Attention-modulated activity in visual cortex—More than a simple ‘spotlight’

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We assessed modulation of retinotopic visual cortex representing peripheral regions of the visual field while subjects engaged in a central attention task. The onset of an attention capturing central letter stream attenuated activity in representations of the peripheral locations. When these locations were empty, the observed reduction was the same whether subjects passively viewed or actively attended the letter stream. For locations containing distracting letters, however, an additional attenuation was observed during the active task. In a second experiment we found that representations of target incompatible peripheral letters were suppressed relative to a control task, whereas at the same time representations of compatible peripheral letters were relatively enhanced. The fMRI results are complemented by behavioral data demonstrating prolonged responses to probes presented at suppressed locations. In sum, our study suggests that activity modulation across the visual field representation not only reflects an attentional spotlight effect but is additionally shaped by the nature of sensory input at unattended locations as well as its relation to task demands.

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Introduction

For decades, the spotlight metaphor (Posner, 1980; Posner and Petersen, 1990; Posner et al., 1980) has dominated our understanding of how attention selects behaviorally relevant information from the myriad of data that hits our senses every second. The metaphor suggests that an attentional beam highlights a region of the visual field so that information in this region is processed more efficiently. The metaphor’s popularity was boosted further at the end of the 1990s when a potential neurophysiological correlate was demonstrated using fMRI in humans (Brefozynski and DeYoe, 1999; Kastner et al., 1998; Müller et al., 2003; Müller and Kleinschmidt, 2003; Somers et al., 1999; Tootell et al., 1998). When subjects direct attention to a certain location in the periphery (while maintaining central fixation) fMRI signals in visual cortex representing the attended location in retinotopic terms become enhanced. It was concluded that stimuli in an attended region are detected more easily because they receive superior sensory processing — triggered by a fronto-parietal network exerting top-down control on visual areas (Corbetta, 1998; Corbetta and Shulman, 2002).

Only recently, functional imaging studies have started to assess unsettled questions surrounding the spotlight metaphor, e.g. whether it can be split (McMains and Somers, 2004) or zoomed (Müller et al., 2003). Yet, other aspects of the spotlight that pertain to its exact organizational structure remain unsolved. For example, an idealized spotlight would only allow two conditions for any stimulus — either inside or outside the spotlight’s beam. Behavioral data, however, clearly demonstrate that the situation is more complex: several studies (Eriksen and Hoffman, 1973, 1974; Eriksen et al., 1990) showed that completely task-irrelevant stimuli placed beyond the assumed focus of attention interfere with target processing. The authors presented central target letters with flankling task-irrelevant letters (distracters). Subjects had to press one button for one set of target letters and another button for another set of target letters. In case the distracter letters were linked with the same response as the target (compatible trial) responses to the target were speeded as opposed to neutral distracters. When the flankling letters were linked with the other response (incompatible trial) they slowed responding. These results indicate that the irrelevant distracters must have attracted some attention or processing resources. Yet other studies demonstrated that subjects obviously try to diminish the deteriorating influence of such distracters: When Cepeda et al. (1998) presented probe stimuli at locations that had previously been either empty or had contained distracters they found that the probes were processed more effectively when the locations had been empty indicating that information processing at distracter locations is inhibited.

To date, there are only few studies that have assessed attention-modulated activity in retinotopic representations of visual field regions outside the attentional focus and these have yielded an inconsistent picture. Smith et al. (2000) reported reduced activity in...
cortical representations of all regions of the visual field except for those coding the position on which attention was focused. This observation obviously cannot account for the behavioral data discussed above which suggested a fine-tuned modulation of activity beyond the center of attention that further distinguishes between empty and filled regions of space. In an earlier study, Müller and Kleinschmidt (2004) observed reduced activity in striate but not extrastriate representations of locations in the vicinity of the attended location indicating an inhibitory surround (see also Schwartz et al., 2005). The latter notion is also supported by behavioral studies that observed increased target–distractor interference with increasing distance (Cutzu and Tsotsos, 2003; Mounts, 2000a,b; Müller et al., 2005). However, these behavioral studies as well as an earlier fMRI study (Müller and Kleinschmidt, 2004), assessed the spatial distribution of attention by distractors and thus could not disentangle whether the observed suppression effects were merely due to spatial distance from the location of attention or required the additional presence of distractors.

