The spatial profile of the focus of attention in visual search: Insights from MEG recordings

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ABSTRACT

The spatial focus of attention has been suggested to resemble a spotlight, a zoom-lens, a simple gradient, or even a more complex center–surround profile. Here we review evidence from neuromagnetic recordings indicating that the spatial profile is not fixed but depends on the particular perceptual demands of the attention task. We show that visual search requiring spatial scrutiny for target discrimination produces a zone of neural attenuation in the target's immediate surround, whereas search permitting target discrimination without spatial scrutiny is associated with a simple gradient. We provide new evidence indicating that increasing the demands on target discrimination without changing the spatial scale of discrimination does not influence surround attenuation, and that surround attenuation is also not influenced by the type of features involved in forward processing, that is whether the target location is defined by color or luminance contrast in visual search. An assessment of the time-course of attentional selection reveals that, when present, surround attenuation onsets with a substantial delay relative to the initial feed-forward sweep of processing in the visual system. The reported observations together suggest that the more complex center–surround profile arises as a consequence of top-down attentional selection in the visual system. The reviewed neuromagnetic evidence is discussed with respect to key notions of the Selective Tuning model of visual attention for which strong support is provided.

1. Introduction

Observations by Helmholtz (Helmholtz, 1896), subsequent seminal work by Posner (Posner, 1980) and many other groups revealed that attention can be focused at will to a circumscribed region in space. This circumscribed region could dissociate from eye fixations, and was associated with a facilitation of sensory processing, both in terms of perceptual sensitivity as well as the speed of stimulus dependent responses. The region of enhanced sensory processing was metaphorically termed a "spotlight" of attention (Posner, Snyder, & Davidson, 1980; Shulman, Remington, & McLean, 1979), and was assumed to represent a contiguous region of space. The idea was extended to the "zoom-lens" methaphor, where the extent of enhancement was variable, depending on what was attended (Eriksen & James, 1986; Eriksen & Yeh, 1985). Systematic assessments of the spatial profile of facilitation typically revealed a simple monotonic gradient with a center maximum falling off gradually (Gaussian-like) in the surround (Downing & Pinker, 1985; Heinze et al., 1994; Henderson & Macquistan, 1993; Shulman, Wilson, & Sheehy, 1985). However, evidence has mounted suggesting that the notion of a simple gradient may not always be appropriate. For example, attention was shown to facilitate sensory processing in a region more complex than a circular spot (Egly & Homa, 1984; Muller & Hubner, 2002), or even in regions that are completely noncontiguous (Awh & Pashler, 2000; McMains & Somers, 2004; Muller, Malinowski, Gruber, & Hillyard, 2003). Furthermore, there is substantial behavioural and neurophysiological evidence suggesting that the focus of attention displays a center–surround structure where a zone of sensory attenuation surrounds a center region of facilitation (Bahcall & Kowler, 1999; Boehler, Tsotsos, Schoenfeld, Heinze, & Hopf, 2009; Caputo & Guerra, 1998; Cave & Zimmerman, 1997; Cutzu & Tsotsos, 2003; Downing, 1988; Hopf et al., 2006; Mounts, 2000a, 2000b; Muller & Kleinschmidt, 2004; Muller, Mollenhauer, Rosler, & Kleinschmidt, 2005; Slotnick, Hopfinger, Klein, & Sutter, 2002; Vanduffel, Tootell, & Orban, 2000). Despite mounting evidence from behavioural and neurophysiological studies, available empirical data, so far, did not provide a satisfying framework for understanding the neural mechanisms that give rise to such center–surround profile. Accordingly, it remained unclear why a center–surround profile is observed under certain but not all experimental conditions.

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This stands in contrast to computational models like the Selective Tuning model (ST) of visual attention (Tsotsos, 1990; Tsotsos, 2005a, 2005b; Tsotsos et al., 1995; Tsotsos, Rodriguez-Sanchez, Rothenstein, & Simine, 2008) which proposes a neural implementation of attentional selection from which such a profile arises as an inherent consequence of top-down selection in visual cortex. Importantly, the neural operations causing surround attenuation are explicitly formulated in the model which makes it possible to test their validity in the real biological system, and ultimately, to facilitate a clarification of the underlying neural mechanisms. The following will summarize our research with event-related magnetic field (ERMF) recordings in human observers that was based on this rationale. Details about the technical realization of recordings and experimental procedures are provided in previous publications (Boehler et al., 2009; Hopf et al., 2006). The following sections headed "Spatial focusing and surround attenuation", "The center–surround profile of attention reflects top-down processing", and "The time-course of surround attenuation" will review data published Hopf et al. (2006) and Boehler et al. (2009). The sections "The center–surround profile and the nature of feed-forward processing", and "Surround attenuation does not depend on the demands on target discrimination within the focus of attention" will report new empirical data.

