $3.1 \times 3.1 \times 4$ mm^3. Images were spatially realigned to the fifth volume (see below) to correct for interscan movement and normalized to the Montreal Neurological Institute (MNI) single-subject template (Ashburner & Friston, 2005; Collins et al., 1998; Evans, Kamber, Collins, & MacDonald, 1994) using the "unified-segmentation" function in SPM5 (see below). This algorithm is based on a probabilistic framework that permits image registration, tissue classification, and bias correction to be combined within the same generative model. The resulting parameters of a discrete cosine transform, which define the deformation field necessary to move the subject's data into the space of the MNI tissue probability maps (Evans et al., 1994), were then combined with the deformation field transforming between "MNI tissue probability maps" and the MNI single-subject template. The resulting deformation was subsequently applied to the individual EPI volumes. The data were then smoothed using a Gaussian kernel of 8-mm full-width half-maximum.

Data Analysis

fMRI data were analyzed using the Statistical Parametric Mapping software SPM5 (Wellcome Department of Imaging Neuroscience, London; Friston et al., 1995; www.fil.ion.ucl.ac.uk/spm5.html). The first four images were

excluded from the analysis, as these were acquired within the time period the MR signal needs to reach a steady state.

Two onset regressors were defined, one for valid- and one for invalid-cue trials, indicating the onset times of individual trials (each considered as a single event). For each onset regressor, an additional regressor for the parametric modulation of target saliency was included. The hemodynamic response to each type of event was modeled using a canonical synthetic hemodynamic response function (HRF) and its first derivative. The six head movement parameters were included as confounds.

First-level linear baseline contrasts were calculated comparing each onset regressor with the implicit baseline (i.e., those time periods that were not explicitly modeled and where no event occurred). These contrasts were then taken to the second level, where they were subjected to a within-subject analysis of variance (ANOVA) with the single factor cue condition (invalid, valid), using a corrected threshold of $p < .05$ at the cluster level ($p < .001$ cutoff at the voxel level). Unequal variances between participants and conditions were compensated for by nonsphericity correction. Differential contrasts were calculated in both directions (i.e., valid > invalid and invalid > valid).

Likewise, the first-level effect of the parametric modulation of target saliency was calculated, followed by a second-level, random-effects within-subject ANOVA with the single factor cue condition, using a corrected threshold of $p < .05$ at the cluster level ($p < .001$ cutoff at the voxel level) and allowing for unequal variances between subjects and conditions. Parametric modulation regressors were set to "1" to test for voxels that exhibited an increased BOLD signal amplitude along with increasing saliency. Analogously, parametric modulation regressors were set to "−1" to reveal those voxels that displayed a decrease of BOLD signal amplitude with increasing target saliency.

To test whether signal increases and decreases differed between valid and invalid trials, the parametric modulation regressors for both trial types were contrasted. This analysis was restricted to those areas that exhibited a significant main effect (whether positive or negative) related to the saliency modulation. To correct for multiple comparisons, a small volume correction (cutoff FWE-corrected $p < .05$) was performed, which was based on a binary mask including all voxels that exhibited significant saliency effects based on the criteria described above (corrected threshold of $p < .05$ at the cluster level, with a $p < .001$ cutoff at the voxel level).

Furthermore, in order to report parameter estimates separately for each saliency level, a new fMRI model was estimated which included separate onset regressors for each saliency level separately for the different cueing conditions.

In order to test for effects of the identity of the target-defining and the cued dimensions, another model was set up with the regressors for valid- and invalid-cue trials split according to the target dimension (color and orientation, respectively, i.e., valid color trials, invalid color trials, valid orientation trials, invalid orientation trials) and including, for each of these regressors, an additional regressor for the parametric modulation of target saliency. Moreover, to test for effects of the variable CTI, an additional parametric regressor for CTI was included. Furthermore, target-absent trials were included separately dependent on whether the cued dimension was orientation or color. Analogously to the analysis above, first-level linear baseline contrasts were calculated comparing each onset regressor with the implicit baseline. Then, at the second level, these contrasts were examined in an ANOVA with the factors cue condition (color cue, orientation cue) and target dimension (color target, orientation target), using a corrected threshold of $p < .05$ at the cluster level ($p < .001$ cutoff at the voxel level). Unequal variances between subjects and conditions were controlled for by nonsphericity correction. Differential contrasts were calculated in both directions. In this way, it was possible to compare the differential effects of color versus orientation targets as well as the effects of color versus orientation cueing.

RESULTS

Behavioral Results

Figure 2A and B presents the group mean target-present RTs and percentages of target misses (i.e., errors), separately for valid- and invalid-cue trials (Figure 2A) and the various target saliency levels (Figure 2B). The RT and miss rate data were examined by separate repeated measures ANOVAs, with the factors cue validity (valid, invalid) and target saliency (levels 1–10). The ANOVA of the RTs revealed both main effects to be significant [validity, $F(1, 12) = 5.5$, $MSE = 53,784$, $p < .05$; saliency: $F(9, 108) = 2.7$, $MSE = 3730$, $p < .01$]. The Validity × Saliency interaction was not significant [$F(9, 108) = 0.95$, $MSE = 1432$, ns]. An ANOVA of the miss rates revealed no effect of saliency [validity: $F(1, 12) = 2.19$, $MSE = 4.55$, ns; saliency: $F(9, 108) = 1.70$, $MSE = 3.247$, ns; Validity × Saliency: $F(9, 108) = 0.98$, $MSE = 5.4$, ns], indicating that the slight numerical reduction in miss rates at intermediate saliencies was not reliable. It was not possible to analyze the false alarm rates as a function of saliency because (due to the randomized presentation of targets of variable saliency within the same block) errors on target-absent trials could not be assigned to a particular saliency condition. Given that the miss rates were statistically balanced across the various saliency levels, we assume that the RT data are not confounded by a systematic speed–accuracy tradeoff as a function of target saliency.