Here, we aimed at correlating neural activity in visual cortex representations of peripheral locations with the behavioral impact of stimuli presented at these locations on a central attention task. Crucially, we varied the content at the peripheral locations: they could be empty or contain distractors (experiment 1) or contain stimuli that were either compatible or incompatible with the target that had to be detected at the center (experiment 2). We found a robust relation between fMRI signal strength in representations of peripheral stimuli in early retinotopic visual areas 1 to 3 (V1–V3) and these stimuli’s impact on probe detection in the behavioral experiments. These results go beyond the classic spotlight metaphor for visuospatial attention and support a flexible mechanism in enhancing and suppressing visual field regions depending on their content.

Methods — general

Four experiments with a similar experimental design were conducted. In all experiments subjects had to detect target letters within a rapid serial visual presentation (RSVP) presented at the center of fixation. Four peripheral locations were defined (one at each corner of an imaginary square centered at fixation) at which distractors could be presented. In the behavioral experiments (1a, 2a) additional probe stimuli were presented occasionally at one of the four peripheral locations in order to estimate the distribution of attention in the periphery (Cepeda et al., 1998; Klein, 1988). The fMRI studies (experiments 1b and 2b) measured the BOLD signal change within the neural representations of the peripheral locations in V1 to V3. To do so, the visual cortex representations of the four peripheral and the central locations served as regions of interest (ROIs) and were mapped in separate sessions through passive stimulation with alternating checkerboards presented at the respective locations.

Experiment 1a and b compared peripheral locations that were either empty or contained distractors, whereas experiments 2a and b compared peripheral locations that either contained target compatible or incompatible letters.

All experiments were conducted in conformity with the Declaration of Helsinki and all participants gave written informed consent in compliance with the protocol approved by the local ethics committee. All participating subjects were right-handed and reported normal or corrected-to-normal vision and unimpaired color vision. All subjects were naive as to the purpose of the experiments. No subject took part in more than one of the experiments. No eye movements were recorded as subjects were engaged in a demanding task presented at the center. Moreover, in case peripheral probes were used, their presentation times were too short (50 ms) for saccades to be performed.

Experiment 1a

Experiment 1a assessed the distribution of attention across peripheral locations that were either empty or contained interfering distracter letters. We expected probes presented at distracter locations to be detected slower than those presented at empty locations.

Subjects, stimuli and task

Twenty-two subjects (12 females, mean age 30.8 years) participated in the experiment for course credit. They were seated 60 cm in front of a 17° CRT screen (60 Hz) connected to a standard IBM compatible PC running the Experimental Runtime System (ERTS, Berisoft, Frankfurt, Germany) for stimulus presentation. As in all the following experiments, they fixated the center of the screen during the whole experiment. At the beginning of each block an instruction was displayed reading either the letters "XXX" or the word "RED" (see Fig. 1). This indicated to the subjects that they had to respond either to the letter X or to any red letter in the subsequent RSVP. Subjects could end the instruction and start the central RSVP by pressing the space key.

In half of the blocks, during presentation of the RSVP two clusters of distracter letters were presented either in the upper left and lower right or in the lower left and upper right quadrant in the periphery. Occasionally, a probe stimulus (the character # against a black background that would cover the distracters) was presented at one of the four peripheral locations. Subjects had to press the space bar if they detected such a probe. In order to avoid interference with responding to RSVP targets probes were presented only after a non-target RSVP letter had been displayed. Subjects were instructed to respond to the targets and probes as fast as possible, minimum and maximum RTs were set to 100 ms and 1000 ms, respectively.

Each RSVP letter comprised 1.7° of visual angle and was presented for 250 ms. Distracter letters had the same size as the RSVP letters and were arranged in matrices of nine letters placed at a center-to-center distance of 4.8°. They were static once they had appeared at the beginning of a block. In the RSVP the letters ‘HBLIVRSA’, for distracters the letters ‘DYTJFMDQ’ were used.