2. The Selective Tuning model (ST)

The Selective Tuning model of visual attention represents a 'first principles' modelling approach developed to solve complexity issues of vision, in particular combinatorial problems associated with input representation and feature/location binding (Tsotsos, 1990, 1993, 2005b; Tsotsos, Culhane, & Cutzu, 2001; Tsotsos et al., 1995). A core notion of the model is that the computational problems of vision would be intractable unless recurrent processing is critically involved (Tsotsos, 2005a). While other theoretical frameworks have dealt with attention (Olshausen, Anderson, & Van Essen, 1993; Treisman, 1996), and top-down processing in vision (Ahissar & Hochstein, 2004; Bullier, 2001; Di Lollo, 2010; Lamme & Roelfsema, 2000), few have proposed an inherent link between top-down processing and attention (Deco & Zihl, 2001; Spratling & Johnson, 2004; Tsotsos, 1990). ST emphasizes the importance of top-down processing in attention for solving a large class of binding problems associated with the necessity to link features, objects and locations in vision. Importantly, ST offers an explicit implementation of attentional (featural and location) selection based on biologically realistic assumptions about connectivity (divergent and convergent) in the visual cortex hierarchy (Felleman & Van Essen, 1991; Salin & Bullier, 1995). Moreover, it proposes a realistic implementation of the temporal organization of involved selection stages (Tsotsos et al., 2008). Fig. 1 provides an illustration of the model's implementation in a simplified four-level hierarchy. Connectivity across hierarchical levels in visual cortex is modelled as pyramidal structure with feed-forward and feed-back connections forming upward-diverging (inverse) and downward-diverging (regular) pyramids. Surround attenuation arises as an inherent consequence of top-down directed modifications of connectivity in this hierarchy. For example, the red (target) and blue (distractor) input units at layer n-3 in (A) give rise to a diverging projection field of feed-forward activated units across hierarchical levels. The projection field of the red input at the top layer of the pyramid (n) contains many units that represent the red input but also units that represent the blue input from the distractor. This results in a rather coarse and ambiguous representation. As illustrated by the dashed bracket in (A), the effective spatial resolution at this stage of processing is too low to permit precise target discrimination. To regain resolution and localize
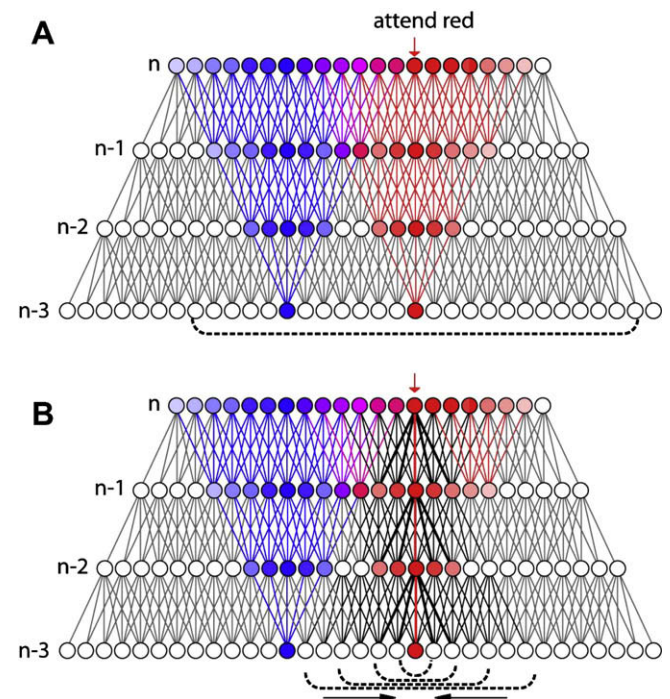
Fig. 1. Illustration of the Selective Tuning model. Shown are four layers of units (n-3 through n) representing four hierarchical levels of the visual system. Divergent and convergent connectivity between layers is represented by gray lines. Panel (A) shows diverging forward projection fields of two input units (red, blue) with red units representing relevant input and blue units representing irrelevant input from a distractor. Violet coloration highlights overlap of the projection fields at higher levels of the hierarchy (n, n-1). The dashed bracket marks the effective spatial resolution of the input representation when the forward projection field of the target just reached the top layer of the visual hierarchy. The red arrow highlights the global winner in the top-layer. Panel (B) shows the altered connectivity in the visual hierarchy after the top-down propagating pruning operation reached the input layer of the system. Pruned connections are shown in black. Dashed brackets highlight the progressive increase in spatial resolution produced by the downward propagation of the WTA process.

the input, ST proposes that at the top layer a winner-take-all (WTA) process is started which selects one unit (or more) as being the one(s) that best represent(s) the input (red arrow). This WTA can be based on feed-forward driven activity differences (e.g. the strongest forward-driven units) solely, but can also be biased by top-down influences (e.g. the instruction to attend the red not the blue item). The winner at the top layer then determines a sub-pyramid of forward projecting units (afferents to that winner) from the next lower level (n-1, black solid connections in panel B), in which a further WTA is started. The resulting winner at level n-1, in turn, determines a sub-pyramid at the next lower level (n-2) where, again, a WTA is initiated. This process propagates downwards until the input layer is reached (n-3) (see Tsotsos et al. (1995) for details of implementation).