As can be seen from Figure 2A, RTs were significantly faster, and response accuracy was numerically higher, for valid- compared to invalid-cue trials (RTs: 591 (*SEM =*
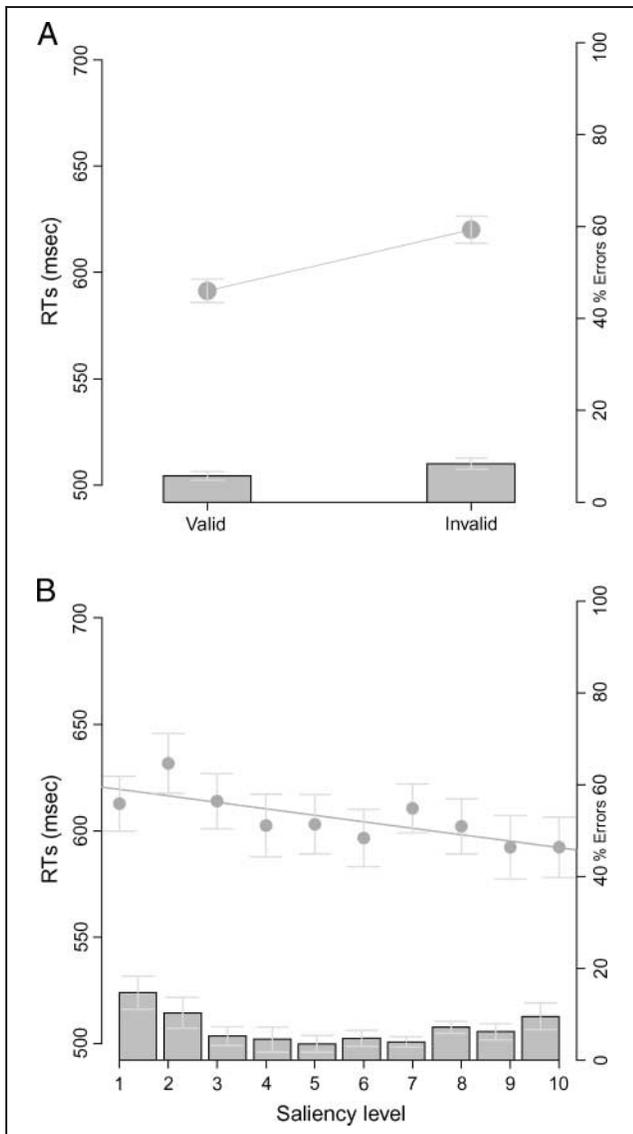
Figure 2. Behavioral data: (A) RTs (dots) and percentage misses (bars) are shown separately for valid- and invalid-cue trials. (B) RTs (dots) and percentage misses (bars) for the different saliency levels (dots), and the linear regression function for the RTs (black line) are depicted. Error bars reflect standard errors of the mean.

17.3) vs. 620 (20.15) msec; miss rates: 5.7% (1.07) vs. 8.4% (1.39)]. Furthermore, as illustrated from Figure 2B, RTs decreased with increasing target saliency. The slope of the decrease was 3 msec per saliency level, with an intercept at 622 msec [linear regression, $r^2 = .59$, $F(1, 8) = 11.59$, $p < .01$]. Misses showed a decrease of 0.3% per saliency level, which was, however, not significant [linear regression, $r^2 = .12$, $F(1, 8) = 1.05$, ns].

Functional Imaging Results

Target Saliency-related Effects

The neural effects associated with enhanced top–down guidance of visuospatial search were examined by ana-

lyzing the regressors for the parametric target saliency modulation. Increasing BOLD response amplitudes associated with decreasing target saliency were found bilaterally in occipital and parietal cortex as well as in frontal cortex. In right parietal and occipital cortex, two clusters of activation were observed: one large cluster in middle and superior occipital areas extending to superior parietal cortex and including large parts of the IPS and inferior parietal cortex, and a second cluster in the postcentral gyrus. Frontal activation was found in the precentral gyrus at the junction with the superior frontal sulcus extending to the middle frontal gyrus.

In the left hemisphere, three occipital and parietal activation clusters were observed: one reaching from the middle occipital gyrus to superior parietal cortex including the posterior part of the IPS and angular gyrus, which was extending medially toward the precuneus; a second cluster in the precuneus; and a third cluster located in the supramarginal gyrus and a more anterior part of the IPS. Frontal activation was found along the middle frontal gyrus at its anterior end, extending to the triangular part of the inferior frontal gyrus (Figure 3, Table 1).

Neural effects related to increases of BOLD signal amplitude with increases of target saliency were observed in medial anterior prefrontal cortex, extending to pregenual anterior cingulate cortex and to the middle orbital gyrus.

Cue Validity-related Effects

The effect of dimensional reorienting—when the cue indicated the incorrect, rather than the correct, target dimension—was assessed comparing invalid- and valid-dimension cue trials. This contrast revealed activations in left and right medial and lateral prefrontal cortex as well as in left parietal areas and bilaterally in the cerebellum. A left-lateralized activation in fronto-polar cortex was observed at the border of the fronto-marginal gyrus and the superior orbital gyrus, extending to the inferior transverse fronto-polar gyrus. Bilaterally, activations were observed at the orbital part of the inferior frontal gyrus extending to the anterior insula. Furthermore, large areas of activation were found bilaterally within the inferior frontal sulcus, which extended dorsally to the middle frontal gyrus and were bounded posteriorly by the precentral sulcus and anteriorly by the pars triangularis of inferior frontal cortex. Medial activation was observed in the medial part of superior frontal cortex at the border to the right pre-SMA (Picard & Strick, 1996) and superior to the rostral cingulate zone. This cluster extended to the left hemisphere. In left lateral posterior parietal cortex, an activation was observed in the supramarginal gyrus, extending to the IPS (Figure 4, Table 1). Furthermore, activation was observed in the left cerebellum.