Probes were presented for 50 ms. Stimulus onset asynchronies between non-target RSVP letters and probes varied between 50, 100 and 150 ms. All stimuli were white and presented against a black background.

In every block, 648 RSVP letters and 36 peripheral probes were presented. Among the RSVP letters were 72 targets. There were eight blocks with the target letter ‘X’, and eight blocks where any red letter served as target. Half of the blocks contained two peripheral distracter clusters; the remaining blocks did not contain any distracters. The blocks were presented in randomized order.

Data analysis

A repeated measure ANOVAs for the mean reaction times (RTs) was calculated for the central RSVP with the factors ‘task’ (X or red letter) and ‘distracter’ (present or absent). For RTs to the
probes, the ANOVA included the factors ‘location’ (distracter vs. empty) and ‘SOA’ (50, 100, and 150 ms). As in the remaining experiments, paired t-tests were used for post hoc analyses.

Results

Reaction times (RTs) to targets within the RSVP were slower during presence than during absence of distracters ($F(1, 21)=13.09, p<0.01$, Table 1). In addition, RTs were faster for red letters as opposed for the letter X ($F(1, 21)=81.17, p<0.001$) but there was no significant interaction target $\times$ distracter presence ($p>0.2$). Hence, in the following fMRI experiment only one target type was used.

The main finding of experiment 1a was that subjects reacted faster to probes presented at empty than at distracter locations [$F(2, 42)=41.36, p<0.001$] (Table 2). In the present study it made no difference whether probes appeared at empty locations that were opposed by distracters or whether probes appeared while no distracters were presented at all ($p>0.2$). Hence, the empty locations seem to have received the same amount of attention irrespective of the presence or absence of distracters at other locations in the visual field.

Experiment 1b

In this experiment we compared activity at early visual cortex representations of empty vs. distracter locations. We aimed at minimizing sensory driven fMRI activation by using a static display instead of rapidly reversing stimuli. Modulation of activity in visual representations of the distracters should, therefore, mainly be top-down driven. Hence, we expected that during active search for a target activity in these representations should decrease as previous data suggested distracter suppression under focused attention (Caputo and Guerra, 1998; Cepeda et al., 1998; Eriksen and Hoffman, 1974; Facoetti and Molteni, 2000; Pinks et al., 2004; Rees et al., 1997; Schwartz et al., 2005).

Subjects, stimuli and task

Eight subjects (four females, mean age 24.6 years) were paid to participate in the study. Almost the same stimuli as in experiment

<table>
<thead>
<tr>
<th>Target</th>
<th>Distracter</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Present</td>
</tr>
<tr>
<td></td>
<td>Experiment 1a</td>
</tr>
<tr>
<td></td>
<td>Red letter</td>
</tr>
<tr>
<td></td>
<td>Experiment 1b</td>
</tr>
<tr>
<td></td>
<td>X</td>
</tr>
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<td></td>
<td>O</td>
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<tr>
<td></td>
<td>Interruption</td>
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<tr>
<td></td>
<td>Experiment 2a</td>
</tr>
<tr>
<td></td>
<td>X</td>
</tr>
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<td></td>
<td>O</td>
</tr>
</tbody>
</table>

In experiment 1a distracters could be present or absent during target identification whereas in all other experiments distracters were always present.

In experiment 1b probes could occur on a distracter location, opposite a distracter location or in empty locations. In experiment 2a probes were the offset of an X or O distracter.

