

The Role of Top–Down Focused Spatial Attention in Preattentive Salience Coding and Salience-based Attentional Capture

Sabine Bertleff¹, Gereon R. Fink^{1,2}, and Ralph Weidner¹

Abstract

■ Selective visual attention requires an efficient coordination between top–down and bottom–up attention control mechanisms. This study investigated the behavioral and neural effects of top–down focused spatial attention on the coding of highly salient distractors and their tendency to capture attention. Combining spatial cueing with an irrelevant distractor paradigm revealed bottom–up based attentional capture only when attention was distributed across the whole search display, including the distractor location. Top–down focusing spatial attention on the target location abolished attentional capture of a salient distractor outside the current attentional focus. Functional data indicated that the missing capture effect was not based on diminished bottom–up salience signals at unattended distractor locations.

Irrespective of whether salient distractors occurred at attended or unattended locations, their presence enhanced BOLD signals at their respective spatial representation in early visual areas as well as in inferior frontal, superior parietal, and medial parietal cortex. Importantly, activity in these regions reflected the presence of a salient distractor rather than attentional capture per se. Moreover, successfully inhibiting attentional capture of a salient distractor at an unattended location further increased neural responses in medial parietal regions known to be involved in controlling spatial attentional shifts. Consequently, data provide evidence that top–down focused spatial attention prevents automatic attentional capture by supporting attentional control processes counteracting a spatial bias toward a salient distractor. ■

INTRODUCTION

The processing capacities of the visual system are limited. Accordingly, only a subset of the large amount of visual information available can be selected. The decision, which information is prioritized for further processing and which one is to be ignored, is often referred to as selective attention and is to some extent controlled exogenously by visual stimulus features. A stimulus that stands out from its background is more likely to grab an observer's attention. Its salience is largely determined by a local difference from surrounding items with regard to certain visual features such as color, orientation, brightness, etc. (Wolfe, 1998; Nothdurft, 1991). Computational models of focal visual attention take into account such feature differences to quantify the strength of bottom–up activation underlying stimulus-driven attention selection (Itti & Koch, 2000; Wolfe, 1994; Koch & Ullman, 1987). In particular, salience is assumed to be calculated separately for different visual features and to be represented in topographic feature-salience maps. These maps are then integrated to an overall salience map or supra-feature salience maps (Itti & Koch, 2001; Wolfe, 1994; Treisman & Gelade, 1980), constituting the representational

basis of attentional selection. In particular, peaks indicating locations with a high overall salience attract attention and are hence more likely to be selected. Accordingly, the allocation of the attentional spotlight is—at least to a large degree—controlled exogenously by stimulus features.

Moreover, selective attention can be guided voluntarily by internal settings of the observer. Attention can be directed endogenously to specific features or to specific locations (see, e.g., Weidner & Müller, 2013; Bichot, Rossi, & Desimone, 2005; Martinez-Trujillo & Treue, 2004; Sàenz, Buraças, & Boynton, 2003; Chawla, Rees, & Friston, 1999). Electrophysiological evidence (Hopfinger & West, 2006) as well as behavioral results suggest that exogenous and endogenous attention (Berger, Henik, & Rafal, 2005; Juola, Koshino, & Warner, 1995) is controlled by separate but interacting functional systems that partially share stages of information processing.

This view is further substantiated by current knowledge of the functional neuroanatomy underlying attentional control. Attentional selection has been suggested to be controlled by two cortico-cortical mechanisms (Corbetta, Patel, & Shulman, 2008; Corbetta & Shulman, 2002): a bilateral dorsal frontoparietal network involving dorsal parietal and frontal brain regions that has been suggested to host endogenous top–down mechanisms and a second system that responds along with the dorsal network particularly when detecting behaviorally relevant stimuli,

¹Cognitive Neuroscience (INM-3) Research Centre Jülich, ²University Hospital Cologne

especially at unattended locations and during reorienting (Corbetta et al., 2008). These control networks seem to host both feature- and space-based mechanisms (Egner, Etkin, Gale, & Hirsch, 2008; Vandenberghe, Gitelman, Parrish, & Mesulam, 2001). Importantly, although located in the same brain regions, space-based and feature-based control processes are implemented independently within these regions (Egner et al., 2008) and can accordingly, at least in part, be altered independently by focal TMS (Schenkluhn, Ruff, Heinen, & Chambers, 2008).

It has been speculated that endogenous attentional modulation operates via top-down priority maps in intraparietal sulcus, combining feature and space preferences (Egner et al., 2008). This priority map could then be used to weight bottom-up representations (Weidner & Müller, 2013; Weidner, Krummenacher, Reimann, Müller, & Fink, 2009; Found & Müller, 1996; Müller, Heller, & Ziegler, 1995) or to bias competition between bottom-up representations as suggested in the bias competition model (Desimone & Duncan, 1995; Bundesen, 1990). The latter framework suggests that attentional effects are best understood in the context of competitive interactions among stimulus representations and that these interactions can be biased in favor of behaviorally relevant stimuli (Desimone, 1998). These mechanisms are particularly relevant when exogenous and endogenous control signals are incongruent. There is conflicting evidence whether in these situations attentional selection is dominated by bottom-up rather than by top-down mechanisms. Experimentally, the interaction of top-down and bottom-up control is often investigated using the irrelevant distractor paradigm (Theeuwes, 1991, 1992, 1994). When searching for a singleton target shape among homogeneously shaped distractors, the presence of a singleton color distractor typically increases RTs indicating automatic attentional capture. This notion is supported by ERP data (Hickey, McDonald, & Theeuwes, 2006) providing evidence that attention is involuntarily shifted toward a highly salient, albeit task-irrelevant distractor before being reoriented toward the target. However, controversial findings exist whether or not salience-based attentional capture can be top-down controlled (Müller & Krummenacher, 2006; Bacon & Egeth, 1994; Theeuwes, 1994; Folk, Remington, & Johnston, 1992). To account for this competing evidence, Theeuwes (2004, 2010) highlighted the role of top-down focused spatial attention, suggesting that it acts to prevent attentional capture by reducing salience coding of distractor stimuli outside the spatial focus. Accordingly, only salient items within the attentional focus are assumed to capture attention.

This study investigated the effects of top-down focused spatial attention on the neural coding of salience as well as on behavioral and functional aspects of attentional capture by means of fMRI. Spatial cueing and the irrelevant distractor paradigm (Theeuwes, 1991, 1992, 1994) were combined to vary simultaneously the size of the attentional focus and salience. The cues were either 100%

valid, generating a small attentional focus around the target location, or spatially nonpredictive, thereby encouraging participants to distribute their attention across the whole search display, including the salient distractor location.

Four VOIs representing visual processing at four spatial locations, each in a different quadrant of the visual search display, were identified and used to extract signals induced by salient and nonsalient distractors. These signals were then compared separately for conditions of highly focused versus diffused spatial attention. In addition, whole-brain analysis was performed to identify brain regions activated by a salient distractor located outside the spatial focus or within a widespread attentional spotlight.

Theoretically, top-down focused spatial attention may affect attentional capture at various levels of processing. For instance, it may directly prevent salience coding on relatively early levels of visual processing. If this notion holds (Theeuwes, 2004, 2010), one may expect reduced signal differences between salient and nonsalient distractors when the target location was validly precued (i.e., when distractors were located at an unattended position).