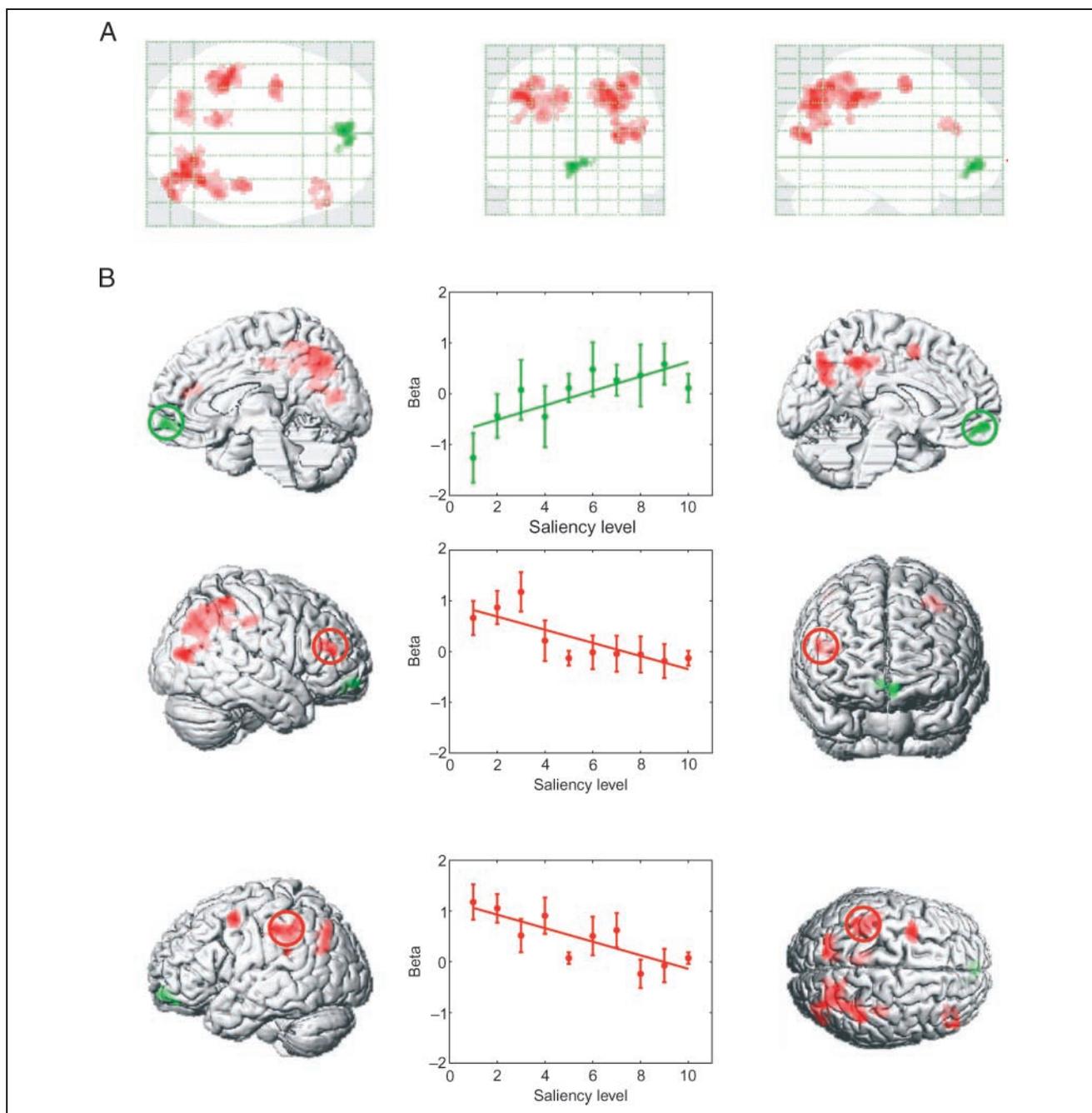The reverse contrast (valid- vs. invalid-cue trials) revealed significant activations at the superior frontal gyrus,

Figure 3. (A) Glass-brain images (top) and (B) surface renderings (left and right column) and signal change patterns (middle column) of functional contrasts for brain areas showing increased activity along with decreasing saliency (red) and areas showing increasing signal changes along with increasing target saliency (green). The graphs in the middle column present the estimated beta values for the brain areas marked by colored circles separately for different saliency levels. Error bars reflect standard errors of the mean.

located slightly anterior to its junction with the precentral gyrus (FEF).

Modulations in Saliency Processing Dependent on Top–Down Control

To examine whether valid and invalid attentional settings would lead to differential processing of saliency, the modulation regressors for valid and invalid trials were con-

trasted. This analysis was restricted to voxels that had shown a significant (positively or negatively correlated) effect related to saliency in the previous analysis. To correct for multiple comparisons, an FWE correction was applied based on a binary mask containing all voxels that showed a significant saliency-related effect. This analysis revealed significantly more positive slopes for valid-compared to invalid-cue trials in the left supramarginal gyrus at the junction between temporal and parietal cortex

Table 1. List of Activations Related to Top–Down Controlled Search Processes, Dimensional Reorienting (Invalid > Valid), and Greater Saliency-related Increases on Valid Trials (Saliency-related Increases Valid > Invalid)