Table 1

Mean RTs and standard errors (ms) for target detection in the central task in experiments 1a–2b

<table>
<thead>
<tr>
<th>Target</th>
<th>Distracter</th>
<th>Probe At distracter</th>
<th>Opposite Dis</th>
<th>Empty</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Experiment 1a</td>
<td>X</td>
<td>480.8 (61.6)</td>
<td>452.9 (75.5)</td>
</tr>
<tr>
<td></td>
<td>Red letter</td>
<td>456.5 (50.8)</td>
<td>436.7 (72.0)</td>
<td>436.9 (47.6)</td>
</tr>
<tr>
<td></td>
<td>Experiment 2a</td>
<td>X offset</td>
<td>451.6 (67.7)</td>
<td>475.9 (75.5)</td>
</tr>
<tr>
<td></td>
<td>O</td>
<td>466.1 (77.2)</td>
<td>436.7 (72.0)</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>Interruption</td>
<td>426.8 (83.4)</td>
<td>425.1 (83.3)</td>
<td>–</td>
</tr>
</tbody>
</table>

In experiment 1a, probes could occur on a distracter location, opposite a distracter location or in empty locations. In experiment 2a probes were the offset of an X or O distracter.
1a were used. However, some adjustments were made for the fMRI experiment: RSVP letters were presented only for 200 ms in order to adjust task difficulty as no probes were shown; passive blocks, in which subjects only watched the RSVP without the need to respond, were introduced to assess bottom-up driven activity; in active blocks, always the letter ‘X’ served as target; and a pair of distracters was present in every block.

Each of the 36 blocks used in this experiment started with the presentation of the instruction with the words “passive” or “active” presented above the central fixation cross for 20 s. At the beginning of the instruction phase the two diagonally opposing clusters of distracters switched positions. Hence, always two quadrants contained distracters while the other two remained empty. Passive and active blocks lasted for 40 s (20 volumes) each and were presented in randomized order. In every active block the target letter ‘X’ was shown 10 times.

**fMRI procedure**

Data were acquired with a 3T Siemens (Erlangen, Germany) Trio scanner. Stimuli were back-projected onto a screen using a Sanyo Pro XtraX Multiverse projector placed outside the scanner room and equipped with a customized lens. Participants viewed the display through a mirror attached to the head coil. Custom-made response keys with fiber optics were used for report.

Functional images were acquired via a 64×64 gradient T2* echo echoplanar imaging sequence (resolution 3×3×3 mm; slices=32; gap=0.3 mm; TR=2000 ms; TE=30 ms; flip angle 60°). The experiment consisted of three 12 min runs corresponding to 3×360 volumes. Retinotopic mapping was conducted in separate runs. 240 volumes were acquired to map the meridians and 350 volumes to define the different ROIs.

A T1-weighted MPRage sequence (resolution 1×1×1 mm³; slices=144; TR=2250; T1=900 ms) was used to create 3D anatomical images.

Brainvoyager QX software (BrainInnovation, Maastricht, The Netherlands) was used for all fMRI analyses. The first two volumes of each functional run were discarded, the remaining corrected for slice scan time differences within a volume, motion-corrected and temporally high-pass filtered (3 cycles per run). The functional data were co-registered with the three-dimensional MPRAGE data sets obtained in the same session which were then 3D–3D aligned to the MPRAGE data set acquired in the first session and transformed into stereotactic space (Talairach and Tournoux, 1988) such that volume–time courses from different sessions could be compared.

The cortical surface of each subject was reconstructed from the 3D data set. The white matter was segmented using a grow-region function, then a sphere was covered smoothly around the segmented region, and the reconstructed white matter was expanded into the gray matter. After separation of the hemispheres, the sulci were smoothed using a cortical inflation procedure.

**Regions of Interests (ROIs)**

Neural activity during the experimental task was assessed in pre-defined ROIs. These ROIs were determined in each subject individually in extra experimental runs. In these runs subjects fixated a central cross and passively watched flickering checkerboards (8 Hz) presented at the same peripheral visual field regions that could contain distracter letters in the attention experiment. Each position was stimulated separately for 6×20 s. The activated regions were shown on inflated and flattened surface representations of the brain (Fig. 2). They were assigned to visual areas V1, V2 and V3 in yet another experiment in which wedge shaped checkerboard stimuli were presented along the horizontal and vertical meridians (Sereno et al., 1994, 1995). Note, that we did not assess area V4 because this area has only representations for the upper visual field.