A key mechanism proposed by the model is that forward connections in the sub-pyramids that project from non-winning units to the winner at the next higher level are pruned, while forward connections that project between winners across levels remain unchanged (solid red connections). On its way downwards the hierarchy, the pruning operation gradually narrows the zone of relevant (permitted) projections to the winner at the top layer. In a very real sense, this process traces back neural activation responsible for the attended stimulus response from higher to lower levels of the visual hierarchy. The result of this tracing-back is manifold, but most importantly it: (1.) refines location information about the attended input from layer to layer, and (2.) it eliminates spatial blurring and ambiguities of feature coding, both inevitably entailed by the con-
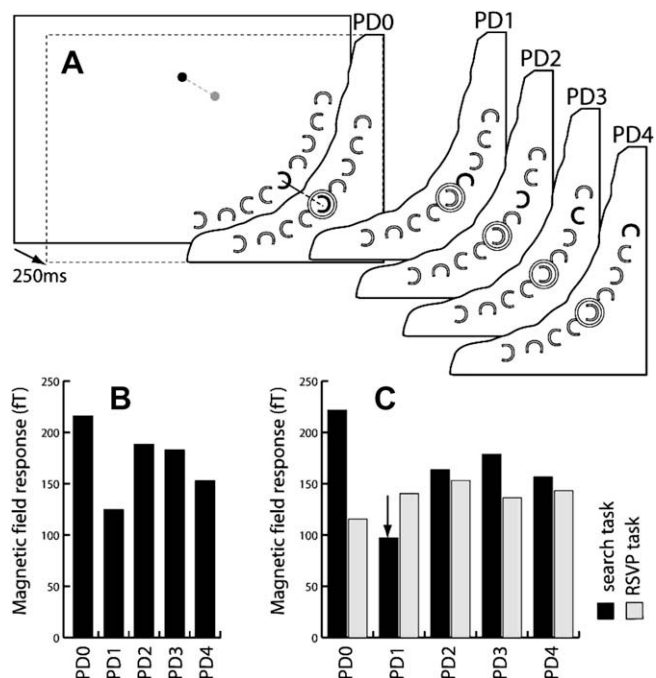
vergent computations during the initial feed-forward sweep of processing. Take the illustration in Fig. 1: once the downward selection process has reached layer (n-2), the location information about red input is narrowed from 13 down to 5 units in the input layer (n-3). In addition, at layer (n-2) the overlap from the forward projection field of the blue distractor is completely eliminated, such that the global winner now exclusively (i.e. unambiguously) represents the red input.

ST posits that discrimination tasks that require solving the problems just sketched are inherently associated with surround attenuation. Hence, this leads to a number of testable predictions. First, ST predicts surround attenuation to arise when a task requires a narrowing of the focus of attention. Second, if the visual task is one of simple feature discrimination then it requires neither spatial attention nor a narrowing of the focus of attention, and no suppressive surround is predicted to appear. Not all visual discrimination tasks require spatial resolution and scrutiny. Reporting the presence of a particular color (among simple alternatives) would not require one to localize the colored object with precision.[1] Color information computed by the feed-forward sweep of processing would already be sufficient to perform correctly. Take the illustration in Fig. 1A. What remains to be done after the feed-forward sweep of processing has passed the cascade is simply to identify the presence of red (i.e. decide the competition between red and blue units at the top level). Recurrent processing for explicitly localizing the red item in the input layer (n-3) as illustrated in Fig. 1B would not facilitate color-discrimination performance. In fact, it would deteriorate performance in terms of temporal efficiency. Hence, assuming that attentional selection in visual cortex does not unnecessarily waste processing resources, ST would predict that a suppressive surround would not appear. Finally, given that surround attenuation arises as a consequence of recurrent processing in the visual system it is predicted to appear with a temporal delay relative to the initial feed-forward sweep of processing. The work reported below, has addressed these predictions explicitly.

3. Spatial focusing and surround attenuation

In a first study published in Hopf et al. (2006) we asked whether focusing attention in space is, in fact, associated with a suppressive zone surrounding the location of an attended item. To assess the spatial profile of cortical excitability, we measured the neuromagnetic response of the visual cortex to a task-irrelevant probe as a function of this probe's distance to the focus of attention (probe-distance, PD). We varied the location of the focus of attention relative to a spatially fixed location where the probe appeared. Specifically, subjects performed a visual search task in which the target appeared at one of nine possible item locations that differed by distance to the location of the probe (Fig. 2A). While the probe's location was held constant (center item position) the location of the target changed randomly from trial to trial, such that it appeared with equal probability either at the probe's location (PD0) or at a location between one to four items away from the probe (PD1–PD4) towards the horizontal or vertical meridian. The target, a red C (black in panel (A)), and eight distractor items (blue Cs (gray in panel (A)) were always presented at isoeccentric locations in the right lower visual quadrant. Subjects had to report the orientation

Fig. 2. Stimulus setup and results of experiments reported in Hopf et al. (2006). (A) While fixating the center (black dot), subjects searched for a red C (shown in black) among eight blue Cs (shown in gray) presented at an isoeccentric distance in the right lower visual quadrant. On 50% of the trials, a white ring was flashed 250 ms after search frame onset always around the center C for 50 ms; on the remaining trials no probe was presented. The target C appeared randomly at any of the nine item locations, thereby directing the focus of attention randomly to locations subtending different distances to the probe (probe-distances, PD0–PD4). (B) Average event-related magnetic field response elicited by the probe (frame-probe minus frame-only response) as a function of probe-distance. (C) Results of a control experiment with two attention conditions. The probe-response is shown as a function of distance to the search target when subjects performed the search task (black bars), or when attention was withdrawn from the search items by a demanding RSVP task at fixation (gray bars).

of the target's gap (left/right) – a task that required that some level of accurate location information be associated with the target's visual features. The probe was a small white ring flashed around the center item 250 ms after search frame onset. It appeared on 50% of the trials (frame-probe trials, FP trials), while on the remaining trials the search frame was not followed by a probe. Obtaining frame-probe and frame-only trials (FO trials) permitted the cortical response to be isolated to the probe proper (i.e. the passive cortical excitability) by simply subtracting the neuromagnetic response to frame-only trials from that of frame-probe trials at corresponding target locations (FP-minus-FO difference). The bar-graph in Fig. 2B summarizes the size of the neuromagnetic response to the probe as a function of distance from the search target (distances towards the vertical and horizontal meridian are collapsed). Apparently, the smallest probe-response was elicited when attention was focused one item position away from the probe (PD1). Item positions farther away (PD2–PD4) and the position coinciding with the probe (PD0) showed significantly larger responses (Hopf et al., 2006). Hence, the search task indeed produced a zone of attenuation in the immediate surround of the target consistent with the prediction of ST.

