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2010

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citation for published version (APA)

Munneke, J. (2010). *Spatial Attention in Early Visual Cortex*. [PhD-Thesis - Research and graduation internal, Vrije Universiteit Amsterdam].

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Chapter 5

Preparing for distractors: neural correlates
of attentional suppression

Munneke, J., Heslenfeld, D.J., Mangun, G.R., Theeuwes, J. (in preparation). Preparing for distractors:
Neural correlates of attentional suppression.

Abstract

Spatial selective attention is the mechanism that facilitates the selection of relevant information over irrelevant information presented in the visual field. The current study investigated whether foreknowledge concerning the presence or absence of distractors surrounding a target modulates early visual cortex. We cued the location of the target and the presence or absence of distractors surrounding the target. We measured changes in blood oxygen level dependent (BOLD) signals. Our findings indicate that top-down spatial attention resulted in an increased contralateral BOLD response evoked by the cue throughout early visual cortex (V1, V2 and V3). Furthermore, cues indicating distractor presence evoked a stronger BOLD response in regions of visual cortex contralateral to the cued location in visual area V3, but not in V2 or V1. The observed effects for location and distractor cueing were retinotopic in nature. The study shows that prior knowledge of distractor presence results in modulation of 'mid-level' areas of visual cortex where neuronal receptive fields are large enough to encompass both targets and distractors.

Introduction

Spatial selective attention is the mechanism that allows us to focus on information relevant for ongoing behaviour while ignoring unimportant events. It is generally assumed that spatial attention acts by facilitating processes related to the selection of relevant information (Hillyard, et al., 1998; Posner & Petersen, 1990). However, because the visual environment also contains information that is irrelevant for ongoing behaviour, it has been hypothesized that selective attention attenuates possible interfering effects of irrelevant information (Moran & Desimone, 1985; Reynolds, et al., 1999). A number of behavioural studies have shown that spatial cueing effects were larger in conditions in which a target was surrounded by irrelevant information (Awh, et al., 2003; Awh & Pashler, 2000; Shiu & Pashler, 1994). Therefore, attentional selection may be accomplished by a mechanism that facilitates processing of relevant information while at the same time suppressing interference caused by irrelevant information (Pinsk, et al., 2004; Somers, et al., 1999).

Previous research has shown that selective attention can operate in a spatially specific manner, acting on a limited part of the visual field (e.g. Posner, 1980). Voluntary (top-down) control of this mechanism can be accomplished covertly, without making overt eye or head movements. Theories of spatial selective attention have mostly focused on attentional mechanisms that enhance the neural response in parts of visual cortex that code the attended location. These models of spatial selective attention have compared the attentional mechanism to a spotlight (Posner, et al., 1980), zoom lens (Eriksen & Yeh, 1985) or a gradient (Laberge & Brown, 1989), all sharing the assumption that when more processing resources are directed to a relatively small visual area, information processing at that area is improved.

Contrary to improved processing of target-related information, some studies have focused on the suppressive effects of attention on irrelevant information. An example of these effects can be found in studies showing that information presented close to the focus of attention gets suppressed compared to items presented further away from the attended location (Bahcall & Kowler, 1999; Mounts, 2000a). This has led to the hypothesis that the spotlight of attention has a Mexican-hat distribution (Muller, Mollenhauer, Rosler, & Kleinschmidt, 2005), facilitating information processing at

attended locations, whereas information surrounding the focus of attention gets suppressed. Information presented even further away from the attended location is neither facilitated nor suppressed.

Studies that show suppression surrounding the focus of attention confirm the notion that spatial selective attention does not merely facilitate target processing, but also suppresses effects of surrounding irrelevant information (Bahcall & Kowler, 1999; Mounts, 2000a; Muller, et al., 2005). However, these studies specifically deal with the operation of attentional selection and do not specifically address the properties and neural mechanisms of attentional suppression.

Facilitated visual information processing due to spatial selective attention has also been studied using neuroimaging methods. Results of fMRI studies have shown increased patterns of activity in striate and extrastriate cortex as a result of top-down control of attention (Brefczynski & DeYoe, 1999; Corbetta, et al., 2000; Gandhi, et al., 1999; Hopfinger, et al., 2000; Kastner, et al., 1999; Somers, et al., 1999). The increased BOLD response in visual cortex is assumed to reflect enhanced processing of visual information as a result of attention. Top-down attentional control signals are thought to derive from higher order areas in a dorsal fronto-parietal network. This network is commonly found to be active during tasks of spatial attention (reviewed in Corbetta & Shulman, 2002; Kanwisher & Wojciulik, 2000). These top-down signals modulate in visual cortex the neural response that reflects sensory processing.

