

Distraction and target selection in the brain: An fMRI study

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ABSTRACT

To attend successfully, a specification of what is currently relevant is necessary, but not sufficient. Irrelevant stimuli that are also present in the environment must be recognized as such and filtered out at the same time. Using functional magnetic resonance imaging, we showed that posterior brain regions in parietal, occipital and temporal cortex are recruited in order to ignore distracting visual stimuli, while the specification and selection of relevant stimuli is associated with differential activity in frontal cortex and hippocampal areas instead. The results thus suggest that the selection of relevant objects can be anatomically dissociated from the handling of competing irrelevant objects. The dissociation between the increased involvement of parietal and occipital cortex in handling distraction on one hand, and that of frontal cortex in target specification on the other provides neurophysiological support for models of attention that make this functional distinction.

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In order to deal effectively with the sensory wealth of our environment, we rely on the process of attention to select only what is presently relevant to us so that we can ignore the rest (Bundesen, Habekost, & Kyllingsbæk, 2005; Pashler, Johnston, & Ruthruff, 2001; Raymond, Shapiro, & Arnell, 1992; Wolfe & Horowitz, 2004). Given its functional importance, it is of little surprise that attention has been studied extensively in both classical psychology and neuroscience. Recent neuroscientific studies have shown that neuronal activity associated with selective attention in the visual domain can be observed in relatively widespread brain regions, including parietal, temporal, and prefrontal cortex (Leonards, Sunaert, Van Hecke, & Orban, 2000; Nobre, Coull, Walsh, & Frith, 2003). The concurrent co-activity of these regions has led to the idea that a relatively large frontoparietal network is involved in the allocation of attention (Corbetta, 1998; Indovina & Macaluso, 2007).

Given the extent of the observed cortical activity, it seems likely that attention is a broad phenomenon in the brain, and may involve different sub-functions of the mind. One hypothesis that has been put forward is that the frontoparietal network can be functionally divided into a dorsal and a ventral part; the former is involved in goal-directed selection, while the latter acts as an interrupter driven by salient stimuli (Corbetta & Shulman, 2002; Fox, Corbetta, Snyder, Vincent, & Raichle, 2006). Others have pro-

posed a somewhat similar distinction between the involvement of prefrontal cortex in instantiating top-down control and that of posterior parietal regions in bottom-up processing, based on studies conducted with monkeys (Buschman & Miller, 2007). One issue with both of these definitions of functional specificity is that stimulus salience is strongly influenced by current task settings, and thus it can be maintained that perception is realized through a continuous interplay between both endogenous (top-down) factors and exogenous (stimulus-driven) ones (Folk, Leber, & Egeth, 2002; Folk & Remington, 1998; Folk, Remington, & Johnston, 1992; Folk, Remington, & Wright, 1994). Indeed, supporting neurophysiological evidence has shown that both frontal and parietal brain regions respond to contextual and (target) location-specific modulation (Serences et al., 2005; Peers et al., 2005). Thus, it seems that the concepts of top-down and bottom-up control may prove hard to isolate by virtue of their tendency to intermix.

A view on attention championed by Duncan (1980), Desimone and Duncan (1995), Duncan and Humphreys (1989) offers a way out of the difficulties with finding 'pure' top-down or bottom-up processing. One can logically define two attentional sub-functions. Attending to something requires (1) the *selection* of the target stimulus, by matching it to a target template, and (2) the *filtering* or rejection of distracting stimuli that are also perceived. The concepts of top-down and bottom-up control are neutral to this classification. In particular the notion of a filtering function has inspired neurophysiological studies. As a result, the hypothesis has been put forward that parietal regions in the brain serve the function of filtering out (spatially) distracting stimuli (Friedman-Hill, Robertson, Desimone, & Ungerleider, 2003; Wojciulik & Kanwisher, 1999; also

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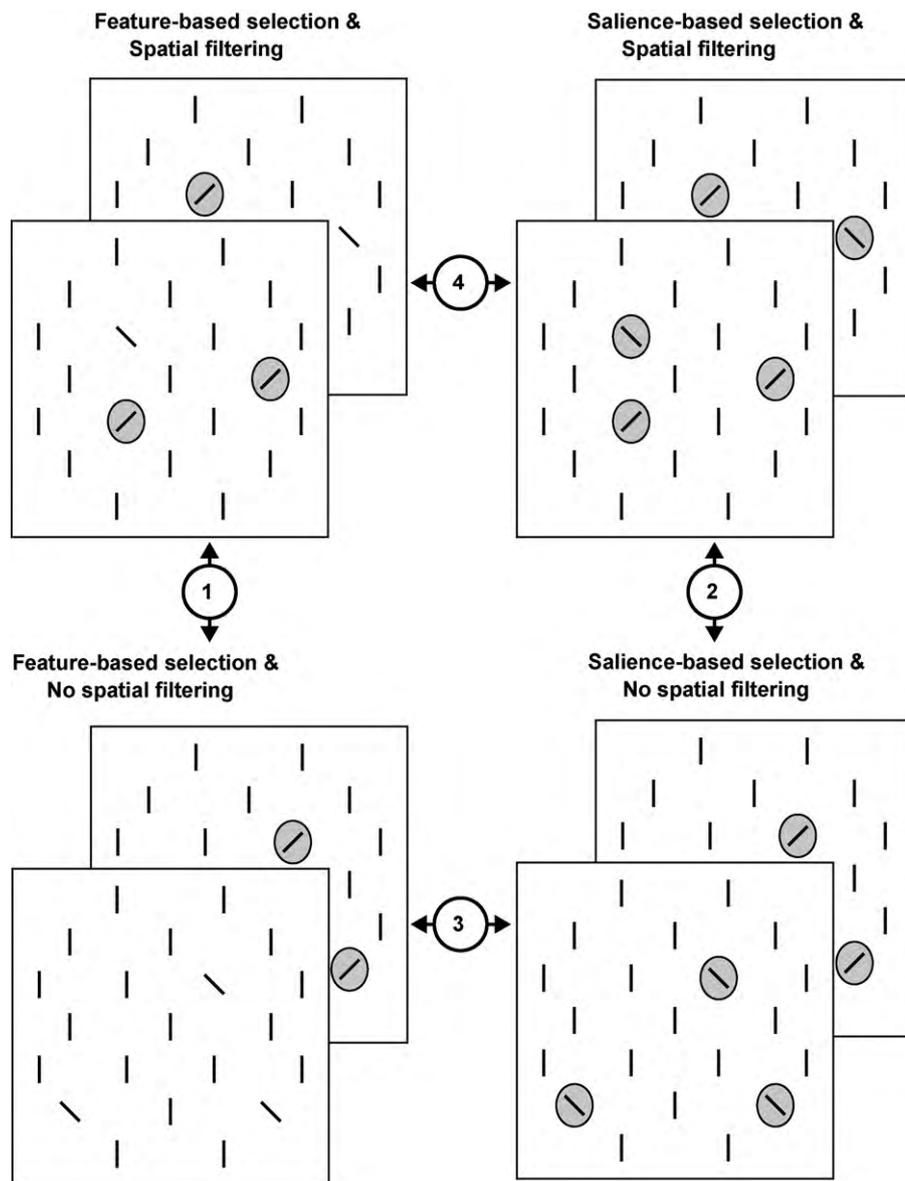