Structure	t Score	Side	MNI
Saliency Negative			
Middle frontal gyrus/inferior frontal sulcus pars triangularis	4.98	R	52 36 22
Precentral gyrus	5.52	L	−36 0 52
Postcentral gyrus	5.26	R	38 −24 46
Supramarginal gyrus	6.96	L	−36 −40 42
Middle occipital gyrus/superior parietal gyrus	4.98	L	−26 −74 32
Precuneus	5.21	L	−8 −46 46
Superior middle occipital gyrus/precuneus/superior parietal gyrus/ angular gyrus/supramarginal gyrus	7.26	R	30 −70 40
Saliency Positive			
Middle orbital gyrus/pregenual anterior cingulate cortex	4.79	L	−2 50 −6
Valid > Invalid			
Superior frontal gyrus	4.6	R	16 −16 48
Invalid > Valid			
Superior orbital gyrus/lateral fronto-polar cortex	4.49	L	−30 60 −4
Inferior frontal gyrus pars orbitalis/anterior insular cortex	5.95	L	−36 24 −12
Inferior frontal gyrus	4.65	L	−44 8 40
Inferior frontal gyrus pars orbitalis/anterior insular cortex	4.73	R	52 24 −4
Middle frontal gyrus/inferior frontal sulcus	5.77	R	32 2 42
Medial frontal gyrus	4.63	R	6 32 46
Supramarginal gyrus	5.38	L	−46 −46 56
Cerebellum	5.39	L	−10 −82 −30
Cerebellum	5.87	L	−26 −76 −44
Saliency (Invalid > Valid)			
Temporo-parietal junction	4.63	L	−44 −42 28
Color > Orientation Targets			
Cuneus/Precuneus	4.12	L	−4 −54 40
Middle occipital gyrus/angular gyrus	4.35	L	−36 −68 30
Lowered Threshold (.001 Uncorrected)			
Fusiform gyrus	3.36	L	−24 −52 −16
Fusiform gyrus	3.28	R	30 −46 −16
Parahippocampal gyrus	3.41	L	−30 −28 −18
Inferior temporal gyrus	4.23	R	58 −30 −22
Orientation > Color Targets Lowered Threshold (.001 Uncorrected)			
Inferior occipital gyrus	3.96	R	52 −64 −12

Coordinates are defined within MNI space.

Figure 4. Glass-brain images and surface rendering of functional contrasts for invalid- compared to valid-cue trials (red), and for the reverse contrast (green).
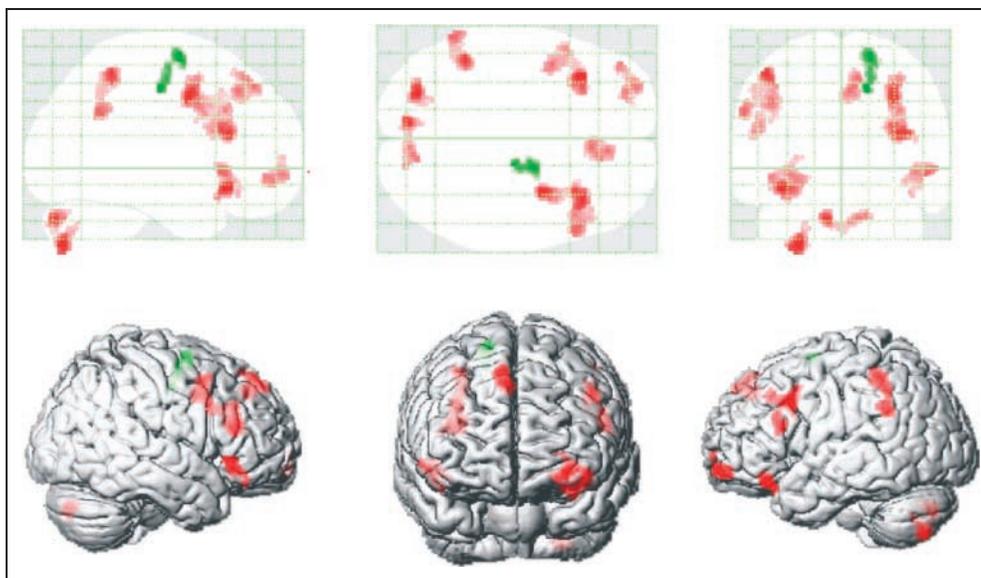
(temporo-parietal junction, TPJ) (Figure 5, Table 1). Extracting the beta values separately for the different cueing conditions and the different saliency levels revealed an opposite signal change pattern for valid- and invalid-cue trials: Valid cueing resulted in an increase of signal changes along with higher saliency, whereas invalid cueing induced decreasing signal changes along with higher saliency levels.

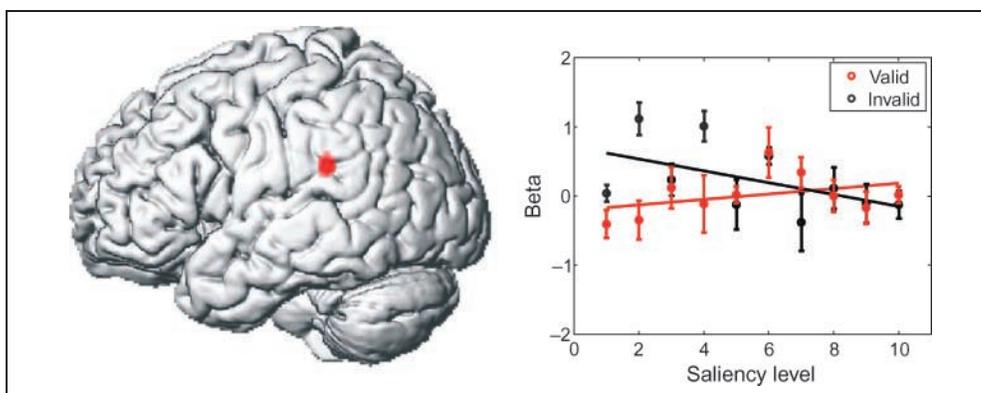### Color versus Orientation Targets

In a further comparison, processing was examined for color versus orientation targets, using the same threshold as for whole-brain analysis (corrected threshold of $p < .05$ at the cluster level, with a $p < .001$ cutoff at the voxel level). This comparison revealed two activations: a midline activation with a maximum in the left cuneus and precuneus, which—overlaid on the cytoarchitectonic probability maps—involved Brodmann's area 18 (Amunts, Malikovic, Mohlberg, Schormann, & Zilles, 2000) as well as dorsal V3 (Rottschy et al., 2007). Furthermore, there was an activation in the left middle occipital gyrus ex-