Strictly taken, this observation is at best suggestive of spatial focusing being associated with surround attenuation. An unambiguous demonstration would require manipulating attention and showing that without focused attention surround attenuation does not appear. This was done in a further MEG experiment (experiment 2 in Hopf et al. (2006)), in which the search task and probe presentation was identical to the just reported experiment while

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[1] Evidence has been provided that attending item-color may necessarily involve attending an item's location (Tsal and Lamy, 2000). Attending to an object's color entails attending to its location: support for location-special views of visual attention. *Percept Psychophys, 62* (5), 960-968. While some elementary form of location information may always be required when processing feature information, the present argument is about spatial scrutiny, narrowing the focus of attention for decoding item detail – a demanding operation not automatically entailed when processing simple features.

an additional RSVP stream of characters was presented close to fixation. In different trial-blocks, subjects were either instructed to ignore this RSVP stream and perform the visual search task as in the previous experiment, or to ignore the search items in the periphery and perform the RSVP task at fixation (report the occurrence of designated character in a stream of 11 different characters). Performing the RSVP task was perceptually demanding and would bind attention to fixation, i.e. effectively withdraw attention from the peripheral items. Hence, if surround attenuation reflects a truly attention-related effect, it should disappear in this situation. Fig. 2C summarizes the neuromagnetic response to the probe under both experimental conditions. Obviously when subjects performed the RSVP task, no surround attenuation appeared (gray bars). In contrast, performing the visual search task (black bars) gave rise to a surround attenuation effect at PD1 (arrow) as in the first experiment. Notably, this experiment also rules out a possible sensory confound of the first experiment. The fact that the probe was flashed around the red target in only 1 out of 9 trials (while on most of the trials a blue item appeared with the probe) may have led to sensory interactions and a reduced response at and around the probe. (Fig. 2C reveals that this was, in fact, the case to some extent.). If this sensory attenuation at the probe's location would combine with a spatially narrower gradient of enhancement due to attention, we would see surround attenuation, but not due to attention. However, as visible in Fig. 2C, the response of the search task at PD1 is significantly smaller than the corresponding response of the RSVP task (see arrow), which is incompatible with this possibility. In sum, the data of both experiments clearly confirm ST's prediction that surround attenuation is a direct consequence of attentional focusing in space.

## 4. The center–surround profile and the nature of feed-forward processing

An issue to consider is whether surround attenuation depends on the type of forward-processing that defines the location of the target. In the experiments reported above, it was a popout based on color contrast that defined target's location. It remains to be clarified whether attention to a target defined by other feature-contrasts would give rise to surround attenuation in the same way. ST predicts that the size of the pass-zone and the zone of surrounding attenuation is defined by the extension of the top-layer winner's downward projection field, no matter what ultimately defines the winner during the feed-forward sweep of processing. In other words, any feature contrast giving rise to the same spatial extension of activation reflecting the winner at the top-layer will be expected to produce the same surround attenuation effect. However, contrast effects in different feature dimensions are not equivalent in their relation to attention, and locus of computation in visual cortex. Attention to color contrast, for example, has been shown to draw on different attentional resources than attention to luminance contrast (Morrone, Denti, & Spinelli, 2002, 2004). Moreover, fMRI investigations of color, chromaticity, and luminance contrast sensitivity in human visual cortex revealed that color/chromaticity contrast produces a response maximum in ventral exstrastriate area V4 (Hadjikhani, Liu, Dale, Cavanagh, & Tootell, 1998; McKeefry & Zeki, 1997; Wade, Augath, Logothetis, & Wandell, 2008), whereas sensitivity to luminance contrast was more evenly distributed across retinotopic visual areas up to V4 (Wade et al., 2008). It is possible, therefore, that location selection based on color contrast engages V4, while location selection based on luminance contrast arises at cortical levels earlier than V4, that is, the location of selection depends on the task. In terms of ST, this could mean that the ultimate top-layer winner is determined at different hierarchical levels in the visual system, which would

predict that surround attenuation for color and luminance popouts differs in spatial extent, with the latter producing a narrower surround.

To address this issue, we performed an MEG experiment similar to the one in Hopf et al. (2006), but with the modification that on half of the trial blocks, the target was defined by luminance contrast (all items blue with the target C being brighter)(luminance-blocks). On the other half, the target was defined by color contrast (red target C among blue distractors)(color-blocks). General stimulus setup, event timing, and task were identical to the experiment reported in Hopf et al. (2006, first experiment), except for the following modifications. Search items were presented on a black background. The luminance of the red target in the color-blocks was adjusted to match the luminance of the distractors (1.3 cd/m^2) based on heterochromatic flicker photometry (Lee, Martin, & Valberg, 1988). The luminance of the distractor items was identical in the color- and luminance-blocks, with the luminance-target being defined by a 10 cd/m^2 increase in luminance (13 cd/m^2). As before, a probe stimulus (a small white ring around the center item) was flashed for 50 ms, 250 ms after search frame onset randomly on 50% of the trials (FP trials). On the remaining trials no probe appeared (FO trials). Subjects ($n = 10$, 6 female) performed 10 experimental blocks (5 luminance, 5 color) amounting to a total of 100 trials per condition. MEG data recording, artifact rejection, and data analysis were identical to Hopf et al. (2006). *Behavioural performance.* The subjects' performance accuracy was excellent under both conditions (both 96% correct). A rANOVA with the factor target-type (color vs. luminance) confirmed that there was no significant difference ($F[1, 9] = 0.4$, $p = 0.84$). Subjects responded slightly faster to luminance- than color-targets (507 vs. 514 ms), but this difference was not statistically significant ($F[1, 9] = 3.01$, $p = 0.12$).