Fig. 1. Schematic representation of the experimental design. Top left panel represents the feature-based selection & simultaneous (target-related) spatial filtering condition. Target lines (circled in gray) are drawn simultaneously with distractor lines (with the opposite orientation offset). Top right panel shows the saliency-based selection & (stimulus-level) filtering condition. Both orientations are shown simultaneously, and both are targets. Bottom left panel shows the feature-based selection & no filtering condition. Targets and distractors are shown sequentially. Bottom right panel shows the saliency-based selection & no filtering condition. All sequentially presented orientation offsets are targets.

cf. LaBerge, Carlson, Williams, & Bunney, 1997, who proposed a similar division between control and preparatory processes). Some evidence for at least a rudimentary form of spatial filtering was obtained by reports of an interaction between lateral inhibition and attentional goals in closely coupled areas such as V4 and inferior temporal cortex (IT) in monkeys (Desimone & Duncan, 1995; Reynolds & Desimone, 2003). Although these results to date indeed support (one half of) the hypothesis of Duncan and colleagues, to our knowledge there has not been an attempt to find the neurophysiological correlate of both the filtering as well as the selection function. In order to successfully distinguish target selection from distractor filtering, both of those aspects should be studied and dissociated within one design. To do so was the purpose of the present study.

To study how the brain deals with distraction and target selection we used functional magnetic resonance imaging (fMRI) to scan the brains of our participants while they performed a simple atten-

tional search task. A multi-target visual search paradigm was used. Participants were asked to look for and count and report a number (0–4) of $\pm 45^\circ$ tilted lines in an array of vertical lines (21 in total). The task was designed to decompose the classic contrast between feature search and singleton detection (Bacon & Egeth, 1994), by breaking it down to functions of filtering and target selection. In feature search mode, observers have to select specific target stimuli, defined by specific feature values, and have to process or filter out all non-targets. In singleton detection mode, observers can select any salient stimulus, and thus do not need to filter salient non-targets at the same time (as these do not exist).

In the present design, these two conditions were instantiated so that participants were either performing feature-based selection or saliency-based selection (Fig. 1; left vs. right panels). That is, they were either looking for target stimuli, defined by a particular feature (i.e., a specific orientation), or they were simply looking for salient stimuli in the visual field. Furthermore, the need to perform

simultaneous spatial filtering was manipulated. In one condition, the tilted lines in each individual search display had both left- and rightward orientations, whereas in the other only one orientation was presented in a single display (but both orientations were used across displays). The addition of this spatial filtering variable had two consequences. Firstly, when observers were performing a feature-based search they were looking for only one type of line orientation (i.e., leftward or rightward), and the simultaneous presence of relatively salient lines oriented in the alternative direction constituted a distraction that had to be filtered out (Fig. 1; top left panel). This need to perform spatial filtering was not required when line orientations were not varied within a single display. In this case, either all salient lines were targets, or none were (Fig. 1; bottom left panel). Secondly, when observers were performing salience-based search they were looking for any tilted line, so that the simultaneous presence of both line orientations within one display would not require spatial filtering to perform the task successfully (Fig. 1; top right panel). At the stimulus level, however, the different line orientations might still evoke some degree of spatial filtering compared to the condition in which only one line orientation was present at the same time, even if such filtering was not necessary for target selection due to the use of a salience-based search criterion (Fig. 1; bottom right panel).

The relative simplicity of the search task was intended to keep task difficulty as constant as possible across conditions. The target template was always defined by simple orientation offset to prevent differential brain activation caused by engaging in inefficient feature conjunction search (Nobre et al., 2003). Similarly, to prevent contingent capture of attention by distractors that share features with targets (Serences et al., 2005), this possibility was eliminated in the present design. Finally, the number of relevant locations was variable, but consistent across all conditions, negating possible differences due to the reorienting of attention and differential eye movements (Corbetta, 1998; Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000).

1. Method

1.1. Participants

Seventeen right-handed students (10 female, 24.6 years average) with normal or corrected vision and no history of neurological problems participated in a behavioral training session and a subsequent fMRI session (approximately 1 week interval) for monetary compensation, after having given informed consent.