Alternatively, retinotopic salience coding could also be largely unaffected, with potential effects on attentional capture related to activation changes in higher-level attentional and cognitive control regions.

Candidate regions would be the superior parietal cortex as well as left inferior frontal gyrus, because these regions have been suggested to support the neural systems' attempts of resolving conflicts between target and salient distractor information (De Fockert, Rees, Frith, & Lavie, 2004).

METHODS

Before the fMRI experiment, each participant engaged in a behavioral training session to practice and familiarize with the task. Within 1 week after the training session, each participant performed the same task in the fMRI session.

Participants

Twenty-six participants (eight men, mean age = 26.38 years, age range = 20–43 years) took part in both the pretest and in the fMRI experiment. They were all right-handed as measured using the Edinburgh Handedness Inventory (Oldfield, 1971) and reported normal or corrected-to-normal visual acuity. In all participants, color vision was normal as assessed by pseudoisochromatic color plates (Velhagen & Broschmann, 2003). No neurological or psychiatric disorders were reported. All participants gave written consent for participation and were remunerated for their time. The study was approved by the ethics committee of the German Society of Psychology.

Stimuli

During behavioral training, stimuli were presented on a 22-in. Samsung SyncMaster 2233 (Samsung Electronics Co., Ltd., Seoul, South Korea) screen at a distance of 72 cm. Distance was controlled by a forehead and chin rest. In the fMRI session, stimuli were presented on a 30-in LCD screen behind the scanner at a distance of 245 cm. Participants saw the monitor via a movable mirror installed on top of the head coil.

Because of the different distance and with the limited size of the screen, the visual angles for the fMRI experiment and the training (angles in brackets) differed from each other. To ensure visibility of the stimuli in the fMRI part, the size of the stimuli was increased to encompass the whole screen. All stimuli were presented on a black background with a white fixation cross of 0.1° (0.2°) for each segment in the center of the screen. Participants were instructed to fixate the cross throughout the experiment. In every trial, a spatial cueing display preceded the search display to modulate the size of the attentional window (small vs. wide) for both distractor conditions (present vs. absent).

Spatial Cueing Display

The cueing display consisted of either a white circle with a radius of 0.407° (0.9°) and with its center at fixation or a white arrow with a length of 0.814° (1.8°) and with its endpoint at fixation. Each cue was presented together with eight gray dots, each with a radius of 0.05° , arranged in a circular shape and centered at fixation, indicating the exact position of the upcoming element of the visual search display. The white arrow pointed to one of the eight possible target positions, which randomly varied

across the experiment. Because the white arrow indicated target positions with 100% validity, we hypothesized that it would generate a small focus of spatial attention around the target location. In contrast, the white circle was nonpredictive regarding the target location, thereby encouraging participants to widen their attentional focus and thus to attend to the whole search display. Spatial cueing displays are illustrated in Figure 1A.

Visual Search Display

The visual search display consisted of eight colored shapes presented equally spaced along the circumference of an imaginary circle with a radius of 1.57° (3.1°) centered at fixation. Each shape contained a white vertical line with a length of 0.25° (0.36°) that was either tilted 45° to the left or to the right. The target shape was a circle with a radius of 0.332° (0.568°) that was presented in green (CIE coordinates .300/.600) or red (CIE coordinates .640/.330). The remaining elements were diamond shapes with a height and width of 0.701° (1.27°) presented in the same color as the target circle. In the salient distractor-present condition, one of the diamonds was colored contrary to the remaining diamond shapes constituting a unique and salient color distractor among homogeneously colored and therefore nonsalient distractor shapes (see Figure 1B).

Target shapes were presented at one of the eight possible stimulus positions in the visual search display. The target location randomly varied trial-by-trial across the experiment. Importantly, the salient distractor was never presented at positions next to the target location. Thus, the salient distractor's location randomly varied between

Figure 1. The cueing display (A) consisted either of an arrow indicating the upcoming target location with 100% validity or a spatially nonpredictive circle. The eight gray dots indicated the exact positions of the stimuli in the upcoming visual search display. Visual search displays (B) showing any possible combination of distractor and color condition and two samples of the position localizer (C) coding four possible distractor positions in the visual search display.

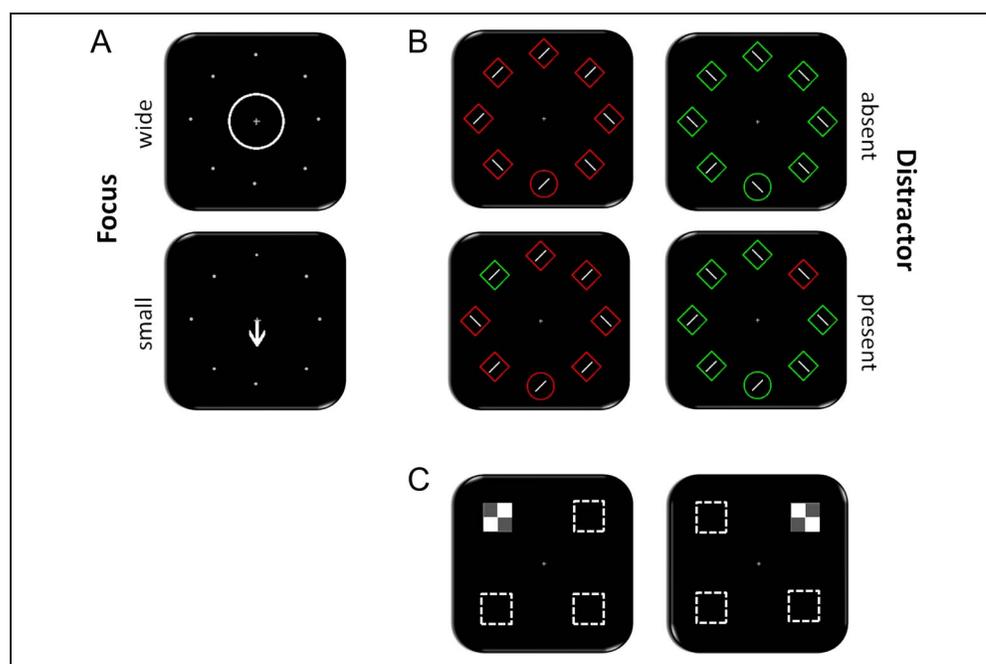
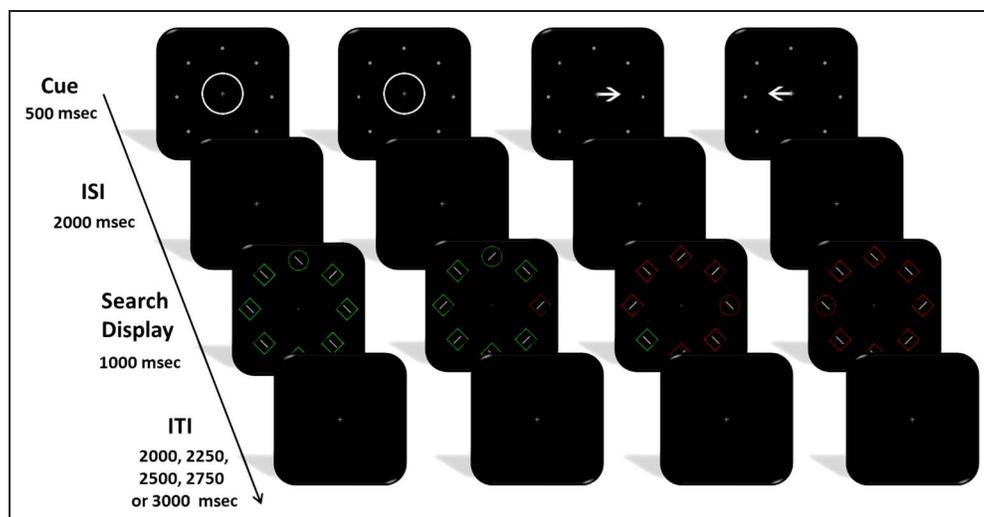