4.1. Event-related magnetic field (ERMF) response

The ERMF response to the probe (average FP-minus-FO difference between 124 and 132 ms after probe-onset) is shown in Fig. 3. Note, the FP-minus-FO difference computed for each probe-distance eliminates the magnetic response to the search frames including activity reflecting attentional focusing onto the target. It leaves the purely passive cortical response to the probe as a function of distance to the focus of attention. Fig. 3 displays responses collapsed for equivalent probe-distances towards the vertical and horizontal meridian. Apparently, both luminance-(A) and color-targets (B) produce fairly similar spatial profiles with clear evidence for surround attenuation at PD1. That is, the probe-
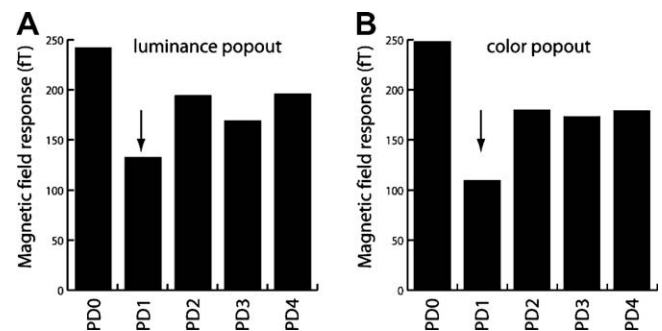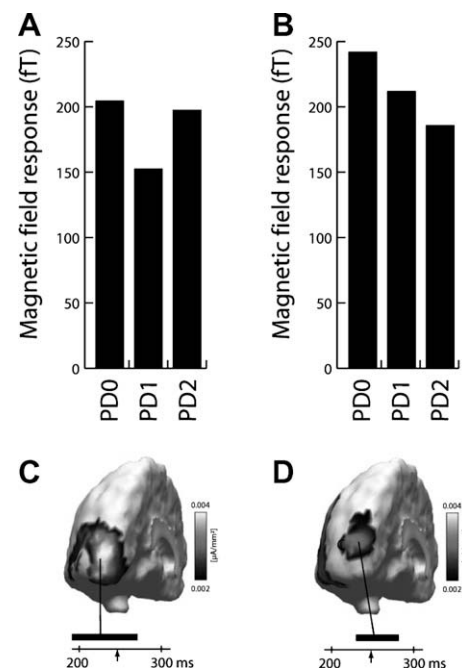

Fig. 3. Probe-response (frame-probe minus frame-only response) as a function of distance to the search target when the location of the target is defined by luminance (A) or by color-popout (B). Stimulation and experimental task were identical to the experiment shown in Fig. 2A (Hopf et al., 2006), except that the target's location was defined by color or luminance contrast. As visible, both conditions produce a comparable surround attenuation effect at PD1 (arrows).

response at PD1 is smaller than at PD0 and also smaller than at PD2 (arrows). Planned two-way rANOVAs with factors target-type (color/luminance) and probe-distance (PD0/PD1, or PD1/PD2) validate this impression. Significant main effects were observed for probe-distance (PD0/PD1: $F[1, 9] = 13.9$, $p = 0.005$; PD1/PD2: $F[1, 9] = 9.7$, $p = 0.012$), but not for target-type (PD0/PD1: $F[1, 9] = 0.15$, $p = 0.71$; PD1/PD2: $F[1, 9] = 1.3$, $p = 0.28$) and the target-type - probe-distance interaction (PD0/PD1: $F[1, 9] = 0.17$, $p = 0.69$; PD1/PD2: $F[1, 9] = 0.6$, $p = 0.82$). Additional comparisons between color- and luminance-targets at each individual probe-distance yielded no significant difference (all F-values <1). In sum, both color- and luminance-targets produced comparable surround attenuation effects, suggesting that the latter does not depend on the nature of the bottom-up feature contrast defining the target location during forward processing in the visual system. Instead, we will see below, that surround attenuation depends on top-down processing for narrowing of the focus of attention as suggested by ST. Furthermore, these observations are consistent with the interpretation that the top-layer winning unit for the luminance and color contrast was determined at the same hierarchical level in visual cortex. Of course, it remains to be shown whether this holds true for feature dimensions other than color and luminance.

5. The center–surround profile of attention reflects top-down processing

In ST surround attenuation results from a top-down propagating selection process that involves pruning of connections not contributing to the selected neurons at the next higher hierarchical level. This top-down process is launched to regain spatial resolution, that is, to narrow the pass-zone of relevant input from level to level such that it matches the decreasing size of receptive fields at progressively lower levels of the hierarchy. This leads to a further simple prediction that we addressed in Boehler et al. (2009). If the visual task can be successfully completed based on the lower spatial resolution at the higher layers of the visual pyramid, then this top-down selection process is not required. Such a situation – referred to as convergence binding in a recent development of the model (Tsotsos et al., 2008) – would not be expected to produce surround attenuation. There is considerable evidence showing that item features can be processed very rapidly even for item categorization (Grill-Spector & Kanwisher, 2005; Thorpe, Fize, & Marlot, 1996), but at the cost of remaining spatially unbound (Evans & Treisman, 2005; Treisman, 1998; Treisman & Gelade, 1980; Treisman & Schmidt, 1982). In contrast, binding of features at a particular location, i.e. making explicit that features are owned by a particular item is suggested to involve an additional more time-consuming operation that demands attentional focusing - termed recurrence binding in Tsotsos et al. (2008). We have recently provided neurophysiological data showing that in visual search feature-based attentional selection is a distinct location-unbound operation that appears prior to the spatial selection of the target item (Hopf, Boelmans, Schoenfeld, Luck, & Heinze, 2004). Hence, with respect to ST's notions, a simple feature discrimination task that does not require precise feature-location binding is predicted to not produce surround attenuation. This prediction was tested in a further MEG experiment (Boehler et al., 2009). The set-up of this experiment was similar to the one reported in Hopf et al. (2006), but the search task was modified such that on each trial the target was randomly assigned one of two possible popout colors (red or green) among blue distractors.[2] The experiment was run un-