tending to the angular gyrus, covering parts of the IPS (Choi et al., 2006).

Processing of color is known to involve areas along the ventral visual pathway. In line with this, we found activation in the ventral visual stream when lowering the statistical threshold to an uncorrected level of $p > .001$. Specifically, there was activation bilaterally in the fusiform gyrus, which corresponds well with the coordinates previously reported for V4α (Bartels & Zeki, 2000). Furthermore, there was a left-lateralized activation in the parahippocampal gyrus and an additional activation in the right inferior temporal gyrus.

Modulation of activation in these areas was examined by testing for effects related to the processing of validly versus invalidly cued color targets, and to the reverse contrast. To restrict the statistical analysis to color-sensitive areas only, the results of this contrast were inclusively masked with the contrast comparing color target detection with a masking threshold of $p > .05$. These comparisons did not reveal any significant activation. Irrespective of the precue, color targets elicited larger BOLD signals compared to orientation targets, most markedly in areas

Figure 5. Estimated beta parameters for the different saliency levels in the left TPJ, separately for valid- (red) and invalid-cue (black) trials. Error bars reflect the standard error of mean.

that passed the cluster-level correction: the left cuneus/precuneus and the middle occipital/angular gyrus (Figure 6A). The difference between valid and invalid cueing was small and not significant.

Orientation versus Color Targets

Comparing the processing of orientation versus color targets did not reveal any significant activations exceed-ing a corrected threshold of $p < .05$ at the cluster level, with $p < .001$ cutoff at the voxel level. Decreasing the threshold to an uncorrected level revealed only one cluster of activation within visual brain areas: the right inferior occipital gyrus. Analogously to the procedure described above, attentional modulation within this area was examined by testing for differential activations in the processing of orientation targets depending on the valid-ity of the precue. This comparison, which was inclusively
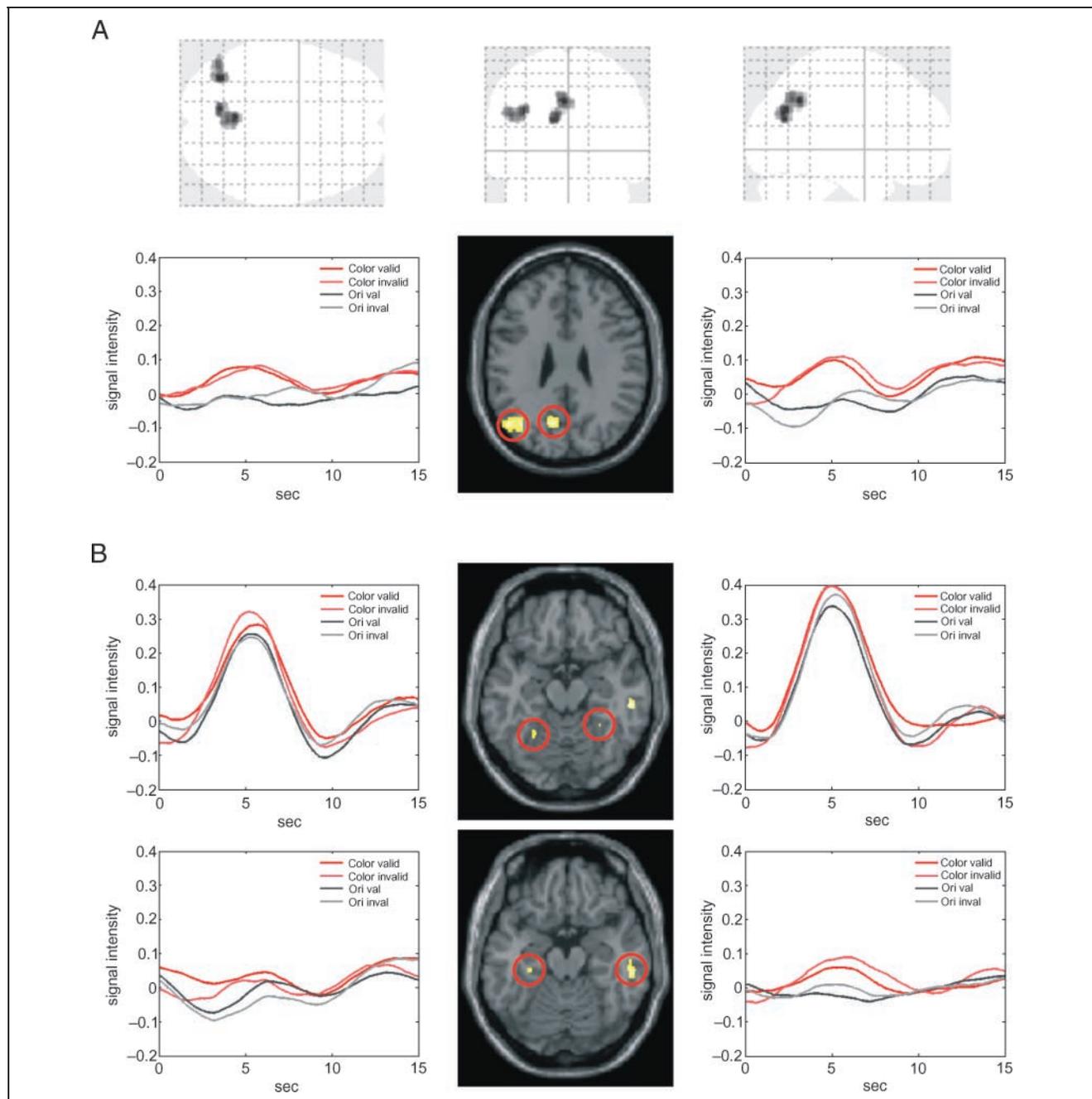