Figure 2. Example trial sequences for the different experimental conditions. In 50% of the trials, a perfectly valid cue pointed to one of the eight possible target positions; on the remaining trials, a spatially nonpredictive circle preceded the visual search display. Within the search display, a color distractor could be either absent or present at one of the eight possible stimulus positions. Note that the color distractor never appeared on a position next to the target position.



five possible positions as a function of the target location in the corresponding trial.

Position Localizer

In the fMRI part of the experiment, a position localizer session followed the visual search task. The localizer was a small reversing checkerboard with a height and width of 0.701° presented at four possible distractor locations in each visual field quadrant (see Figure 1C).

Design and Procedure

A 2×2 factorial design combining the two independent factors Salient Distractor (present, absent) and Attentional Focus (small, wide) resulted in four different experimental conditions, which varied blockwise across the experiment. Because there were two possible color combinations of the stimuli in the search display (red items and green distractor vs. green items and red distractor), each condition was presented twice. Consequently, the experiment consisted of eight blocks, each comprising 36 trials, resulting in a total of 288 trials. Blocks alternated between salient distractor conditions. Half of the participants started with the salient-distractor-present condition, the other half with the salient-distractor-absent condition. The attentional focus alternated between small and wide in ABBA or BAAB order, randomized across participants. The color combination alternated between green target/red distractor and vice versa in AABB or BBAA order, also randomized across participants.

Each trial started with a spatial cueing display that lasted 500 msec. The cueing display was followed by a 2000-msec interval. Then, the visual search display was presented for 1000 msec. An intertrial interval, which randomly varied between 2000, 2250, 2500, 2750, and 3000 msec, separated the trials. In the training session, the next block started via button press, whereas in the fMRI session, the break between blocks was fixed for 5000 msec.

Thus, the duration of the training session differed individually, whereas the fMRI session lasted around 30 min.

Participants' task was to attend to the target circle and to report the orientation of the line within the target. By pressing the response button with the left or right index finger, participants indicated whether the line was tilted to the left or right, respectively (see Figure 2).

To functionally identify VOIs corresponding to the visual cortical representations of four different distractor locations, a position localizer session was performed in which participants viewed alternating 16-sec blocks of a reversing checkerboard, presented at one of the four possible locations each in one of the different quadrants. Each localizer was presented twice at each of the four positions resulting in a total of eight blocks. Blocks were separated by an interval of 16 sec during which a fixation cross was presented. Thus, the duration of the localizer session lasted 4.27 min. During the entire session, participants' task was to fixate the cross in the center of the screen.

fMRI Measurement

Data Acquisition

Functional imaging data were collected using a 3-T TRIO MRI system (Siemens, Erlangen, Germany) and T2* weighted EPI (with a repetition time of 2.2 sec and an echo time of 30 msec). For the main experiment a total of 819 volumes and for the position localizer a total of 128 volumes of 36 axial slices were acquired using an interleaved slice mode. Slice thickness was 3 mm with an interslice distance of 15%, corresponding to 0.45 mm. A 64×64 image matrix and a field of view of 200 mm were used resulting in a voxel size of $3.1 \times 3.1 \times 3.0 \text{ mm}^3$.

Preprocessing

The Statistical Parametric Mapping software SPM (Wellcome Department of Imaging Neuroscience, London,

United Kingdom; www.fil.ion.ucl.ac.uk/spm/software/spm8) was used for preprocessing and analyzing functional imaging data. The first nine images were excluded from analysis, as these were acquired before the first stimulus display appeared and before the BOLD signal had reached a steady state.

The remaining images were spatially realigned to correct for interscan movements. Then, images were normalized to the mean image, which was previously computed using the segmentation function. Finally, data were smoothed using a Gaussian kernel of 8 mm FWHM.

Data Analysis

Three of the 26 participants were excluded from data analysis because of movement artifacts. For another nine participants, error trials were not recorded because of technical problems. However, their behavioral and fMRI data were included for the sake of statistical power. Additionally, five of those subjects participated a second time to account for the technical problems during their first scanning session. Consequently, 28 behavioral and functional data sets derived from 23 participants were analyzed.

Behavioral Data Analysis

The free statistical software R (R Foundation for Statistical Computing, Vienna, Austria; www.r-project.org) was used for the analysis of the behavioral data collected in the fMRI experiment. Repeated-measures ANOVAs of RTs and error rates were conducted with the within-subject factors Salient Distractor (present, absent) and Attentional Focus (small, wide). Error trials, trials following errors and breaks, as well as trials with RTs faster than 200 msec and slower than 1000 msec were excluded from RT analysis. For nine participants, error trials were not recorded and therefore could not be removed from RT analysis. Five of these nine participants volunteered to repeat the experiment. Accordingly, for these participants, two RT data sets were available effectively doubling the amount of trials. A Welch two-sample *t* test was calculated to compare the mean RTs of data sets from which error trials were removed with those that include error trials. There were no significant differences in RTs, $t(61.223) = -0.3939$, $p = .695$, between the data sets.

Because there was no accuracy data for nine participants, calculation of mean error rates was only based on data of 19 participants. To ensure that each participant did the fMRI task as instructed, we additionally analyzed accuracy data collected in the training session. A Welch two-sample *t* test was conducted to compare error rates of participants who produced data sets including ($n = 19$) and data sets excluding error trials ($n = 9$) in the subsequent fMRI session. Results revealed no significant differences, $t(83.88) = 1.7119$, $p = .095$, between both samples (including errors: $M = 5.7\%$, $SD = 4.6\%$; excluding errors: $M = 6.4\%$, $SD = 3.7\%$), suggesting that

accuracy data of participants who produced data sets excluding error trials in the subsequent scanning session were not different from the other participants.

Functional Analysis: Main Experiment

Four onset regressors were defined reflecting the four different experimental conditions. Because the cueing phase and the search phase implemented in the experimental design were temporarily relatively close, a combined BOLD signal was modeled starting with the onset times of the spatial cueing display. Accordingly, the duration was set to 3.5 sec to cover the period from cue onset until the offset of the visual search display. Similar to the behavioral analysis, trials after breaks and trials with RTs faster than 200 msec or slower than 1000 msec were excluded. Additionally, erroneous trials and trials thereafter were omitted. For nine participants, error trials were not recorded and therefore could not be excluded. However, because five of those subjects participated a second time and to keep between- and within-subject variance separated for each of those participants, data sets were combined on the first level with explicitly modeling the two scanning sessions. The hemodynamic response was modeled using a canonical hemodynamic response function and a time derivative. Linear and quadratic effects of the six head movement parameters were included as confounds (Lund, Nørgaard, Rostrup, Rowe, & Paulson, 2005).