der two different instructions. One required subjects to discriminate the gap-orientation (left/right) of the color-popout as in the experiment reported above (gap-orientation task). This task depended on spatial scrutiny, i.e. on the narrowing of the focus of attention to perform correctly. The second instruction required subjects to simply report the color of the popout target (color task). Successful performance on this task does not require narrowing of the focus of attention as in the gap-orientation task. Task-critical color information is already available with the feed-forward sweep of processing, and further localization of the target item is not needed. Fig. 4A and B shows the size of the neuromagnetic response elicited by the probe (frame-probe minus frame-only difference) for both conditions. Apparently, and confirming ST's prediction, the gap-orientation task (A), but not the color task (B) produced an attenuation of the probe-response in the immediate surround of the target (PD1) (Boehler et al., 2009). Hence these observations make a rather strong point in favour of the notion that surround attenuation is a direct consequence of recurrent processing for narrowing the focus of attention in visual cortex. In fact, this conclusion is further supported by a source localization analysis of our data illustrated in Fig. 4C and D. This analysis revealed a strong recurrent activity modulation shortly *before* probe-onset in the gap-orientation task as compared to the color task. Specifically, current source activity elicited by search frames of the gap-orientation task (C) and the color task (D) was estimated between 200 and 300 ms after search frame onset, that is, in a time-range where attention-driven recurrent activity modulations in early visual cortex are typically seen in visual attention tasks (Boehler, Schoenfeld, Heinze, & Hopf, 2008; Di Russo, Martinez, & Hillyard, 2003; Hillyard, Vogel, & Luck, 1998; Martinez et al., 1999, 2001; Noesselt et al., 2002). A comparison between (C) and (D) reveals that the gap-orientation task elicited strong recurrent activity in early visual cortex areas, while the color task showed a much weaker response.

Fig. 4. Results of experiment 1 reported in Boehler et al. (2009). (A) Probe-response (frame-probe minus frame-only response) as a function of distance to the search target when subjects performed the gap-discrimination task. (B) Probe-response when subjects performed the color-discrimination task. Panels (C) and (D) show current source maxima of recurrent activity in early visual cortex for the orientation- and the color task, respectively. Black horizontal bars indicate the time-range of recurrent activity. Arrows mark the onset of the probe stimulus.

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[2] Another modification of the experiment with respect to Hopf et al. (2006) was that data were only obtained from three probe distances (PD0–PD2), which turned out to suffice to demonstrate surround attenuation. This was done in order to increase the signal-to-noise ratio of the ERMF signal.

In sum, those results indicate that not all forms of attentional selection are associated with surround attenuation, as suggested by ST (Tsotsos et al., 2008). It is the specific need to narrow the spatial focus of attention for increasing the resolution of discrimination and item localization that gives rise to a center–surround profile. This conclusion is clearly in direct support of ST's computational mechanism of visual attention.

6. Surround attenuation does not depend on the demands on target discrimination within the focus of attention

The just reviewed experiments suggest that surround attenuation is a direct consequence of top-down selection for increasing the spatial resolution of discrimination – an operation indispensible for the orientation task, but not important for the color task. A closer look at the evidence from the previous experiment, however, reveals that our conclusion requires further evaluation. It is important to be aware that the orientation task differed from the color task not only with respect to the requirement to increase spatial resolution (in the sense that the spatial focus had to be narrowed for precise localization of the target), but also regarding the type of feature discrimination itself. Subjects had to discriminate the gap - a perceptually more demanding operation than color discrimination. While it is arguably most parsimonious, and in line with ST, to conclude that surround attenuation is linked with the need to increase spatial resolution, it remains possible that it is a consequence of the increased demands on discrimination posed by the orientation task. It would therefore be important to see whether changing task difficulty without changing demands on the spatial resolution of the discrimination influences the surround attenuation effect.

To address this possibility, an MEG experiment was performed in which the difficulty of the gap discrimination task was varied from trial to trial randomly within experimental blocks, while the spatial scale of discrimination was held constant. Presentation protocol and general task requirements were identical to experiment 1 reported in Hopf et al. (2006). On one type of trials the search items were identical to the ones used in Hopf et al. (2006). The target and the distractors contained just one gap, and

subjects were required to discriminate the orientation of the gap (**single gap task,** Fig. 5A). On another type of trials search items were modified in the following way to render orientation discrimination more difficult: Search items contained two gaps, one on the left and one on the right side, with the size of the gaps differing slightly (**double gap condition**, Fig. 5B). Subjects ($n = 14$, 12 female) were required to report the orientation of the larger gap (left/right), which appeared randomly either at the left or right side of the target on a given trial. This task did not change the spatial scale of discrimination nor the general requirement to perform an orientation discrimination task, but as attested by the behavioural performance below, it increased the demands on discrimination significantly. Except for this modification, the stimulus configuration and task instruction were identical to the easy task. Subjects performed a total of 9 experimental runs with easy and hard targets being randomly intermixed yielding 108 trials per condition. MEG data recording, artifact rejection, and data analysis were identical to Boehler et al. (2009).