In order to test whether we would obtain the usual enhancement for the attended visual field region, we also mapped the central region where the RSVP was presented. Note, however, that within foveal representations it is very difficult to identify individual visual areas (Dougherty et al., 2003), so that we refrained from attempting to separate the activated clusters near the occipital pole into areas V1, V2 and V3.

For the data of the ROI mapping experiment, after z-transformation a fixed-effects general linear model was calculated with each location serving as a predictor. The model contained an idealized reference function as predictor of the effect of interest. This reference function was generated by convolving a model of the hemodynamic impulse response with a square-wave function representing the experimental protocol. Then contrasts between the location of interest and all other locations were calculated employing a significance level of \( p<0.0001 \) (uncorrected).

**Data analysis**

The aim of the experiment was to assess activity in early visual cortex representations of peripheral visual field regions depending
on whether they were empty or contained distracter letters. Note, that we confined our analysis to the ROI approach; hence no whole brain analysis was performed on the RSVP task. For each pre-defined ROI the BOLD response was averaged from the volume-time-courses covering both the instruction and the RSVP phase whereby the 6 s preceding the instruction served as baseline. The data were then collapsed across the upper and lower and the right and left quadrants. For statistical analysis the mean of the BOLD response during the 40 s RSVP was computed and entered into a repeated measure ANOVA with the factors “location” (filled vs. empty) and “task” (passive vs. active) and ‘area’ (V1–V3) was calculated. For the single ROI representing the fovea a separate ANOVA without the factor area was calculated.

Results

Behavioral results for the central task are presented in Table 1, fMRI results are presented in Fig. 3. A t-test that compared RTs to ‘X’ targets between experiment 1a and 1b showed no significant difference between the experiments (p > 0.2).

At the visual cortex representation of the fovea we observed a strong signal increase with the beginning of the RSVP that was considerably more pronounced when subjects actively engaged in the task as opposed to passively watching it (F(1,7)=17.23, p < 0.01).

In the representations of the peripheral locations the onset – and to a lesser extent – the offset of distracters at the beginning of a block induced a marked signal increase. With the subsequent start of the RSVP activity decreased considerably whereby the cortical representations of the distracter locations remained more active than those of the empty locations (F(1,7)=82.85, p < 0.001). This effect, however, was solely due to the initial difference related to stimulus onset vs. offset and disappeared when the signal from the early phase (i.e. the first 6 s after onset of the RSVP) was subtracted from the later signal (t = 0.17, df=7, p > 0.4).

While the RSVP was on, the signal for the distracter representations was more attenuated in the active than in the passive task in all visual areas, whereas representations of the empty locations evoked the same signal levels in both tasks (F(1,7)=8.31, p < 0.05 for task × location, see Fig. 3B). Hence, the representations of the distracters but not the empty locations were modulated by intentionally focusing attention on the central task.

Experiment 2a

Like in experiment 1a, subjects had to respond to targets within a RSVP as well as to infrequent probe stimuli at the peripheral locations. However, distracter letters were now placed in each quadrant of the visual field and the distracters were compatible, incompatible or neutral with respect to the target. In the line with previous studies (Flowers and Wilcox, 1982) we expected that target incompatible distracters (e.g. search for X within the RSVP, distracter=O) would cause distraction as opposed to target compatible distracters (e.g. search for X within the RSVP, distracter=X).

Subjects, stimuli and task

Nineteen subjects (11 females, mean age 24.6 years) participated for course credit. Positions of stimuli as well as timing were identical to experiment 1a. However, there were now three types of targets: X, O or an interruption of the central RSVP; two diagonally opposing peripheral locations contained the letters ‘X’, the other two contained the letters ‘O’ (size ~4°).
The distractor letters switched positions between blocks. Hence, depending on which letter was defined as target two distracters were compatible and two were incompatible as they corresponded to the central letter that had to be ignored in the respective block. For example, when subjects search for a central X, the peripheral X letters are compatible, while the peripheral Os are incompatible as whenever a central O occurs responses have to be withheld. In blocks in which subjects had to detect an interruption within the RSVP, all peripheral letters were neutral with respect to the central task. Probes in this experiment were defined as short offsets (50 ms) of the peripheral distracters.