Figure 6. (A) Functional contrast for brain areas showing increased activation along with color target, relative to orientation target, processing, presented on a glass-brain image and overlaid on the MNI single subject, as well as signal time courses extracted from these locations for color (red) and orientation targets (gray), separately for valid (dark) and invalid trials (light). (B) Functional activations from the same contrast presented at an uncorrected threshold ($p < .001$) and the extracted signal time courses.

masked by the main effect of target dimension (orientation > color) with a masking threshold of $p > .05$, did not reveal any significant effects (Figure 7).

Effects of the Cue Dimension

In order to test whether there were differential activations when preparing for precued color and orientation targets, target-present trials were compared dependent on whether they were preceded by a color or an orientation cue. This analysis revealed no significant differences between the two types of dimension cue. An analogous analysis for target-absent trials also failed to reveal any differential activations between color and orientation cues.

Effect of the Cue–Target Interval

Signal increases related to an increased CTI were observed in the right hippocampus (42 −36 −10).

DISCUSSION

Active Search Guidance

Detection of a singleton feature target was hypothesized to require more top–down guidance of visuospatial attention when target saliency is low. Consistent with this, increasing target saliency decreased the RTs required to discern target presence, and decreased the BOLD signal amplitude in a number of brain areas, including the left FEF (Luna, 1998; Paus, 1996) and superior and inferior parietal cortex bilaterally, that are part of the fronto-parietal attention network (Corbetta & Shulman, 2002). Recently, this network has been subdivided into a right-lateralized ventral part, which is thought be involved in stimulus-driven attentional selection, and a more bilaterally organized dorsal part involved in maintaining top–down (endogenous) attentional sets (Corbetta & Shulman, 2002). In part, our data agree with this proposal: the need for endogenous control activated parietal cortex bilaterally. However, these activations were not restricted to superior parietal areas and the IPS, but also involved inferior parietal cortex.

In addition to the visuospatial control areas, the need for enhanced top–down control led to signal modulations in frontal cortex at the right middle frontal gyrus. Hitherto, this brain region has been discussed mainly in the context of working memory (Haxby, Petit, Ungerleider, & Courtney, 2000), although there is also evidence for a role of dorsolateral prefrontal cortex in the top–down control of sensory processing: Chao and Knight (1998) reported that patients with lesions in dorsolateral prefrontal cortex show altered patterns, relative to healthy controls, in auditory evoked brain potentials related to the processing of irrelevant sound. The present data support the role of dorsolateral prefrontal cortex in top–down control, in relation to visual (as well as auditory) processing.

Furthermore, activation was observed in the middle occipital gyrus involving high-level visual processing areas. Interestingly, activation in occipital areas correlated negatively (rather than positively) with stimulus saliency, arguing that it is top–down control, rather than stimulus saliency, that drives activation in these areas during visual search. It is generally known that neural processing in visual cortex can be modulated by top–down control (Noesselt et al., 2002; Brefczynski & DeYoe, 1999; Tootell et al., 1998) and that target detection involves an ongoing interaction between bottom–up and top–down areas (Weidner, Shah, & Fink, 2006). The present data confirm these findings and extend them by showing that the top–down influence determines bottom–up signal coding in the middle occipital gyrus.

Readout of Saliency

In order to identify regions that are more related to stimulus-driven (rather than endogenous) search guidance, we tested for regions that showed an increase of BOLD signal changes with increasing saliency. Such areas are likely to reflect saliency coding per se, or the reading

Figure 7. Functional contrast for brain areas showing increased activation along with orientation target, relative to color target, processing, overlaid on the MNI single subject at an uncorrected threshold ($p < .001$), as well as signal time courses extracted from these locations for color targets (red) and orientation targets (gray), separately for valid (dark) and invalid trials (light).
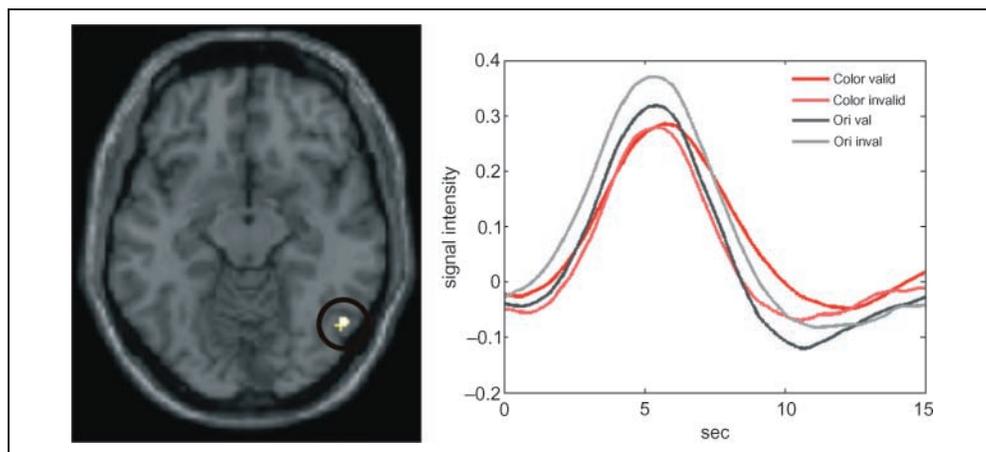
out of saliency information to make it available for further processing, such as discerning the presence of a target and initiating a detection response. Direct saliency coding would be expected to activate posterior brain areas where saliency-based information is extracted—in the present case, in primary visual areas as well as color-sensitive areas along the ventral pathway. However, as reported above, posterior brain areas involved in visual stimulus analysis were activated more with decreasing (rather than increasing) target saliency—indicative of a top–down modulation. This suggests that brain areas in medial anterior prefrontal cortex, where activation increased with increasing target saliency, are likely to be involved in ''secondary'' effects of saliency processing.