6.1. Behavioural performance

Performance was very accurate in the single gap condition (96% correct), and decreased for the double gap condition (70% correct), indicating that the intended manipulation of task difficulty was effective. Response time was also slower on double (580 ms) versus single gap trials (520 ms). RANOVAs with the factor task (single/double gap) confirmed the significance of those differences in performance (accuracy: $F[1, 13] = 400.2$, $p < 0.001$, RT: $F[1, 13] = 59.5$, $p < 0.001$). Importantly, while the proportion of correct responses was clearly reduced for the double versus the single gap condition, performance was still significantly above chance (50%, one-sample t test: $T[13] = 36.3$; $p < 0.001$).

6.2. Event-related magnetic field (ERMF) response

Fig. 5C shows the size of the ERMF response elicited by the probe (FP-minus-FO response) at the five probe distances from the focus of attention (distances towards the horizontal and vertical meridian are collapsed) separately for double (gray) and the
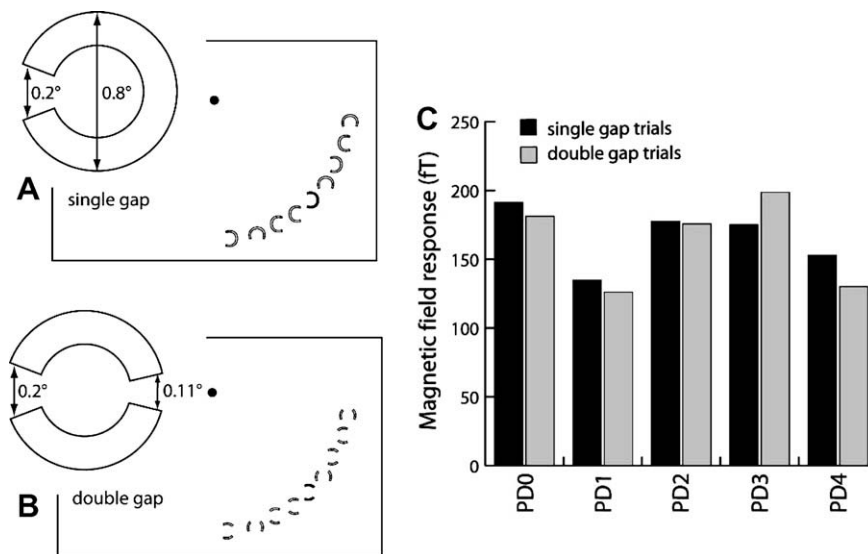
Fig. 5. Results of an experiment manipulating the difficulty of target discrimination without changing the spatial scale of discrimination. (A) illustrates the setup of the search frame and the geometry of the search items (arrows and numbers indicate dimensions in degree of visual angle) presented at the perceptually easier trials (single gap trials) that were identical to the experiment reported in Fig. 2 (Hopf et al. (2006). (B) illustrates the stimuli used on the perceptually more demanding trials where subjects had to discriminate the orientation of the larger of two gaps at opposite sites of the circle (double gap task). (C) shows the probe-response (frame-probe minus frame-only response) as a function of distance to the search target for the single (black) and the double gap trials (gray).

single gap trials (black). The size of the effect was quantified as the average response between 115 and 130 ms after probe-onset where the response had its amplitude maximum. A rough inspection indicated that the size of the response at each probe distance does not show obvious differences between conditions at probe-distances PD0 and PD2. While both conditions produce a clear surround attenuation effect at PD1, the extension of the effect does not differ between them. This general impression is confirmed by a statistical validation. An overall two-way rANOVA with the five-level factor probe-distance (PD0-PD4) and a two-level factor trial type (double/single gap; degrees of freedom adjusted when sphericity correction necessary (Greenhouse-Geisser)) yielded a significant effect of probe-distance ($F[2.7, 34.7] = 3.1$, $p < 0.05$), but no effect of trial type ($F[1, 13] = 0.2$). There was also no significant interaction ($F[2.8, 36.5] = 0.45$). The effect of the type of discrimination task on surround attenuation was further analyzed by planned comparisons between probe-distances. To this end, separate rANOVAs with the factors probe-distance (PD0/PD1; PD1/PD2) and trial type (double/single gap) were performed yielding significant main effects of probe-distance (PD0/PD1: $F[1, 13] = 4.7$, $p < 0.05$; PD1/PD2: $F[1, 13] = 8.2$, $p < 0.05$), but no effects of trial type (PD0/PD1: $F[1, 13] = 0.4$; PD1/PD2: $F[1, 13] = 0.2$). There was also no probe-distance × trial type interaction (both F-values <0.1). In sum, both types of discrimination tasks led to surround attenuation consistent with the requirement for recurrent top-down processing to narrow the focus of attention in both tasks. Importantly, while the discrimination task was substantially more difficult in the double than the single gap condition, the extension and amount of attenuation in both conditions was found to be roughly identical. This clearly indicates that the specific perceptual demands imposed by the orientation discrimination do not determine surround attenuation, and that it is rather the operation of narrowing the focus of attention to increase the resolution of discrimination that is important for surround attenuation to appear.