The experiment comprised two sessions of 18 randomized blocks (six per target type) that lasted for 162 s each.

Data analysis

RTs faster than 100 ms or slower than 1000 ms were rejected from further analysis. The data from the central task was submitted to a repeated measure ANOVA with the factor ‘target’ (X, O, interruption). For the probes, paired t-tests were calculated to compare the mean RTs for probes at different locations.

Results

The statistical analysis of the data revealed no RT differences for the different targets (X, O, interruption; F(2, 36) = 1.93 > 0.1) indicating that task difficulty was matched between the three conditions (Table 1).

During letter search, probes presented on compatible letters were detected faster than probes on incompatible letters (t = 4.52, df = 18, p < 0.001, see Fig. 4B). When subjects instead watched for an interruption within the RSVP, X and O offsets in the periphery were detected equally fast (t = 0.40, df = 18, p > 0.5).

Experiment 2b

In experiment 2b we measured activity in neural representations of peripheral visual field regions containing compatible or incompatible distracters. We expected that locations with target incompatible distracters should be activated less than target compatible distracters. No such distracter type dependent effects should occur in a control condition, in which subjects had to detect an interruption within the RSVP rather than a specific target letter.

Subjects, stimuli and task

Eleven subjects (four females, mean age 23.8 years) were paid to participate in the study. Some adjustments to experiment 2a were necessary to make the experiment functional imaging: No probes were used and the presentation time per letter was reduced to 200 ms. Hence, the experimental procedure was close to experiment 1b. An experiment consisted of 36 blocks, in each block 10 targets were presented.

fMRI procedure

Retinotopic mapping, the fMRI measurement and the analysis of the functional data were conducted the same way as in experiment 1b. The experiment comprised 36 blocks presented within three runs of 360 volumes.

Data analysis

For the ROIs representing the center, a single-factor ANOVA with the factor ‘target’ (X, O, interruption) was calculated. In order to account for the effects in the periphery, paired t-tests were calculated that compared activity at compatible with neutral and incompatible with neutral locations, respectively.

Results

Behavioral data are presented in Table 1. As in experiment 2a, there was no significant RT difference between the three different target types (X, O, interruption; F(2, 36) = 0.81 > 0.1). The BOLD signal at the representation of the central target showed similarities to that observed in experiment 1b (see Fig. 5): The BOLD signal increased with the beginning of the RSVP irrespective of which target had to be searched for. The different search tasks had no significant influence on the mean BOLD signal at the representations of the fixation location (F(2, 36) = 1.93, p > 0.1).

The time courses of the BOLD signals at the peripheral distracter locations are presented in Fig. 6A. The signal for compatible distracters was relatively enhanced compared to neutral distracters (V1: t = 4.47, df = 10, p < 0.001; V2: t = 4.65, df = 10, p < 0.001; V3: t = 4.58, df = 10, p < 0.001) whereas it was suppressed for incompatible distracters (V1: t = −3.58, df = 10, p < 0.01; V2: t = −3.74, df = 10, p < 0.01; V3: t = −3.26, df = 10, p < 0.01). The results held when instead of the pre-instruction baseline a baseline comprising the first 6 s of the RSVP baseline was chosen (see comment on experiment 1b) indicating that the RSVP effects were not simply driven by signal changes during the preceding instruction phase.

In order to illustrate our findings we subtracted the signal for a given peripheral letter during neutral trials (interruption task) from those trials in which the same peripheral letter was either compatible or incompatible with respect to the target (Fig. 6B). This calculation eliminates any potential difference in sensory processing between X and O letters. The subtraction between compatible and neutral letters yielded positive, the subtraction between incompatible and neutral letters yielded negative values corresponding to the t-tests reported above.

In sum, experiment 2b demonstrated that activity in early visual cortex representing peripheral distracter locations is modulated as a function of target–distracter relation.

General discussion

Four experiments were conducted to investigate the distribution of neural activity in visual cortex representing regions outside the focus of attention. Behavior as assessed by RTs for infrequent probe stimuli at peripheral locations was correlated with neural activity in retinotopic representations of the peripheral locations as measured by fMRI.