To specify the first-level contrasts, each experimental regressor was compared with the implicit baseline. At the second level, the resulting contrast images were subjected to a second-level flexible factorial design with “conditions” as within-subject factor and participants as a random factor using a random effects analysis. First, contrasts were calculated reflecting the main effects for the factors Salient Distractor (present > absent, absent > present) and Attentional Focus (small > wide, wide > small). In addition, the interaction was calculated comparing Salient Distractor present versus absent condition for small versus wide Attentional Focus. Furthermore, to test for a distractor effect inside and outside the spotlight of attention, differential contrasts for the factor Salient Distractor were calculated within both Attentional Focus conditions (i.e., small: present > absent, absent > present; wide: present > absent, absent > present).

Functional Analysis: Position Localizer Experiment

Four different VOIs in visual cortical areas were identified by means of localizer stimuli at four of the eight possible distractor positions, each in a different quadrant of the visual search display. Four regressors indicating the onsets of visual stimulation (duration = 16 sec) at the four different localizer positions were defined. The hemodynamic response for each block was modeled using a hemodynamic response function and its time derivative.

The six movement parameters were included into the model.

First-level analysis was conducted comparing each onset regressor with the remaining three onset regressors. These differential contrasts were then taken to the second level where they were subjected to one sample *t* tests. A statistical threshold of $p < .05$, corrected for multiple comparisons, was achieved using a family-wise error (FWE) correction at the peak level. Second-level contrasts for each regressor were then considered as VOIs, which were used to extract beta values in the VOI analysis described below.

VOI Analysis

VOI analysis was performed to compare salience coding under conditions of attention and inattention at specific locations in the visual field. Therefore, an additional first-level model was estimated with separate regressors representing the different experimental conditions, separately for the four potential distractor locations, and baseline contrasts were calculated for each condition. Functional activation induced by a salient distractor within a given VOI (as derived from the position localizer experiment) was identified by contrasting distractor present and absent trials at the respective position in the visual field. The coordinates of the maximum *t* value within the VOI were then used to extract estimated BOLD amplitudes when either a salient or a nonsalient distractor was presented at the corresponding position in the visual field. This was done separately for the wide and small attentional focus condition. Beta values were then taken to a three-factorial within-subject ANOVA with the factors Localized VOI (1, 2, 3, 4), Salient Distractor (present at

the specific position within the VOI, absent from display), and Attentional Focus (small, wide).

RESULTS

Behavioral Data

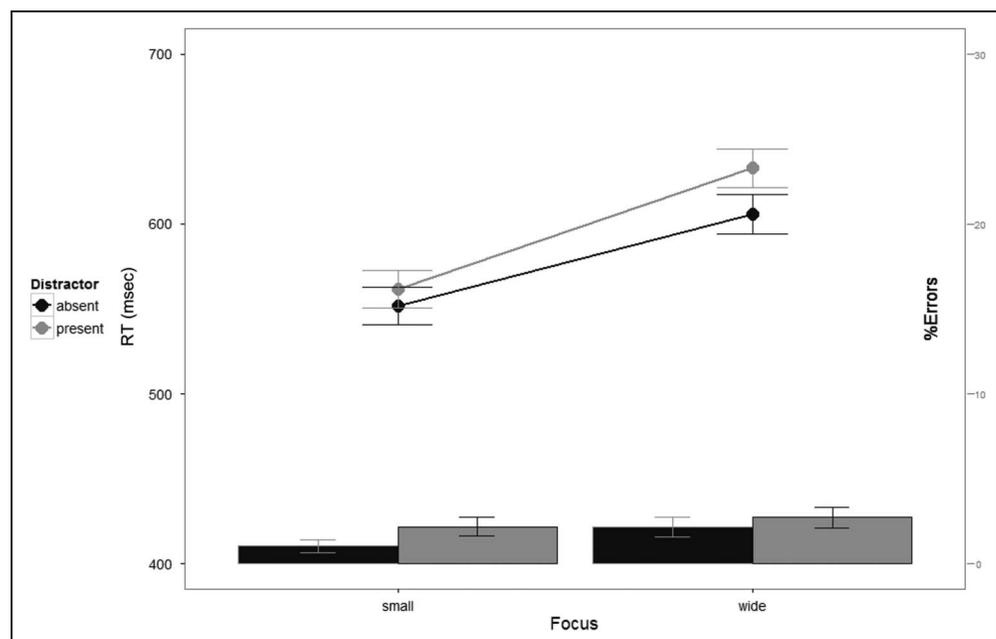
Mean RTs and responses were collected during the fMRI session. RTs and error rates were subjected to separate repeated-measures ANOVAs with the within-subject factors Salient Distractor (present, absent) and Attentional Focus (small, wide).

Error rates and mean RTs are depicted in Figure 3 for the factors Salient Distractor and Attentional Focus. Please note that the calculation of mean error rates is based on data of 19 participants.

Participants made significantly more errors on average, $F(1, 18) = 12.86, p < .01$, when a salient distractor was present ($M = 3.6\%$, $SD = 3.2$) compared with when it was absent ($M = 2.4\%$, $SD = 2.9$). In addition, mean error rates were significantly higher, $F(1, 18) = 7.985, p < .05$, in the wide-focus condition ($M = 3.6\%$, $SD = 3.3$) than in the small-focus condition ($M = 2.4\%$, $SD = 2.8$). The interaction of Salient Distractor and Attentional Focus was not significant, $F(1, 18) = 1.445, p = .245$, suggesting that there was no difference in accuracy when the salient distractor was presented under conditions of widespread (present: $M = 4\%$, $SD = 3.3$; absent: $M = 3.2\%$, $SD = 3.2$) or small focused attention (present: $M = 3.2\%$, $SD = 3.1$; absent: $M = 1.5\%$, $SD = 2.3$).

Computation of mean RTs was based on data of 23 participants. For five of those participants, two RT data sets were available, doubling the amount of trials analyzed. As described above, error trials, trials following errors and breaks, as well as trials with RTs faster than 200 msec or

Figure 3. Mean RTs (lines) and percentage misses/errors (bars) are shown separately for each attentional focus (small, wide) and salient distractor (present, absent) condition. Error bars reflect the standard errors of the mean.



slower than 1000 msec were excluded from RT analysis. Overall, 96.5% of the trials survived the exclusion criteria and were subjected to a repeated-measures ANOVA of mean RTs.