1.2. Apparatus, stimuli, and procedure

Data were recorded using a 3-Tesla Siemens Allegra head scanner (Siemens, Erlangen, Germany). Each run consisted of 1120 continuous volumes with 30 interleaved slices (10% distance factor) covering the whole brain using a T2-weighted echo-planar imaging sequence (TR = 2000 ms; TE = 30 ms; flip angle = 90°; 64 × 64 matrix size; 192 mm FOV; 3 × 3 × 3 voxel size). For the anatomical structure, high-resolution T1-weighted images were acquired using a fast low-angle shot sequence (FLASH; TR = 2250 ms; TE = 2.6 ms; 1 mm isotropic voxel size). Stimulus presentation was controlled by a standard PC running E-Prime 1.2 (Psychology Software Tools, Pittsburgh, USA). The stimuli were projected at a resolution of 1024 by 768 pixels in 16 bit color with a JVC DLA-G20 digital projector onto a translucent screen (34 cm diameter) mounted inside the scanner gantry, which could be seen by subjects through a set of mirrors mounted on the head coil. The viewing distance was approximately 60 cm. Participants responded with a 5-key fiber-optic response box, on which they could rest their dominant hand.

Each trial consisted of the appearance of a fixation cross (“+”) for 200 ms, followed by the presentation of the stimulus display that lasted for 600 ms. A white background was maintained throughout the experiment. The stimulus display consisted of 21 black line segments of 30 by 4 pixels arranged in a semi-circular array with 50 pixels inter-stimulus distance, centered on the screen. Each line in the array was independently displaced by a random jitter of 0–7 pixels in both horizontal and vertical directions. The majority of these lines had a vertical orientation, but two–four randomly chosen lines were tilted 45° in either left or right direction. These orientation offsets were quite salient amongst the otherwise vertical line segments in the visual field (see Fig. 1). After the array had been shown, participants viewed a question mark (“?”) for 800 ms, after which the response interval would end and the next trial in the block commenced. The task was to report the number of target

lines in the array (0–4). Whether a line with an orientation offset was a target or not was determined by block-wise instructions.

1.3. Design

As mentioned, there were four types of experimental blocks, implemented by crossing the simultaneous appearance of both left- and rightward tilted lines with the selection criterion of either one direction of tilt, or both. These conditions may be thought of as the result of two experimental variables with two levels each. The first variable varied target selection criteria. Participants were either asked to attend to only one of the possible orientation offsets (e.g., only leftwards tilted lines), or to attend to all lines with both orientation directions. The former case was thought to require feature-based target selection, as observers had to distinguish between different orientations and to consider only one of these as targets. The latter case was thought to require salience-based selection, as the detection of any salient stimulus (i.e., those that were tilted) was all that was required. The second variable varied the spatial filtering requirements, determined by the presence of (increased) distraction or diversity within the stimulus array. Distraction was considered to be present when arrays contained orientation offsets in both directions (e.g., one leftward tilted line, and two rightward tilted lines in a single display). Distraction was considered to be absent when the tilted lines in a display were all oriented in the same direction. Note that even in the blocks of the latter condition, both orientation directions were used within a block, but not simultaneously within one trial. The condition with distraction was thought to require (increased) spatial filtering, and the condition without was thought to require ‘no’ spatial filtering (other than the rather trivial exclusion of the vertical lines). Note again that when salience-based selection was used, the presence of both orientations in a trial did not require target-level filtering, as all stimuli were targets. It may be taken to require different stimulus-level filtering compared to displays containing just one type of orientation, however. Simply put, two different types of stimuli had to be processed at the same time rather than just one. The entire design is shown in Fig. 1, with the stimulus arrays of two trials displayed per condition to highlight the design logic both within and between trials. The order of blocks was counterbalanced between participants. One experimental session consisted of 48 blocks, each containing 18 trials, for a total of 864.

1.4. Analysis

Pre-processing and statistical analyses were done in SPM5 (Wellcome Department of Imaging Neuroscience, London, UK). The functional data were realigned to the first image and slice timing correction was applied. The structural image was co-registered with the mean functional image. All images were normalized to MNI-152 space and resampled to 2 mm × 2 mm × 2 mm. The realigned and normalized functional images were spatially smoothed with a 6 mm FWHM Gaussian kernel. A canonical hemodynamic response function was convolved with a box car model of the on- and offsets of the experimental conditions and tested against a general linear model of the time series extracted from the voxels. A main effect contrast was made first, to investigate the effects of feature-based and salience-based selection. This analysis was followed by four individual contrasts between the cells of the design, as indicated in Fig. 1. All contrasts were estimated in a random effects analysis and thresholded at a family-wise error (FWE) corrected $p < 0.05$. Additionally, only clusters of at least 10 voxels in size were taken into consideration. The resulting voxels were superimposed on an inflated average landmark- and surface-based standard brain (PALS-B12) using Caret 5.5 (Van Essen, 2005; Van Essen et al., 2001). In cases where the results were significant with a higher degree of certainty (e.g., $p < 0.01$ or

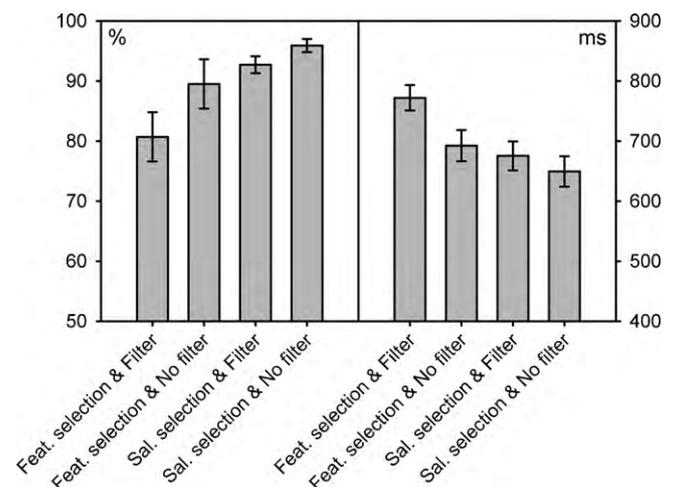


Fig. 2. Behavioral results of the experiment. On the left, bar graphs show mean accuracy in percent correct. On the right, reaction times are plotted. Error bars represent one standard error of the mean.