While activity for the foveal representations increased with onset of the central letter stream, activity in representations of the periphery decreased — irrespective of whether subjects passively watched the stream or actively searched for targets. The latter suggests that this effect was mainly bottom-up driven, i.e. occurred independently from voluntary attentional control through the subject. Recently, it has been shown that salient peripheral stimuli induce exogenous attention shifts that drive activity in early visual cortex (Liu et al., 2005; Müller and Kleinschmidt, 2007). Hence, it can be concluded that neural activity in representations of the fovea reflected processing of sensory input that was further enhanced by an automatic attention shift toward these highly salient stimuli. In
accordance with a push–pull model of visual attention (e.g. Pinsk et al., 2004), the foveal signal increase automatically led to a withdrawal of processing resources from the remaining visual field resulting in a signal decrease in the periphery. This observation is also in line with previous work demonstrating a center-surround modulation of visuospatial attention both behaviorally and with functional imaging (Cutzu and Tsotsos, 2003; Hopf et al., 2006; Mounts, 2000a,b; Schwartz et al., 2005; Slotnick et al., 2002; Smith et al., 2000; Steinman et al., 1995).

On top of this exogenously driven center-surround modulation, however, a more fine-grained modulation of activity in visual cortex emerged as soon as subjects voluntarily directed attention to the RSVP. In accordance with numerous previous studies we observed an attention-driven further enhancement in retinotopic areas coding the attended visual field region (e.g. Brefczynski and DeYoe, 1999; Müller et al., 2003; Müller and Kleinschmidt, 2003; Somers et al., 1999; Tootell et al., 1998) which had been taken as evidence for a physiological correlate of the spotlight model.

Center-surround or push-pull models of attention would have suggested that the further signal increase in foveal representation would simply be paralleled by another signal decrease in representations of all the remaining visual field. However, in active tasks we observed a further suppression of activity only in representations of distracter but not of empty locations. This differential response pattern also goes beyond predictions of Lavie’s theory on attentional load (Lavie, 1995; Lavie and Tsal, 1994). In her model, the amount of processing resources available for surrounding stimuli is negatively correlated with the demands of the central task, i.e. its attentional load. While this theory could explain stronger suppression in the periphery during active (i.e. high load) vs. passive (i.e. low load) conditions, it does not account for the lack of such a modulation at empty locations.

Still, it is conceivable that the stronger attenuation of visual cortex representations of distracter locations was the result of some bottom-up driven effect simply caused by the difference in physical input between distracter and empty locations. Such an explanation could be suspected based on the results of a study by Schwartz et al. (2005). These authors also reported a stronger BOLD reduction in visual cortex coding peripheral stimuli than coding empty space when attentional load was increased at the central task. However, in their study a large, reversing checkerboard stimulus was used as peripheral distracter stimulus that was designed to maximize visual responses. Hence, the bottom-up driven activity in visual areas coding the checkerboard and the empty field differed tremendously. Therefore, the stronger attention-related attenuation for distracter representations could simply be the consequence of this imbalance in bottom-up driven signal magnitude whereby the same relative signal change would result in a much larger net effect in strongly activated as opposed to weakly activated regions. Our design, on the other hand, was aimed at equating differences in bottom-up stimulation for distracter and empty locations. The distracting letters remained static during 60 s and hence only induced a transient signal increase at the beginning of the instruction phase when they switched positions. This transient should not have affected the BOLD signal during the RSVP which followed 20 s later and was the basis of our statistical analysis.