The ANOVA of the RTs revealed significant main effects for both factors. Responses were significantly slower, $F(1, 22) = 34.9, p < .001$, when the salient distractor was present ($M = 595$ msec, $SD = 69.3$) compared with when it was absent ($M = 578$ msec, $SD = 64.7$). Presence of a salient distractor caused a 16-msec interference effect on average, indicating that it captured attention. As illustrated in Figure 3, RTs were significantly faster, $F(1, 22) = 178.3, p < .001$, in the small-focus ($M = 554$ msec, $SD = 56.6$) relative to the wide-focus condition ($M = 618$ msec, $SD = 61.8$), indicated by a 64-msec RT advantage because of valid spatial cueing. Furthermore, the ANOVA of RTs yielded a significant interaction of Salient Distractor and Attentional Focus, $F(1, 22) = 7.036, p < .05$. As depicted in Figure 3, the presence of a salient distractor increased mean RTs significantly ($M = 632$ msec, $SD = 61.5$) relative to its absence ($M = 605$ msec, $SD = 60.1$) when the attentional focus was widespread, $t(1, 27) = 5.302, p < .001$, resulting in a distractor effect of 27 msec. In contrast, when the focus of attention was small, the effect of salient distractor presence (7 msec) was no longer significant, $t(1, 27) = 1.845, p = .076$ (present: $M = 558$ msec, $SD = 55.8$; absent: $M = 551$ msec, $SD = 58.1$). Please note that in approximately half of the distractor present trials, the orientation of the line within the distractor differed from the orientation of the line within the target. Thus, we additionally tested whether such response incongruity between distractor and target information may have modulated the effect of salient distractor presence. The results of the repeated-measures ANOVA with the factors Attentional Focus (small, wide) and Target/Distractor Congruency (congruent, incongruent) revealed neither a significant main effect of Target/Distractor Congruency, $F(1, 22) = 0.88, p = .358$, nor a significant interaction with the factor attentional focus, $F(1, 22) = 0.494, p = .49$, suggesting that Target/Distractor Congruency affected RTs neither when attention was on the target location nor when attention was widespread. Consequently, these results indicate that performance costs were not modulated by any response conflict between target and distractor information but can be solely attributed to the presence of a salient color distractor.

Functional Data

VOI Data

Contrasting activations induced by reversing checkerboards at potential distractor locations each within a different quadrant of the visual search display revealed four different functional VOIs in early visual cortex including areas V1 and V2, which have previously been demonstrated to code salience (Müller & Ebeling, 2008; Somers,

Dale, Seiffert, & Tootell, 1999; Roelfsema, Lamme, & Spekreijse, 1998; Motter, 1993). The locations of activation in visual cortex were derived from the Anatomy Toolbox, which is based on human probabilistic cytoarchitectonic maps (Eickhoff et al., 2005). Figure 4 shows the mean BOLD amplitudes per experimental condition within each of the four predefined VOIs. A repeated-measures ANOVA with the factors Localized VOI (1, 2, 3, 4), Salient Distractor (present at the specific position within the Localized VOI, absent from display), and Attentional Focus (small, wide) revealed a significant difference of BOLD amplitudes associated with distractor presence, $F(1, 22) = 16.69, p < .001$. The presence of a salient distractor increased BOLD signals ($M = 0.399, SD = 0.748$) as compared with its absence ($M = 0.035, SD = 0.407$), $t(1, 22) = 4.085, p < .001$. Importantly, the color combination discerning salient from nonsalient distractors within a search array was also inverted (i.e., a salient red distractor among nonsalient green items and a salient green distractor among nonsalient red items). This procedure ensured that salient and nonsalient distractors were exactly identical, with salience being varied only by context.

Additionally, results revealed a main effect of Attentional Focus, $F(1, 22) = 8.74, p < .01$. BOLD signals were significantly higher when the focus of attention was wide ($M = 0.32, SD = 0.584$) as compared with when it was small ($M = 0.114, SD = 0.655$), $t(1, 22) = 2.956, p < .01$. However, no significant main effect of the factor Localized VOI, $F(1, 22) = 0.598, p = .618$, could be observed. Furthermore, there was neither a significant interaction of the factors Localized VOI and Salient Distractor, $F(1, 22) = 0.159, p = .923$, nor of the factors Localized VOI and Attentional Focus, $F(1, 22) = 1.019, p = .39$, or the factors Localized VOI, Salient Distractor, and Attentional Focus, $F(1, 22) = 2.23, p = .093$, suggesting that the results obtained within the four different localized VOIs were similar. As illustrated in Figure 4 and as qualified by the nonsignificant interaction of the factors Salient Distractor and Attentional Focus, $F(1, 22) = 0.055, p = .814$, salience-related activation patterns were not significantly different between VOIs: The presence of a salient distractor at the specific localizer position caused higher BOLD amplitudes relative to nonsalient distractors for both small, $t(91) = 4.239, p < .001$, and wide attentional conditions, $t(91) = 5.377, p < .001$. Thus, coding of a salient distractor was not found to be different whether or not it was located within the attentional focus.

Whole-brain Data

Neural effects associated with the presence of a salient but irrelevant color distractor were examined contrasting distractor-present and distractor-absent trials. Table 1 illustrates the peak activations associated with the main effect of the factor Salient Distractor and its interaction with the factor Attentional Focus as well as the distractor effect within a small attentional focus. Activations were all