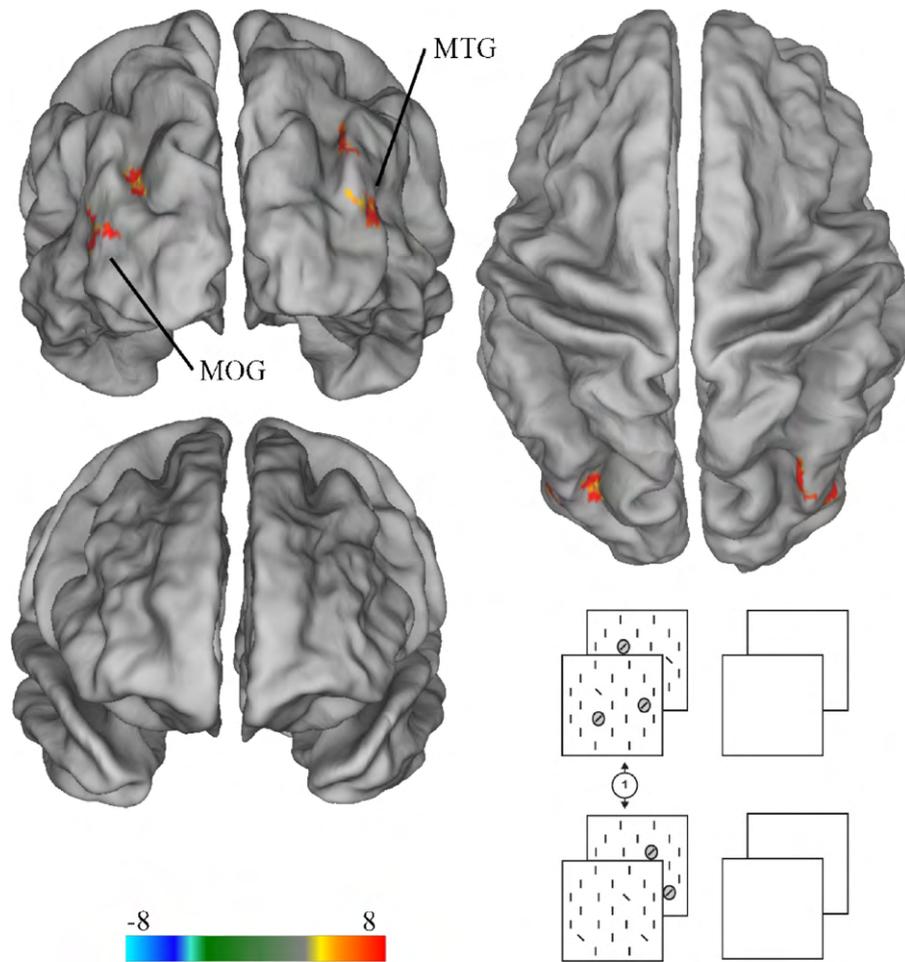


Fig. 3. *t*-Maps of the contrast between the feature-based selection & spatial filtering condition and the feature-based selection & no filtering condition, superimposed on a 3D rendering of a standard brain. In this and subsequent figures, the top left image shows a posterior view, the bottom left image shows an anterior view, and the image on the right a dorsal view. Label abbreviations are explained in the main text.

even $p < 0.001$), this stricter threshold is reported, which still reflects FWE corrected values.

2. Results and discussion

Analysis of variance showed that participants responded more accurately in the conditions that did not require spatial filtering of any kind (92.7%) than in the ones that did (86.7%), $F(1, 16) = 14.76$, $MSE = 0.004$, $p < 0.001$, and similarly more so in the salience-based selection conditions (94.3%) than in the feature-based ones (85.1%), $F(1, 16) = 7.24$, $MSE = 0.020$, $p < 0.05$. Performance was lowest when participants had to both filter and perform feature-based selection (80.7%), $F(1, 16) = 4.54$, $MSE = 0.003$, $p < 0.05$. Reaction times mirrored these results perfectly. Participants were faster when they did not need to filter (671 ms) compared to when they did (724 ms), $F(1, 16) = 37.43$, $MSE = 1266.039$, $p < 0.001$, and were faster when using salience-based selection (662 ms) rather than when they were using feature-based selection (732 ms), $F(1, 16) = 31.32$, $MSE = 2643.245$, $p < 0.001$. The longest reaction times were recorded when participants had to both filter and perform feature-based selection (772 ms), $F(1, 16) = 12.45$, $MSE = 987.623$, $p < 0.005$. The behavioral results are shown in Fig. 2.

In the fMRI data, the comparison of the two feature-based search conditions with the salience-based ones showed that feature-based target selection resulted in increased activity in the right hemisphere in the parietal lobe ($t(16) = 10.32$, $p < 0.001$, MNI 18, -60, 56; extending to 24, -66, 58), and the middle temporal gyrus

(MTG; $t(16) = 8.77$, $p < 0.01$, MNI 34, -80, 16), compared to salience-based selection¹. There was also increased activity associated with the salience-based selection conditions, which took the shape of a rather distributed set of clusters involving hippocampal areas on one end ($t(16) = 12.41$, $p < 0.001$, MNI -24, -34, -8 and $t(16) = 9.31$, $p < 0.01$, MNI 36, -16, -18), and the medial frontal cortex on the other ($t(16) = 9.07$, $p < 0.01$, MNI 0, 60, 22). In-between, the anterior cingulate was also involved in this contrast ($t(16) = 11.08$, $p < 0.001$, MNI 6, 38, 4).