7. The time-course of surround attenuation

The notion that surround attenuation arises from recurrent processing in visual cortex facilitates a further simple prediction regarding the time-course of involved processes which was addressed in Boehler et al. (2009). In ST the top-down process responsible for surround attenuation (the pruning of forward connections) is initiated after the forward projection field of the stimulus reached the top of the processing hierarchy. Surround attenuation should therefore be absent during the initial forward processing phase. From human electrophysiology it is known that the earliest feed-forward driven visually evoked response arises around 50–60 ms in primary visual cortex (Clark, Fan, & Hillyard, 1995; Foxe & Simpson, 2002). It propagates to extrastriate areas within approximately 90–100 ms. Beyond 100 ms, the neuromag-

netic response shows increasing overlap from recurrent activity. Hence, surround attenuation would be predicted to appear not until after 100 ms post search frame onset. In fact, it would be predicted to appear in the neuromagnetic response with an even larger delay because the region of surround attenuation grows with the downward cascade, such that measurable effects will increase with the pruning process passing the hierarchy. The experiments reported so far indicate that surround attenuation is manifest at 250 ms after search frame onset, which is clearly compatible with those assumptions. But to validate a delay beyond the initial feed-forward sweep of processing would require one to assess cortical excitability in a wider time-range that includes frame-probe SOAs shorter than 250 ms. To this end, a further MEG experiment was performed that was, except for two modifications, identical to the one reported in (Hopf et al. (2006)). The first modification consisted in varying the frame-to-probe SOA between 100 and 400 ms in steps of 75 ms (Boehler et al., 2009), which provided five SOAs: 100, 175, 250, 325, 400 ms. The other modification was that the target was defined as a lunminance pop-out. Fig. 6 summarizes the size of the ERMF response (FP-minus-FO difference) to the probe at the five different frame-probe SOAs. No effect of surround attenuation was evident at SOAs of 100 ms and 175 ms. After an SOA of 250 ms, however, a clear attenuation was present at PD1. This effect was also visible but already statistically insignificant at the 325-ms SOA. Hence, the data indicate that surround attenuation arises with a delay of more than 175 ms relative to stimulus onset, and that it is a transient effect confined to a period of less than 150 ms. In line with ST's prediction, this time-course is clearly not compatible with a generation during the initial feed-forward sweep of processing. Indeed, this delay in timing fits with the typical delay of top-down attention effects on cell-firing in monkey extrastriate and striate cortex (Chelazzi, Miller, Duncan, & Desimone, 1993, 2001; Luck, Chelazzi, Hillyard, & Desimone, 1997; Mehta, Ulbert, & Schroeder, 2000; Motter, 1994; Ogawa & Komatsu, 2004).

Moreover, at 325 ms surround attenuation is already tapering off while the probe-response shows a significant enhancement at the focus of attention (PD0). This delayed enhancement is notable, as it fits a further assumption of ST. Top-down processing that demarcates the target location with high spatial resolution may be followed by a second forward pass through the visual hierarchy (Tsotsos et al., 2008). This forward pass may provide an effective way to refine the target's representation, as it now starts from a signal-to-noise ratio at the input level that is improved (by surround attenuation) beyond that of the initial feed-forward pass through the visual system. It is possible, that the center-enhancement at 325 ms reflects such secondary forward refinement of the target representation. Of course, with the data at hand this interpretation must remain a speculation that requires further experimental validation. The prediction is that in these cases successful completion of the visual task that requires such a refinement would take some ∼300 ms or greater to complete.
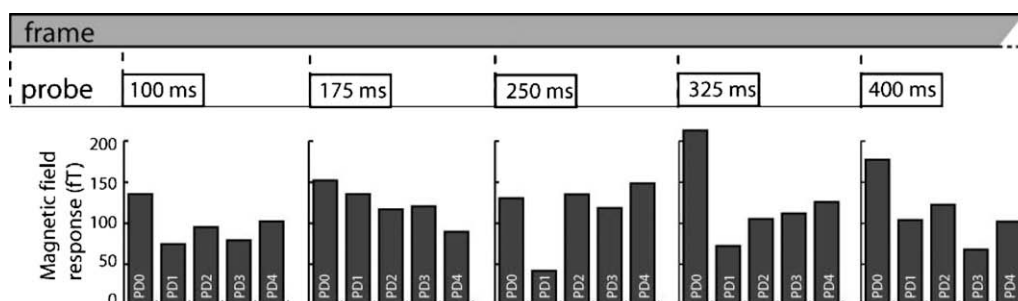

Fig. 6. Results of experiment 2 reported in Boehler et al. (2008). Probe-response as a function of distance to the search target for five different frame-probe SOAs.

To summarize, the time-course of surround attenuation shows a substantial delay relative to the time-course of the initial feed-forward sweep of processing in the visual system. This delay is clearly in line with the temporal organization of attentional selection as revealed by neurophysiological observations in the monkey, in humans, and as proposed by the ST.

8. Conclusion

We have reviewed evidence from neuromagnetic recordings characterizing the focus of attention in visual search, both in terms of its spatial profile and time-course. We observed that the spatial profile is not fixed, but changes depending on the perceptual demands of the search task. Specifically, a simple gradient was seen when search required a simple color discrimination, but a more complex center–surround profile appeared when the search task required item discrimination with scrutiny and spatial precision. Increasing the perceptual demands of item discrimination in the focus of attention without changing the spatial resolution of discrimination did not influence surround attenuation. Furthermore, surround attenuation was independent of the type of forward processing defining the target. Finally, the center–surround profile turned out to appear with a substantial delay relative to the initial feed-forward sweep of processing. Those observations taken together suggest that the center–surround profile arises as a consequence of top-down attentional selection in the visual system, which provides strong support for key notions of the Selective Tuning model of visual attention.

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