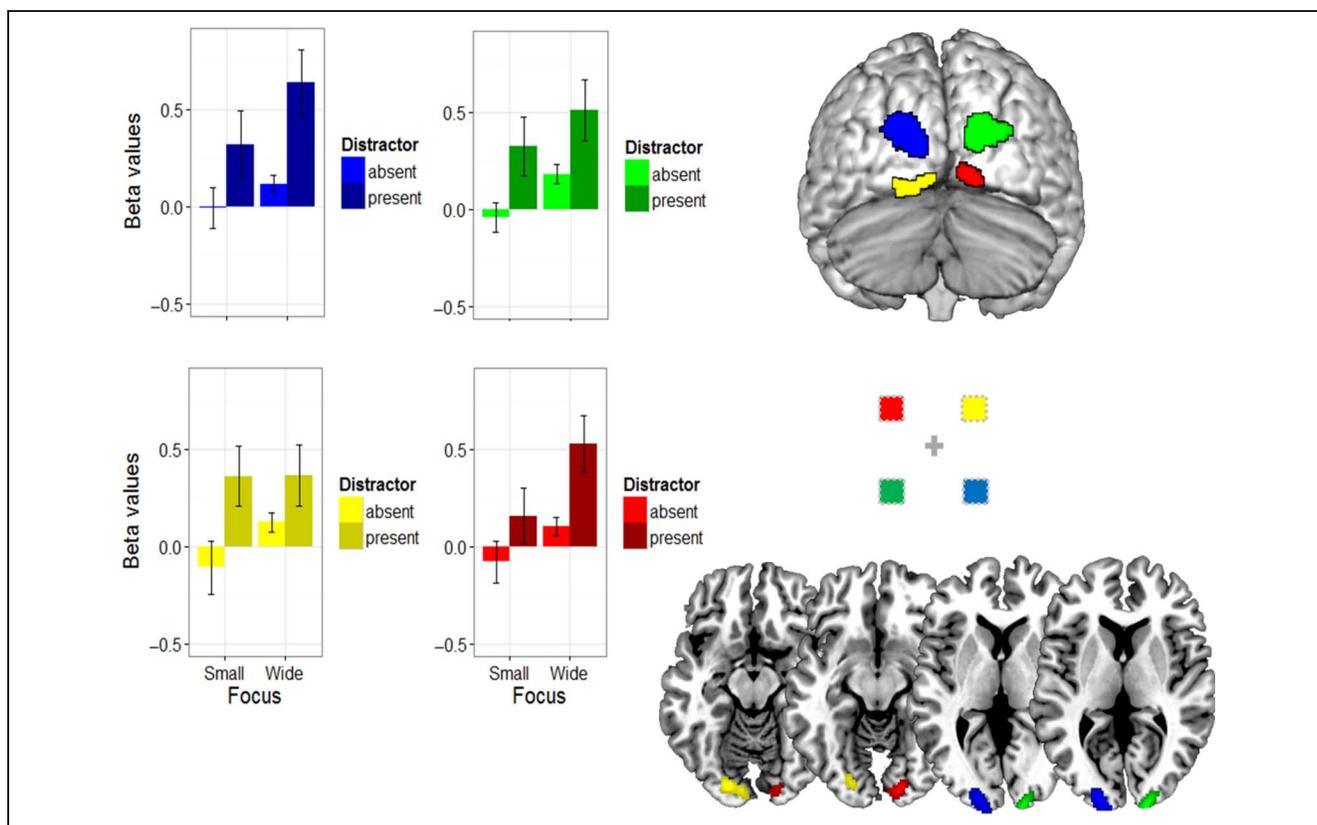


Figure 4. Increased visual activation induced by four different position localizers (right column in the middle) is projected onto a surface rendering (right column, top) and a two-dimensional slice-based medial view (right column, bottom). The graphs in the left column present the mean beta values for each activated brain region per experimental condition. Error bars reflect the standard errors of the mean.

significant at $p < .05$ (FWE) at the cluster level (based on $p < .001$, at the voxel level). No significant activation was found for the main effect of the factor Attentional Focus.

The presence of a salient distractor (as compared with its absence, i.e., presence of a nonsalient distractor) acti-

vated clusters in parietal and frontal cortex. In particular, neural activations were observed bilaterally in the superior parietal lobule reaching medially toward the right precuneus and in the left precentral gyrus at the inferior frontal junction (IFJ; Figure 5). Activity patterns in superior

Table 1. List of Activations Associated with (A) the Main Effect of Distractor Presence (Present > Absent), (B) the Interaction of Salient Distractor (Present > Absent) and Attentional Focus (Small > Wide), and (C) the Effect of Salient Distractor Presence within a Small Attentional Focus (Small Focus: Present > Absent)

Contrast	Region	Cluster Size	Side	Cluster Peak (mm)	Z Score
A. Distractor Present > Absent	Precuneus/superior parietal lobule	779	R	6, -56, 58	4.32
	Superior parietal lobule	310	L	-28, -60, 48	3.89
	Precentral gyrus/inferior frontal gyrus	260	L	-54, 6, 34	4.18
B. Interaction Distractor \times Focus	Middle cingulate cortex/ posterior cingulate cortex/precuneus	355	L/R	0, -46, 34	3.96
C. Small focus Present > Absent	Parahippocampal gyrus/ inferior temporal gyrus	520	L	-20, -2, -28	4.58
	Precuneus/paracentral lobule/ middle cingulate cortex	452	L/R	2, -54, 56	4.06
	Hippocampus/thalamus	295	R	20, -12, -8	4.12
	Superior temporal gyrus	246	R	54, -10, -2	4.67

Coordinates (x, y, z) were defined in MNI space. Activations were all significant at $p < .05$ (FWE) at the cluster level (based on $p < .001$, at the voxel level).

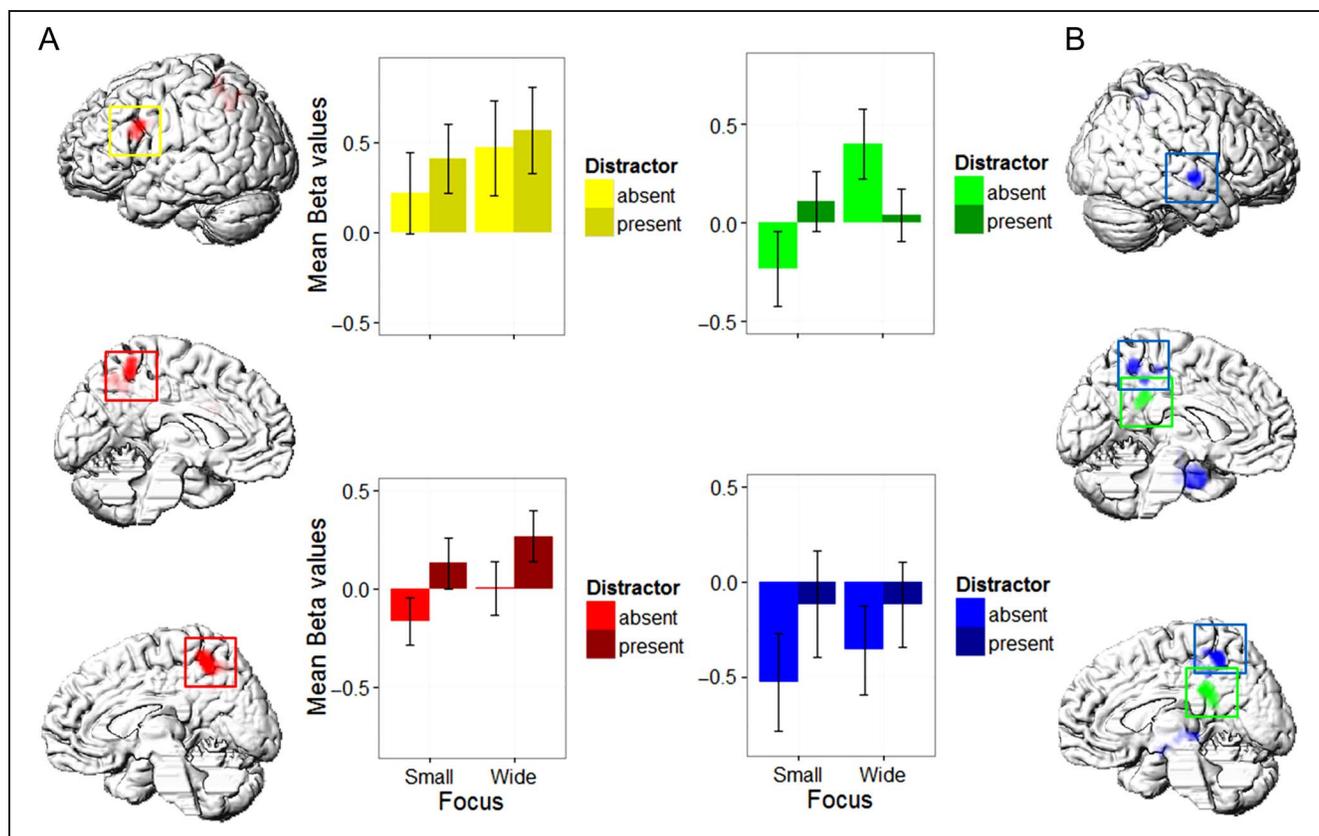


Figure 5. (A) In the left column, surface renderings show increased activation when a salient distractor was present compared with when it was absent. (B) In the right column, surface renderings show higher activity (green) when a salient distractor was present outside the attentional focus as compared with when it was present within the attentional focus. Activation patterns colored in blue reflect increased BOLD signals mainly driven by the first part of the interaction contrast. In the middle column, mean beta values for each experimental condition are illustrated for the relevant brain areas of the three different functional contrasts. Error bars reflect the standard errors of the mean.

parietal and inferior frontal regions matched the attentional capture network reported by De Fockert et al. (2004).