The individual contrasts revealed a pattern of results consistent with the above. In the first contrast, when participants had to filter simultaneously presented salient distractors while performing feature-based selection, compared to the corresponding condition in which distractors were not simultaneously presented (this contrast is labeled as "1" in Fig. 1), regions in bilateral temporal and occipital cortex were more activated (Fig. 3 and Table 1). Activity

¹ Rather than to report the second comparison of the spatial filtering conditions, individual contrasts were examined next. This approach was taken because spatial filtering was not required to perform the search successfully when salience-based selection was used, even if both orientations were presented simultaneously. Thus, the interpretation of this contrast is not as informative as the individual comparisons. For completeness, the results are given here: The comparison showed bilateral clusters of activity, which were more activated in the filtering conditions. Activity peaked in the occipital cortex, near the precuneus ($t(16) = 11.41$, $p < 0.001$, MNI -28, -82, 20), and the MOG ($t(16) = 9.21$, $p < 0.01$, MNI 46, -80, 12). The conditions in which spatial filtering was not required did not reliably show increased activity.

Table 1
Regions of differential activity implicated in the individual contrast (see main text), with MNI coordinates and Z-scores.

Region	Feature-based selection: filtering > no filtering			
	x	y	z	Z-score
Middle temporal gyrus	42	-76	16	5.54
	38	-78	8	5.23
Middle occipital gyrus	-36	-86	8	5.40
	-46	-78	4	5.34

peaked around the MTG ($t(16)=9.92, p<0.005$, MNI 42, -76, 16 and $t(16)=8.75, p<0.01$, MNI 38, -78, 8), and the middle occipital gyrus (MOG; $t(16)=9.37, p<0.01$, MNI -36, -86, 8 and $t(16)=9.16, p<0.01$, MNI -46, -78, 4).

The same comparison while performing salience-based selection (i.e., when attending to any orientation) between simultaneous spatial filtering and its counterpart without filtering showed no reliable differences (contrast 2 in Fig. 1). Note that the physical appearance of these displays was identical to those compared previously in the feature-based selection conditions. In other words, the increased temporal and occipital activity observed in the simultaneous filtering condition compared to the no filtering condition during feature-based selection was elicited by the specific need to filter out simultaneous distractors, and not by aspects of the physical appearance of the stimuli. Thus, the increased posterior activity observed in the feature-based selection condition (contrast 1 in Fig. 1) may be taken as converging evidence for the role

Table 2
Regions of differential activity implicated in the individual contrast (see main text), with MNI coordinates and Z-scores.

Region	No filtering: salience-based > feature-based selection			
	x	y	z	Z-score
Middle temporal gyrus	60	-2	-14	5.74
Hippocampal	38	-22	-14	5.43
	32	-12	-18	5.37

of occipital cortex and adjacent regions as an attentional filter, a notion broadly compatible with previous studies (e.g., Wojciulik & Kanwisher, 1999).

In the third contrast between feature- and salience-based selection in the absence of spatial filtering (see Fig. 1), activity peaked in the right hemisphere in the MTG ($t(16)=10.79, p<0.001$, MNI 60, -2, -14). This locus was more anterior and relatively far away from the MTG clusters implicated in the previous contrast, however. In addition, clusters of activity showed up in hippocampal areas ($t(16)=9.51, p<0.005$, MNI 38, -22, -14 and $t(16)=9.28, p<0.01$, 32, -12, -18). As shown in Fig. 4 (and Table 2), at the same time no reliable differences were significant in parietal and occipital areas, suggesting that distraction played less of a role here. The increased hippocampal activation in the salience-based selection condition may be explained as follows. It may have been a result of all salient stimuli qualifying as targets in those conditions, as compared to the subset of stimuli in the feature-based selection conditions. It may