Therefore, we propose that the reduction of activity for distracter representations during focused attention was top-down driven and aimed at suppressing visual field regions containing distracting information. This assumption also accounts for the observed increase of RTs for probes presented at distracter locations in experiment 1a as visual processing capacity in representations of...
these locations is assumed to be reduced. Top-down control suggests the involvement of higher order fronto-parietal areas that modulate activity in visual subareas depending on the content of the visual field regions that these subareas represent (Barcelo et al., 2000; Hopfinger et al., 2000; Schwartz et al., 2005) contrasting automatic bottom-up attentional capture (Liu et al., 2005; Müller and Kleinschmidt, 2007). Hence, this finding extends prior reports stating that focusing attention at the center simply reduces activation for representations of all the rest of the peripheral visual field (Smith et al., 2000) or that expected distracters enhance activity for the target location (Serences et al., 2004). It also suggests that a previous report of reduced activity in V1 representations of locations neighboring the attended location that was observed in the absence of any relevant stimuli (Müller and Kleinschmidt, 2004) was at least in part driven by the fact that subjects expected distracting stimuli at the unattended locations (Awh et al., 2003).

Fig. 6. fMRI results for experiment 2b. (A) Time course plots of the BOLD responses at distracter locations during instruction and after onset of the RSVP (marked with 0). (B) Difference means of the BOLD responses evoked by the RSVP. Calculated were the differences of the signal for a given distracter during letter search minus the signal for the same distracter during the control task when all distracters were neutral with respect to the central task. In general, the signal for compatible distracters was stronger than for neutral distracters, the signal was weaker for incompatible distracters than for neutral distracters.
In our second series of experiments we observed faster responses to probes at locations containing target-compatible vs. incompatible distractors. Moreover, activity at representations of compatible letters was less attenuated than at representations of incompatible letters. These observations could principally be due to two different processes: The effects could either be based on superior representations of compatible distractors or on suppression of incompatible distractors (or a mixture of both). Enhancement of compatible distractors could be driven by the fact that target and compatible distractor letters were identical or, in other words, shared common features. Only recently, feature based attention has been shown to boost activity in visual cortex representations of ignored stimuli that share a feature with an attended stimulus somewhere else in the visual field (Saenz et al., 2002). With respect to our results, representations of peripheral letters that were task-irrelevant but identical with the target letter may have been enhanced through feature based attention. The assumption that this modulation was top-down driven is supported by the fact that a) the enhancement was observed although the respective target letter was not physically present most of the time and b) the same peripheral letters were not enhanced when subjects watched for non-letter targets, namely an interruption in the central letter stream. In other words, the modulations were solely driven by the subjects’ knowledge.

Now, the parallel signal decrease in representations of incompatible peripheral letters could simply reflect the cost of this feature-based enhancement for compatible letters in terms of a push–pull mechanism. If this was the case, all locations apart from those containing compatible letters should be affected by this withdrawal of resources. Although we cannot rule out this possibility based on the results of experiment 2b alone as we did not asses activity for empty or visual regions with neutral stimuli, with the results from the preceding series of experiments it seems more likely that incompatible distractors were indeed actively suppressed because in experiment 1b no top-down driven modulations were seen at empty locations.

Taken together our experiments indicate that level and sign of neural signal change in representations of peripheral locations under centrally focused attention depend on the degree to which information in the periphery interferes with target processing so that target incompatible distractors elicit the weakest (or most attenuated), target compatible flankers the largest (or least attenuated) and empty locations a medium level signal strength. We suggest that subjects specifically aim at reducing the attentional ‘energy’ devoted to visual field regions with potentially distracting information (Cutzu and Tsotsos, 2003; Facoetti and Molteni, 2000; Schwartz et al., 2005; Smith et al., 2000). The notion that distractor processing is under top-down control is underpinned by previous observations that visual cortex representing an expected distractor’s location is modulated even before the distracter is presented although the exact nature of this anticipatory modulation remains unclear (Awh et al., 2003; Ruff and Driver, 2006).

We did not observe significant differences across the three visual areas addressed in this study. In other words, all effects reported where present in V1 already with no additional modulation observed in later areas. We suggest that only V1 has receptive fields small enough to allow for suppression of nearly neighboring distracters and hence constitutes the major target for fine-tuned spatial attention (Müller and Kleinschmidt, 2004). In conclusion, our data suggest the co-existence of a general surround suppression that occurs as soon as a salient stimulus captures attention and a rather flexible mechanism with which we intentionally enhance and suppress sensory processing of relevant and irrelevant information present at different regions in space.

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References