To test the effects of the attentional focus on the coding of irrelevant distractor information, we compared salient distractor induced activations under conditions of focused and wide attention. The interaction term was evaluated in both directions, testing for stronger distractor-induced activation in small focus as compared with wide focus trials [Focus small (salient distractor present – absent) – Focus wide (salient distractor present – absent)], as well as for stronger activations in wide focus as compared with small focus trials [Focus wide (salient distractor present – absent) – Focus small (salient distractor present – absent)]. Although no significant results were observed for the latter interaction term, the first term revealed one significant cluster of activation covering cingulate and medial parietal regions. In the small focus condition salient distractor presence (relative to its absence) increased BOLD signals bilaterally at the posterior end of middle cingulate cortex reaching into the right posterior cingulate cortex and into the left precuneus (Figure 5).

To further examine the distractor effect, the two parts of the significant interaction [Focus small (salient distrac-

tor present – absent) – Focus wide (salient distractor present – absent)] were investigated separately. A salient distractor located outside the endogenous attentional focus revealed large clusters of activation in parietal and cingulate cortex. Neural activations were observed bilaterally in the precuneus and in the left paracentral lobule reaching medially toward the posterior part of middle cingulate cortex. In temporal cortex, activations were observed along the left parahippocampal gyrus extending to the inferior temporal gyrus. In the right hemisphere, activation was located in the superior temporal gyrus reaching medially toward the hippocampus and the thalamus (Figure 5).

In contrast, a salient distractor presented under conditions of widely distributed attention induced no significant activation. These findings indicate that the interaction was mainly dominated by the differential effects in the small focus condition.

DISCUSSION

This study investigated the behavioral and neural effects of top-down focused spatial attention selection on the

coding of salient singleton color distractors and their tendency to capture attention.

In particular, we tested whether top-down focused spatial attention acts to prevent attentional capture of an irrelevant salient distractor by reducing its salience coding outside the spatial attentional focus. The size of the attentional focus was modulated using two different spatial cues. When a spatially uninformative cue was presented, participants needed to distribute their attention to the whole search display to efficiently detect and respond to the target ensuring that the salient distractor was always within their focus of attention. In contrast, a 100% valid spatial cue allowed participants to optimize their task performance by focusing the spotlight of attention and hence concentrating processing resources at the cued location. This procedure assured that irrelevant distractors were always located at a spatially unattended position. Both RTs and error rates indicate that participants efficiently adopted these search strategies in the different attentional conditions. Accordingly, target detection was significantly faster and more precise when a spatially valid instead of a nonpredictive cue preceded the visual search display, as evidenced by a spatial cueing effect of 62 msec. Hence, participants efficiently directed spatial attention at and around the upcoming target location.

The wide spatial attention condition resembles the classical irrelevant distractor paradigm (Theeuwes, 1991, 1992, 1994) where search displays were presented without any prior information respective the target location. In line with these studies, our results indicate that when spatial attention was widespread the presence of a salient distractor significantly increased RTs relative to its absence. However, a significant interaction revealed that the distractor effect was significantly smaller under endogenously focused attention. In particular, when the salient distractor was presented outside the attentional spotlight no attentional capture was observed: The salient distractor did not affect RTs significantly.

The absence of a significant distractor effect under endogenously focused attention clearly demonstrates that bottom-up driven attentional capture can be affected by top-down control mechanisms. Behavioral data provide evidence that a top-down spatial cue can be efficiently used either to prevent attention from being involuntarily attracted by a salient distractor location or to faster reorient attention toward the target location after it has been initially captured.

It is also possible that the absence of attentional capture may be due to the effect of working memory load on attentional selection (see, e.g., De Fockert, Rees, Frith, & Lavie, 2001). Top-down focusing of attention on the target location may reduce or even abolish the need to search for the relevant target feature, thus reducing the need to actively maintain relevant feature priorities in working memory. Following this line of argument, widespread attention should result in a higher load on work-

ing memory, because relevant feature priorities need to be active during the search process. The need to differentiate between high-priority and low-priority features (i.e., relevant target and salient distractor) in the wide focus condition during the search process may have enabled the salient distractor to capture attention.

Alternatively, assuming that searching for the target shape is not necessary under endogenously focused attention observers may initially not prepare for a singleton target shape before selection but may concentrate on the orientation of the line within the target shape. Thus, observers may prepare to attend to a feature different from a singleton target shape, which may have affected the strength of a singleton color distractor shape to capture attention.

However, the behavioral data are unspecific regarding the underlying functional mechanisms. Theoretically, attentional capture can be inhibited on multiple levels of the processing hierarchy. For instance, it is known that attentional capture critically depends on bottom-up salience coding (see, e.g., Wolfe, 1994). Accordingly, a model assuming that endogenously focusing spatial attention directly acts on preattentive processing of salience signals may account for the absence of attentional capture. This view is in line with a notion put forward by Theeuwes (2004, 2010) according to which salience is calculated within the spotlight of attention only. Within this framework, the absence of attentional capture is reflected by decreased or even abolished salience signals when the salient distractor is outside the top-down defined spatial focus.

Alternatively, top-down focused spatial attention may exert its effect on attentional capture on higher levels of processing, while leaving preattentive salience coding unaffected (see, e.g., Müller & Krummenacher, 2006). This could be achieved by counteracting a spatial orienting bias toward the most salient location by setting up strong endogenous spatial top-down control signals. Importantly, both accounts differ with regard to their prediction related to the coding of salience signals in retinotopic regions. We tested these predictions explicitly by extracting BOLD signals at brain regions coding specific locations in the search display. This was achieved separately for trials where either a salient or a nonsalient distractor was present at a specific location. Importantly, the color-contrast rendering a distractor salient was experimentally varied by changing its context rather than the item itself. In other words, salient and nonsalient distractors were identical, except for their context. As expected and as qualified by a significant main effect of distractor presence, salient distractors induced higher BOLD amplitudes in all functionally defined VOIs in early visual cortex as compared with nonsalient distractors. This finding provides evidence that our experimental setup was efficient in detecting spatially specific BOLD signals induced by salient items in the visual field. This is consistent with findings demonstrating that salience signals based

on simple feature differences are initially generated within early visual areas presumably via suppressive interactions induced by similar stimuli (Kastner, Nothdurft, & Pigarev, 1997; Knierim & van Essen, 1992; Desimone, Schein, Moran, & Ungerleider, 1985). This is also in line with the biased competition model (Desimone & Duncan, 1995), which suggests that stimulus salience acts to resolve competition between multiple elements in the visual field in a winner-take-all fashion, suppressing signals from stimuli not selected by attention.