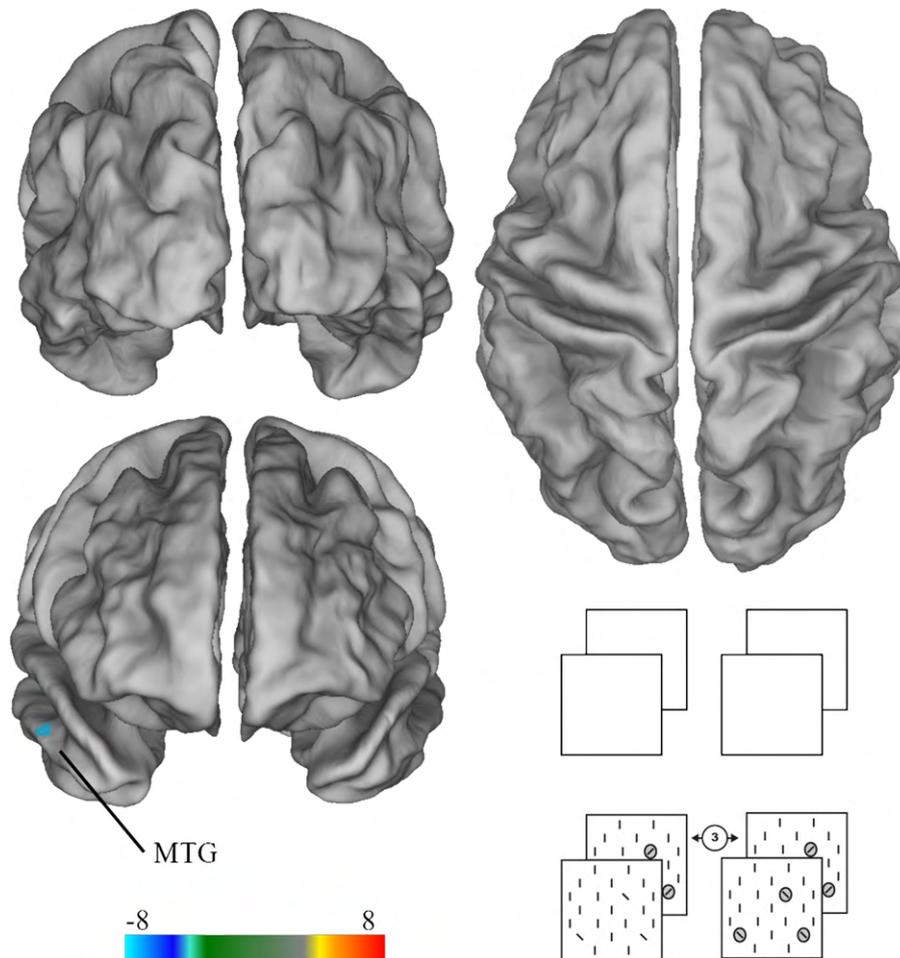


Fig. 4. *t*-Maps of the contrast between feature-based selection & no spatial filtering and salience-based selection & no filtering, superimposed on a 3D rendering of a standard brain.

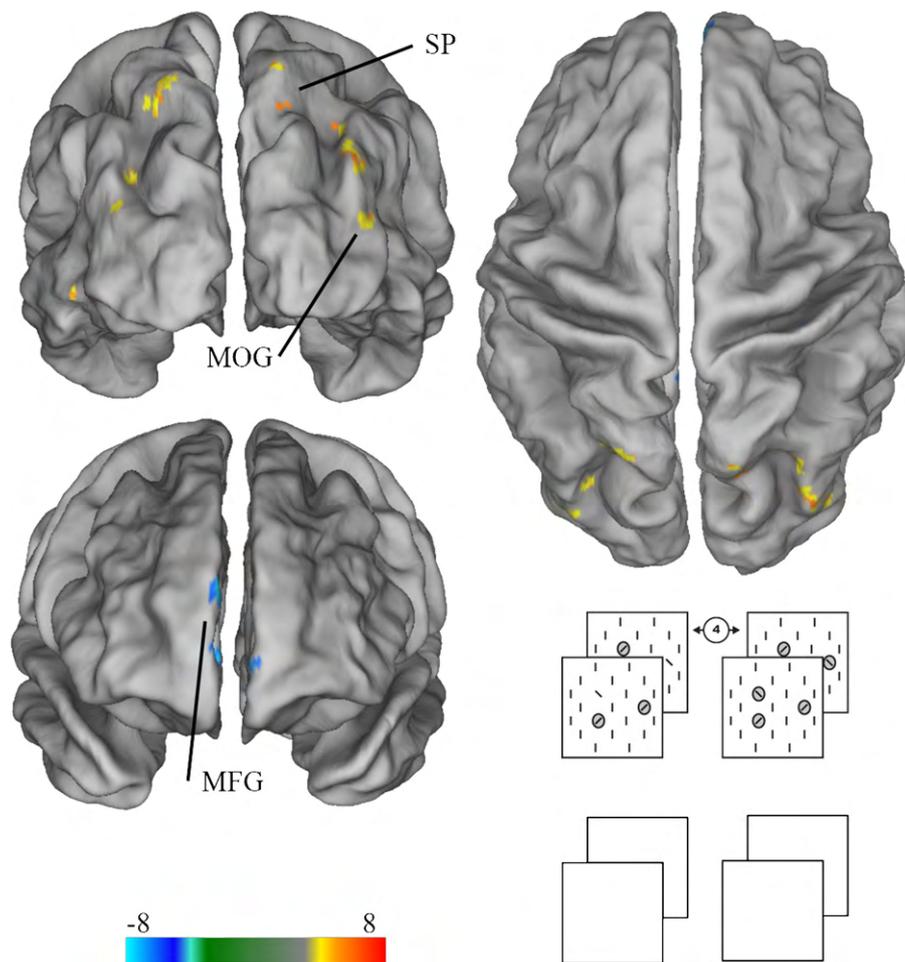


Fig. 5. *t*-Maps of the contrast between feature-based selection & spatial filtering and salience-based selection & spatial (stimulus-level) filtering, superimposed on a 3D rendering of a standard brain. SP=superior parietal lobe.

thus be that more resources related to working memory would be recruited during salience-based selection as well, simply because more stimuli had to be encoded for response selection (cf., Linden et al., 2003). Crucially, this effect was not associated with spatial filtering. In other words, these mechanisms were apparent even when salient distractors were not shown simultaneously with targets.

We finally compared directly between feature-based selection and salience-based selection in the spatial filtering conditions (contrast 4 in Fig. 1). According to our hypothesis, this contrast should reveal both more activity in posterior regions due to the need to perform spatial filtering (observed during feature-based selection), as well as more activity in frontal regions for salience-based selection. This was indeed confirmed, as can be seen from Fig. 5. First, we observed increased activity in the feature-based selection condition, which closely resembled the ones reported previously (in the

main effect analysis and the individual contrast shown in Fig. 3). Activity peaked in the MOG ($t(16)=9.94$, $p<0.005$, MNI 38, -78, 12), in superior parietal regions ($t(16)=9.35$, $p<0.01$, MNI 18, -68, 64 and $t(16)=8.79$, $p<0.01$, MNI 12, -70, 58), and bilaterally in the precuneus ($t(16)=9.60$, $p<0.005$, MNI -20, -68, 52 and $t(16)=8.97$, $p<0.01$, MNI 32, -68, 36). This pattern of parietal and occipital activity resembled the one in the first individual contrast, which supported the idea that these areas are specifically involved in the process of filtering simultaneous distractors. Second, salience-based selection resulted in increased frontal activity compared to when participants were performing feature-based selection, peaking around the medial frontal gyrus (MFG; $t(16)=13.17$, $p<0.001$, MNI 2, 56, 24 and $t(16)=9.51$, $p<0.005$, MNI 4, 64, 20), and extending towards its superior part ($t(16)=9.42$, $p<0.005$, MNI 2, 58, 8). These results were similar to those reported in the ‘main effect’

Table 3
Regions of differential activity implicated in the individual contrast (see main text), with MNI coordinates and Z-scores.