Medial anterior prefrontal cortex has been hypothesized to play a role in integrating the outcomes of two or more separate cognitive operations to achieve a superordinate behavioral goal (i.e., when solving a problem requires the integration of the results of two or more separate operations that compute subgoals only; Ramnani & Owen, 2004). Furthermore, medial rostral prefrontal cortex has been suggested to be a critical node in stimulus-oriented attention processes (Burgess, Dumontheil, & Gilbert, 2007), where cognitive processing is triggered more by sensory input than determined by self-generated thoughts. The present data are consistent with this proposal: Stronger saliency signals permit the processing system to operate in a more stimulus-driven mode, which according to Burgess et al. (2007) is associated with medial prefrontal activation: Activation in medial prefrontal cortex was higher with increasing saliency. Note, however, that anterior medial prefrontal cortex has also been observed to be active on trials on which a target-defining dimension changed in a demanding singleton conjunction search task (Weidner et al., 2002). In this task, the target's saliency signal would not be clearly above those generated by the distractors so that saliency readout from posterior coding areas would be more complex. In particular, signals from different visual dimensions, in which the conjunction target is potentially defined, have to be reweighted and recombined until a good signal-to-noise ratio is achieved. This requires a continuous readout of saliency information. The role of medial prefrontal cortex might therefore be to accumulate evidence for a specific (behavioral) decision, in the present case, on the basis of saliency.

Dimensional Reorienting

In the current experiment, observers were presented with semantic dimension cues, in response to which they were expected to *endogenously* establish an appropriate dimensional weight set. Observers were able to make use of valid precues, thereby speeding up target detection relative to invalid precues (see also Müller et al., 2003). Inappropriate dimension sets (invalid- compared to valid-cue trials) activated left lateral fronto-polar cortex, which

has previously been reported in studies examining dimensional attention switches (Pollmann et al., 2000, 2007; Weidner et al., 2002). In these studies, dimension switches were always elicited by changes of the target-defining dimension across trials, that is, when the target on a given trial was defined in a different dimension to that on the preceding trial. Activation of left lateral fronto-polar cortex has been interpreted as supporting switches between predefined (dimensional) parameter settings. The role of left lateral fronto-polar cortex has been confirmed in the present study. Resetting of dimensional parameters is not only mediated via left lateral fronto-polar cortex when dimension shifts are triggered by dimension changes across consecutive trials, but also when observers endogenously form an explicit dimensional expectation on the basis of a semantic cue.

Burgess et al. (2007) proposed that lateral fronto-polar cortex functions as a weighting mechanism that biases processing to operate in a stimulus-independent (rather than a stimulus-oriented) mode, providing a gateway for connecting different ''cognitive processing units'' such as the top–down control areas consisting of bilateral orbito-frontal cortex and the left supramarginal gyrus.

Enhanced neural activity in orbito-frontal cortex, matching the coordinates in the present experiment, was reported in a study of top–down facilitation of visual object recognition (Bar et al., 2006). Bar et al. (2006) recorded the MEG, in addition to fMRI, so that they could specify the temporal dynamics of the activations observed in orbito-frontal cortex and visual processing areas: Activation in orbito-frontal cortex was found to precede activation in visual areas. On this basis, Bar et al. proposed that the posterior orbital gyrus is a source of top–down control in visual object recognition, and suggested that these top–down influences are invoked by low spatial-frequency representations projected directly to orbito-frontal cortex from early visual areas. In the present study, top–down control was triggered by the semantic dimension cues and the need to reconfigure dimensional weight sets. This argues in favor of a more general role of orbito-frontal cortex in exerting top–down control, specifically: Posterior orbital gyrus is involved in altering endogenous attentional settings, including dimensional weight sets. The altered settings are presumably mediated to posterior areas via left parietal cortex, which has previously been discussed to be involved in nonspatial attention shifts (Weidner et al., 2002, 2006; Coull, Frith, Buchel, & Nobre, 2000; Wojciulik & Kanwisher, 1999).

Top–down control modulated signals in frontal cortex at the posterior part of the right inferior frontal gyrus close to the junction with the precentral gyrus—an area often referred to as the inferior frontal junction (IFJ). In a meta-analysis (Derrfuss et al., 2005), the IFJ was revealed to be involved in a variety of tasks requiring cognitive control, including task-switching and the color–word Stroop task. The role of the IFJ in cognitive control is further supported by findings from a visual-search study

(de Fockert, Rees, Frith, & Lavie, 2004). de Fockert et al. (2004) observed the presence of a task-irrelevant singleton (distractor) item to elicit activation in an area corresponding to the IFJ as described by Brass et al. (2005). de Fockert et al. suggested that this area is involved in preventing interference from irrelevant distractors. Our current data are consistent with this notion. In both the de Fockert et al. and the present study, IFJ activation may be taken to reflect enhanced top–down control during visual search. In the present study, however, distractors were homogeneous so that none of them would have elicited a strong saliency signal. This suggests that the process of top–down control reflected by IFJ activation in visual search is critically related to the signal-to-noise ratio between the target and the distractors (Duncan & Humphreys, 1989), rather than to competition by a single (nontarget) saliency signal.