Furthermore, it has been argued that input signals in early visual areas constitute a first computational stage of salience processing and are relevant for generating bottom-up attention selection of the most salient item in the visual field (Desimone & Duncan, 1995). This view is furthermore consistent with various theoretical accounts postulating that attention is biased toward the location with the highest activity within an overall salience map (Zehetleitner, Krummenacher, & Müller, 2009; Itti, Koch, & Niebur, 1998; Müller et al., 1995; Wolfe, 1994; Koch & Ullman, 1987). In particular, these models uniformly assume a hierarchical coding of salience signals within multiple and feature specific salience maps that are integrated into feature independent neural representations of stimulus signals in the visual field at a later processing stage. Hence, in the current experiment, a uniquely colored item (i.e., the salient distractor) is assumed to generate salience peaks on various levels of the processing hierarchy. Accordingly, the increased BOLD amplitudes observed along with the presence of salient singleton color distractors within the functionally defined VOIs do reflect salience coding at either the level of feature maps or alternatively at the level of a single supra-feature salience map.

Furthermore, two separate post hoc *t* tests revealed significant signal differences between salient and non-salient distractors in both spatial attention conditions. This salience effect was not different for the two attention conditions as indicated by a nonsignificant interaction. These data strongly suggest that salience coding is unaffected by spatial attention and in fact occurred outside the spatial attentional focus. This interpretation is well in line with previous fMRI data (Müller & Ebeling, 2008) as well as with findings from ERP studies (Brignani, Lepsien, & Nobre, 2010; Seiss, Kiss, & Eimer, 2009) that revealed functional markers of attentional capture under endogenously focused attention thus indicating visual processing of stimuli at unattended spatial locations. In summary, these findings together with our VOI data are consistent with the idea that the processes counteracting attentional capture occur at a higher level and may be due to enhanced spatial top-down signals generated within attention control regions.

Our whole-brain analyses corroborated this view. The presence of a salient distractor activated superior parietal and medial parietal regions as well as left inferior frontal gyrus, a network of brain regions that has been associated

with attentional capture (De Fockert et al., 2004). This interpretation implies that these regions should be activated more when a behavioral attentional capture effect was observed. However, our data suggest that this was not the case. None of these regions showed stronger activation induced by the salient distractor in the condition where attention was widespread across the visual display relative to the focused attention condition. If any differential effects were observed, then these were found in the opposite direction, with stronger differential activation in the focused attention condition. Accordingly, our data clearly indicate that these activations either reflect the presence of the salient distractor or result from cognitive efforts to counteract attentional capture, rather than attentional capture per se. The idea of an involvement of cognitive control processes is supported by activations in regions that have been demonstrated to reflect control processes in general (Derrfuss, Brass, & von Cramon, 2004) as well as the allocation of attention in particular (Corbetta et al., 2008). An indicator region for the involvement of top-down control is the IFJ, the brain region at the posterior end of the inferior frontal gyrus. Right-lateralized activation in IFJ has been associated with top-down controlled processing of nonspatial features such as motion or color (Zanto, Rubens, Bollinger, & Gazzaley, 2010) or object-based attentional processes (Baldauf & Desimone, 2014) whereas activation in left IFJ was found to be critically involved in mediating spatial top-down influences to perceptual areas (Weidner et al., 2009). This suggests that in the current experiment activation of left IFJ reflects the need for top-down controlling the allocation of spatial attention when a salient distractor is present within or outside the attentional spotlight.

Increased activation in the left IFJ has also been observed along with stimuli that are incongruent (vs. neutral stimuli) with the relevant response (e.g., in a color-word Stroop task; Zysset, Müller, Lohmann, & von Cramon, 2001; see also De Fockert et al., 2004). However, our behavioral data revealed no significant effect of response incongruity between salient distractor and target information on task performance. Whereas performance costs in Stroop-like tasks are mainly driven by competition between incongruent responses, in our task performance costs may reflect competition for selection between signals of the highly salient yet irrelevant distractor and the relevant but less salient target stimulus. This is in line with the biased competition account (Desimone & Duncan, 1995), which states that visual stimuli act as a whole, that is, as neural representations, which comprise all stimulus features when competing for attentional selection. However, it also argues against the idea that in different attentional states (small focused vs. widespread), observers prepared for different features of the target stimulus before selection, thereby biasing which feature of a distractor might be able to capture attention.

Alternatively, increased activation in the left IFJ may reflect the role of working memory in controlling the

interference of a salient distractor with target selection (De Fockert et al., 2001). Several previous studies (see, e.g., De Fockert & Theeuwes, 2012; Lavie, 2005; De Fockert et al., 2001) reported that the presence of a salient distractor only captured attention under high working memory load suggesting that in the current experiment, spreading attention across the whole visual field generated a high load on working memory. Consequently, activation in the left IFJ should be higher when the distractor was present in the wide focus condition. However, activation in the left IFJ was only observed for the main effect of distractor presence. In line with these findings, left IFJ activation most likely reflects the need for top-down control of spatial attention to resolve the competition for further processing between target and salient distractor even if located outside the spatial attentional spotlight.

Furthermore, successfully ignoring a salient but irrelevant distractor outside the top-down defined spatial coordinates activated medial parietal cortex, which has been suggested to be involved in generating spatial selection biases and/or controlling spatial attention shifts.

For instance, studies using the visual marking paradigm (Watson & Humphreys, 1997) showed an intentional bias against old stimuli that allows efficient target detection among a new subset of stimuli. In particular, in visual marking observers are presented with a preview-display containing a subset of the irrelevant distractor items from an upcoming a visual search display. It has been shown that observers are able to ignore these items, hence rendering upcoming visual search more efficient. Accordingly, visual marking shares similarities with the present experiment in the sense that advance information is used efficiently to restrict selection processes to specific locations. Similar to a small focus of attention as induced in the present experiment, visual marking has the potential to inhibit attentional capture (Olivers & Humphreys, 2003) and involves superior and medial parietal brain regions (Pollmann et al., 2003). Consequently, medial parietal activation may be required when employing spatial top-down control to optimize information selection at relevant locations particularly when a salient but irrelevant distractor is present. This, at least at first sight, may seem at odds with previous work because medial parietal regions have been implicated in supporting endogenous spatial attentional shifts (rather than keeping attention at a particular location; Vandenberghe, Molenberghs, & Gillebert, 2012; Shulman et al., 2009). However, in contrast to previous experiments, in our study keeping attention focused required actively counteracting a bottom-up spatial bias induced by a salient distractor. Hence, the present findings suggest that medial parietal regions may not only support endogenous shifts of attention but are also involved in either inhibiting the initiation of salience-based attentional shifts or at least in correctively adjusting involuntary attentional shifts toward the salient distractor in favor of concentrating spatial attention at top-down defined target coordinates.

In summary, the present data provide evidence that salience calculations of an irrelevant distractor are not restricted to the spatial focus of the observer but occur at an early stage of visual processing, that is, before allocation of focal attention toward the stimuli in the visual field. Only later on in the selection process, cognitive control regions together with regions supporting voluntary shifts of spatial attention resolve the competition between distractor and target information processing. Moreover, our data suggest that top-down focused attention support the neural system's attempts to counteract a spatial bias induced by a salient but irrelevant distractor. Taken together, we propose that top-down focused spatial attention does not override early salience calculation but rather seems to boost attentional control processes to successfully counteract salience-based distraction.

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Reprint requests should be sent to Ralph Weidner, Cognitive Neuroscience, Institute of Neuroscience and Medicine (INM-3), Research Center Juelich, Leo-Brandt-Str. 5, 52425 Juelich, Germany, or via e-mail: r.weidner@fz-juelich.de.

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