Region	Filtering: feature-based > salience-based selection				Filtering: salience-based > feature-based selection			
	x	y	z	Z-score	x	y	z	Z-score
Middle occipital gyrus	38	-78	12	5.54				
Precuneus	-20	-68	52	5.46				
	32	-68	36	5.29				
Superior parietal lobe	18	-68	64	5.46				
	12	-70	58	5.24				
Medial frontal gyrus					2	56	24	6.21
					4	64	20	5.44
					2	58	8	5.41

contrast between feature- and salience-based search. The need to change target selection criteria, or to look for a specific target template match as compared to using an unspecific, salience-based search mode thus affected distinctly different brain regions than those involved in dealing with the presence of salient distractors. Taken together, the functions of both anterior and posterior regions contributed to the contrast between feature- and salience-based selection during spatial filtering. Table 3 lists the clusters of differential activity that were implicated in the analyses presented above.

In conclusion, the present study produced two principal findings. First, when the search task required filtering of (salient) distractors, areas across parietal, temporal, and occipital cortex became (more) involved. Second, when target selection did not require specific matching of a target template (i.e., when any salient stimulus was a target), the differentially involved brain regions were mostly in frontal cortex and hippocampal areas. When both spatial filtering of distractors and feature-based target selection were needed, then both areas were implicated. Our results should not be taken to mean that activity in parietal and occipital cortex are not at all modulated by processes related to target selection or its associated difficulty in other tasks, as shown by others (Donner, Kettermann, Diesch, Villringer, & Brandt, 2003; Martínez et al., 1999; Reynolds & Desimone, 2003), since many factors related to this were explicitly held constant in our study. Indeed, attentional filtering in the inferior parietal sulcus (IPS) is most likely accomplished by boosting target-related visual signals, in contrast to local mutual suppression observed in extrastriate cortex (Kastner, De Weerd, Desimone, & Ungerleider, 1998), as activation in this region has been associated with both perceptual visibility and perceptual interference (Marois, Chun, & Gore, 2003). However, in the present study, given the absence of a comparable difference in these posterior brain areas between feature- and salience-based selection in the absence of spatial filtering, as well as the observed increase in frontal activity observed in both of the salience-based selection conditions, our hypothesis that changing target selection criteria does not directly modulate activity in posterior regions was supported.

The experimental division between target selection and distractor filtering was mirrored by a relatively clear anatomical and functional organization of attention, and can explain recent reports of distinct causal influences of frontal and parietal cortex on activity in the visual cortex (Ruff et al., 2008). The results support the idea that frontal cortex deals with the specification, consolidation, and selection of target stimuli, while parietal cortex deals with filtering those that are not targets. A consequence implicit in this dissociation is that filtering of simultaneously presented distractors is not necessary when selection is salience-based; and indeed did not elicit increased activity in parietal regions. These became more strongly involved only when a feature-based target selection had to be made amongst salient distractors. The increased frontal activity appeared whenever the selection of any salient stimulus was contrasted with the selection of a specific kind, regardless of the composition of the display. One caveat with the interpretation of the results is that the behavioral difficulty of the conditions was also different. Thus, some of the activity observed presently may be attributable to ‘difficulty effects’, and hence potentially implicate the involvement of the so-called “default network” (Shulman et al., 1997). The degree to which this could be the case cannot be easily assessed, but even if difficulty causes brain activity on its own, the cause of this difficulty in the present paradigm still lies in the differences between selection and filtering requirements.

Taken together, the observed degree of functional specificity of the brain supports the framework of attention originally proposed by Duncan (1980), Desimone and Duncan (1995), Duncan and Humphreys (1989) in that the functions defined as “target

selection” and “distractor filtering” were found to modulate distinct cortical sites. This theory is also in line with recent findings of occipital activity elicited by both the location of an expected target as well as that of a distractor, which is more problematic to explain for accounts that focus on the distinction between top-down and bottom-up processing (Brefczynski & DeYoe, 1999; Ruff & Driver, 2006). Thus, the present results suggest that the co-operation of selection and filtering processes provides a comprehensive account of two main functions of attention.