In addition, in the present study, medial prefrontal cortex activation has been observed at the location of the human pre-SMA (Picard & Strick, 1996). The pre-SMA is highly connected with prefrontal cortex, which was also activated in the present study. Functionally, it is associated with visuomotor associations, is active during working memory, and is associated with cognitive input for motor behavior—which is consistent with the bilateral cerebellar activation observed in the present study. Furthermore, the pre-SMA has recently been suggested to be part of a network associated with coordinating voluntary and stimulus-driven attention (Serences et al., 2005).

In summary, dimensional reorienting is associated with activation in brain areas associated with cognitive control, together with top–down facilitation of visual processing as well as the preparation of motor responses. In addition, left lateral fronto-polar cortex was activated, which, following the interpretation of Burgess et al. (2007), might gate processing within these different systems.

Activation differences related to the different target dimensions were weak, supporting the idea that the control networks mediating dimensional reorienting are supradimensional in nature, involving a more general control mechanism.

Top–Down Control and Stimulus Saliency

The network observed for the different sources of top–down control in visual search seem to involve separate brain structures. However, in order to optimize target detection in visual search, both systems are likely to interact. A candidate area for the coordination of top–down guidance within both systems might be the right middle frontal gyrus, which was found to be active in both the visuospatial control network as well as during dimensional reorienting. The right middle frontal gyrus has previously been suggested to act as an interface between the dorsal and ventral attention orienting networks (Corbetta, Patel, & Shulman, 2008).

Furthermore, visuospatial top–down guidance and the calculation of saliency signals are likely to interact as visuospatial search guidance has to be based on the calculated saliency signals, requiring a combination of these signals at some level. The stronger the saliency signal, the less visuospatial guidance is required to detect the target *stimulus*. Valid cueing, therefore, should decrease the need for visuospatial guidance. An area that showed a differential saliency effects as a function of cue validity was the left TPJ.

Left parietal activation has been discussed in the context of mediating nonspatial attention shifts. Within the regions that exhibited a parametric response to stimulus saliency, with either a positive or a negative correlation, a differential cue validity-dependent response was observed in the left TPJ: Saliency was coded differently depending on whether the internal attention set was correct (valid-cue condition) or incorrect (invalid-cue condition). Valid cueing led to increasing signal changes along with higher target saliency, whereas presentation of invalid cues decreased signal changes along with higher target saliency. This pattern indicates that the TPJ is involved in both bottom–up and top–down processing, and is likely to integrate both kinds of signal. More evidence for a role of the TPJ in combining top–down and bottom–up signals comes from a recent fMRI study (Serences et al., 2005), in which participants had to monitor a rapid serial visual presentation stream for the occurrence of a target letter defined by a specific color (e.g., the red letter), whereas two other, task-irrelevant letter streams were presented simultaneously. The TPJ was activated by task-irrelevant distractors that matched the color of the target, but not by salient color singletons defined by a different color feature. Consistent with this, the present data demonstrate that the expectation of (i.e., the attentional set for) a predefined target in a particular dimension alters the processing of saliency within the left TPJ. Hence, the TPJ is a suitable candidate for mediating between top–down and bottom–up signals, along the lines envisaged by Corbetta and Shulman (2002). According to them, the TPJ is part of the ventral fronto-parietal bottom–up network which acts as a "circuit breaker" for the dorsal top–down system, directing attention to salient events.

The TPJ is usually discussed as being part of a right-lateralized attention network (Corbetta & Shulman, 2002), whereas we found TPJ activation only in the left hemisphere. However, left-hemispheric TPJ activation has been reported previously (Kincade, Abrams, Astafiev, Shulman, & Corbetta, 2005). Furthermore, left TPJ activation might be related specifically to the nonspatial nature of the (dimension-based attention) task used in the present experiment, as nonspatial attentional orienting has previously been associated with left parietal involvement (Weidner et al., 2002, 2006; Coull et al., 2000; Wojciulik & Kanwisher, 1999). In summary, the present data suggest that the left TPJ plays a role in integrating an endogenously

formed (dimension-based) attention set with bottom–up generated saliency signals.

Conclusion

We observed two different networks of brain activation related to top–down control in visual search. In agreement with visual-search theories, we dissociated processes related to search guidance acting on the level of an integrated (supradimensional) topographic saliency map. Search guidance involves areas related to visuospatial attentional orienting and, in addition, areas that underlie specific cognitive processes in middle frontal cortex. We propose that neural activity in the middle frontal gyrus is associated with search parameters (i.e., information about potential target stimuli) and the combination with visuospatial orienting of attention. Anterior medial prefrontal cortex is involved in accumulating evidence for target presence and therefore shows a positive correlation of BOLD signal changes with target saliency.

A second network of top–down control was associated with dimension-based selection. Reallocating attentional resources (''weight'') from one dimension to another in response to semantic cues involved left lateral prefrontal cortex, presumably gating processing between areas subserving top–down facilitation of visual processing (posterior orbito-frontal cortex), cognitive control (inferior frontal gyrus), and motor preparation (pre-SMA and cerebellum). Selective enhancement of the coding of saliency signals in the validly cued dimension was observed in the left TPJ. In contrast to previous studies, this area was not related to stimulus-driven attention shifts per se (as proposed by Corbetta & Shulman, 2002), but rather to processes integrating bottom–up generated target signals with top–down attentional control signals.

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