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References

- Bacon, W. F., & Egeth, H. E. (1994). Overriding stimulus-driven attentional capture. *Perception & Psychophysics*, *55*, 485–496.
- Brefczynski, J. A., & DeYoe, E. A. (1999). A physiological correlate of the ‘spotlight’ of attention. *Nature Neuroscience*, *2*, 370–374.
- Bundesen, C., Habekost, T., & Kyllingsbæk, S. (2005). A neural theory of visual attention: Bridging cognition and neurophysiology. *Psychological Review*, *112*, 291–328.
- Buschman, T. J., & Miller, E. K. (2007). Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. *Science*, *315*, 1860–1862.
- Corbetta, M. (1998). Frontoparietal cortical networks for directing attention and the eye to visual locations: Identical, independent, or overlapping neural systems? *Proceedings of the National Academy of Sciences U.S.A.*, *95*, 831–838.
- Corbetta, M., Kincade, J. M., Ollinger, J. M., McAvoy, M. P., & Shulman, G. L. (2000). Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nature Neuroscience*, *3*, 292–297.
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*, 201–215.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, *18*, 193–222.
- Donner, T. H., Kettermann, A., Diesch, E., Villringer, A., & Brandt, S. A. (2003). Parietal activation during visual search in the absence of multiple distractors. *NeuroReport*, *14*, 2257–2261.
- Duncan, J. (1980). The locus of interference in the perception of simultaneous stimuli. *Psychological Review*, *87*, 272–300.
- Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychological Review*, *96*, 433–458.
- Folk, C. L., Leber, A. B., & Egeth, H. E. (2002). Made you blink! Contingent attentional capture produces a spatial blink. *Perception & Psychophysics*, *64*, 741–753.
- Folk, C. L., & Remington, R. W. (1998). Selectivity in distraction by irrelevant featural singletons: Evidence for two forms of attentional capture. *Journal of Experimental Psychology: Human Perception and Performance*, *24*, 847–858.
- Folk, C. L., Remington, R. W., & Johnston, J. C. (1992). Involuntary covert orienting is contingent on attentional control settings. *Journal of Experimental Psychology: Human Perception and Performance*, *18*, 1030–1044.
- Folk, C. L., Remington, R. W., & Wright, J. H. (1994). The structure of attentional control: Contingent attentional capture by apparent motion, abrupt onset and colour. *Journal of Experimental Psychology: Human Perception and Performance*, *20*, 317–329.
- Fox, M. D., Corbetta, M., Snyder, A. Z., Vincent, J. L., & Raichle, M. E. (2006). Spontaneous neuronal activity distinguishes human dorsal and ventral attention systems. *Proceedings of the National Academy of Sciences U.S.A.*, *103*, 10046–10051.
- Friedman-Hill, S. R., Robertson, L. C., Desimone, R., & Ungerleider, L. G. (2003). Posterior parietal cortex and the filtering of distractors. *Proceedings of the National Academy of Sciences U.S.A.*, *100*, 4263–4268.
- Indovina, I., & Macaluso, E. (2007). Dissociation of stimulus relevance and saliency factors during shifts of visuospatial attention. *Cerebral Cortex*, *17*, 1701–1711.
- Kastner, S., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1998). Mechanisms of directed attention in the human extrastriate cortex as revealed by functional MRI. *Science*, *282*, 108–111.
- LaBerge, D., Carlson, R. L., Williams, J. K., & Bunney, B. G. (1997). Shifting attention in visual space: Tests of moving-spotlight models versus an activity-distribution model. *Journal of Experimental Psychology: Human Perception and Performance*, *23*, 1380–1392.
- Leonards, U., Sanaert, S., Van Hecke, P., & Orban, G. A. (2000). Attention mechanisms in visual search—An fMRI study. *Journal of Cognitive Neuroscience*, *12*(S2), 61–75.
- Linden, D. E. J., Bittner, R. A., Muckli, L., Waltz, J. A., Kriegeskorte, N., Goebel, R., et al. (2003). Cortical capacity constraints for visual working memory: Dissociation of fMRI load effects in a fronto-parietal network. *NeuroImage*, *20*, 1518–1530.
- Marois, R., Chun, M. M., & Gore, J. C. (2003). A common parieto-frontal network is recruited under both low visibility and high perceptual interference conditions. *Journal of Neurophysiology*, *92*, 2985–2992.

- Martínez, A., Anllo-Vento, L., Sereno, M. I., Frank, L. R., Buxton, R. B., Dubowitz, D. J., et al. (1999). Involvement of striate and extrastriate visual cortical areas in spatial attention. *Nature Neuroscience*, 2, 364–369.
- Nobre, A. C., Coull, J. T., Walsh, V., & Frith, C. D. (2003). Brain activations during visual search: Contributions of search efficiency versus feature binding. *NeuroImage*, 18, 91–103.
- Pashler, H., Johnston, J. C., & Ruthruff, E. (2001). Attention and performance. *Annual Review of Psychology*, 52, 629–651.
- Peers, P. V., Ludwig, C. J. H., Rorden, C., Cusack, R., Bonfiglioli, C., Bundesen, C., et al. (2005). Attentional functions of parietal and frontal cortex. *Cerebral Cortex*, 15, 1469–1484.
- Raymond, J. E., Shapiro, K. L., & Arnell, K. M. (1992). Temporary suppression of visual processing in an RSVP task: An attentional blink? *Journal of Experimental Psychology: Human Perception and Performance*, 18, 849–860.
- Reynolds, J. H., & Desimone, R. (2003). Interacting roles of attention and visual salience in V4. *Neuron*, 37, 853–863.
- Ruff, C. C., Bestmann, S., Blankenburg, F., Bjoertomt, O., Josephs, O., Weiskopf, N., et al. (2008). Distinct causal influences of parietal versus frontal areas on human visual cortex: Evidence from concurrent TMS-fMRI. *Cerebral Cortex*, 18, 817–827.
- Ruff, C. C., & Driver, J. (2006). Attentional preparation for a lateralized visual distractor: Behavioral and fMRI evidence. *Journal of Cognitive Neuroscience*, 18, 522–538.
- Serences, J. T., Shomstein, S., Leber, A. B., Golay, X., Egeth, H. E., & Yantis, S. (2005). Coordination of voluntary and stimulus-driven attentional control in human cortex. *Psychological Science*, 16, 114–122.
- Shulman, G. L., Fiez, J. A., Corbetta, M., Buckner, R. L., Miezin, F. M., Raichle, M. E., et al. (1997). Common blood flow changes across visual tasks: II. Decreases in cerebral cortex. *Journal of Cognitive Neuroscience*, 9, 648–663.
- Van Essen, D. C. (2005). A population-average, landmark- and surface-based (PALS) atlas of human cerebral cortex. *NeuroImage*, 28, 635–662.
- Van Essen, D. C., Dickson, J., Harwell, J., Hanlon, D., Anderson, C. H., & Drury, H. A. (2001). An integrated software system for surface-based analyses of cerebral cortex. *Journal of the American Medical Informatics Association*, 8, 443–459.
- Wojciulik, E., & Kanwisher, N. (1999). The generality of parietal involvement in visual attention. *Neuron*, 23, 747–764.
- Wolfe, J. M., & Horowitz, T. S. (2004). What attributes guide the deployment of visual attention and how do they do it? *Nature Reviews Neuroscience*, 5, 1–7.