Attentional modulation of visual cortex can be observed prior to the presentation of a target stimulus when a cue directs attention to a specific location. These BOLD response increases have been coined baseline shifts (Kastner, et al., 1999; Ress, et al., 2000). Baseline shifts of attention are thought to prime sensory (visual) cortex by increasing neuronal activity, thereby improving the signal-to-noise ratio of the impending stimulus-evoked response (Ress, et al., 2000). Neuroimaging studies on spatial attention have observed these signals in extrastriate (Hopfinger, et al., 2000) and striate cortex (Jack, et al., 2006; Kastner, et al., 1999; Munneke, Heslenfeld, et al., 2008; Ress, et al., 2000; Silver, et al., 2007). Furthermore, data from these latter studies clearly indicate that primary visual cortex can be biased as a result of directing spatial attention to a location in space. Until quite recently this has been subject to debate (see Posner & Gilbert, 1999).

An issue that has not been addressed adequately concerns the mechanism by which attention facilitates target selection. Target presentation is often accompanied by the presentation of distracting information. Therefore, the increased BOLD response in visual cortex could either reflect the result of enhanced target processing, suppression of interfering information from unattended locations or both. Indeed, studies on the neural correlates of attention have often shown that neural modulation in regions of visual cortex coding unattended locations is attenuated compared to attended and neutral viewing conditions (Silver, et al., 2007; Somers, et al., 1999; Tootell, et al., 1998). These results provide converging evidence that attention does not merely modulate visual cortex in a facilitatory way, but also modulates unattended locations in a suppressive way. However, similar to the behavioural studies showing suppression surrounding the focus of attention (Bahcall & Kowler, 1999; Mounts, 2000a; Muller, et al., 2005), studies that show neural modulation of unattended locations have not specifically addressed the mechanism underlying suppression, but have mainly shown that the suppressive effects observed are basically a by-product of selecting a location in space (Silver, et al., 2007; Somers, et al., 1999).

However, a number of studies have shown that the suppressive mechanism of attention is at least to a certain extent under top-down control (Awh, et al., 2003; Munneke, Van der Stigchel, et al., 2008; Ruff & Driver, 2006; Serences, et al., 2004). These studies show that attentional modulation in early visual cortex may reflect processes related to expected distractor properties, such as their location in the visual field or their presence or absence on a given trial. Furthermore, some of these effects have been observed prior to the onset of the visual information, as changes in baseline activity (Serences, et al., 2004).

Serences et al. (2004) showed that cueing the likelihood of distractor presence influenced baseline signals in visual cortex. On each trial, the location of two target digits was cued. The location cues (100% valid) and subsequent targets were always presented at fixed locations in two quadrants of the visual field at diagonal opposites from the central fixation point (e.g. upper-right and lower-left). The shape of the cues (circle or square) further indicated whether the digits would be presented in a cluttered field of letter-distractors, or whether they would be presented alone (80% valid). Participants were instructed to add the two digits and indicate whether the outcome of the sum was

odd or even. By manipulating the likelihood that targets would be accompanied by distractors, cue-induced neural responses could be measured that reflected preparation for upcoming distractors. Behavioural data showed that participants scored significantly better on distractor-present trials when distractors were expected compared to when distractors were unexpected. Importantly, when distractors were absent, distractor cueing had no effect. These results show that attentional modulation of the target is not the cause of increased performance, as this would have resulted in increased performance when distractors were absent as well. fMRI data showed an increased neural response in early visual cortex (including V1) for attended locations compared to unattended locations. Moreover, the increased neural response was largely caused by cue-evoked responses in trials when distractors were expected. When no distractors were expected, differences in cue-evoked responses between attended and unattended locations were small, irrespective of the presence or absence of distractors. The fMRI data agreed with the behavioural data, showing that preparatory effects of attention were larger in conditions in which the level of distractor suppression was higher.

Additional evidence for top-down control of distractor suppression comes from a study by Ruff and Driver (2006). Ruff and Driver employed a paradigm in which both the location of a target was cued as well as the presence or absence of a distractor in the hemifield opposite to the target. In order to separate target and distractor evoked neural responses, target and distractor were presented in opposite hemifields. Ruff and Driver showed that cueing the expectancy of a distractor lead to a behavioural advantage in target selection in terms of faster response times. Moreover, this effect was only significant when a distractor followed the cue, but not when the distractor was absent. fMRI data of the study by Ruff and Driver showed a preparatory increase in BOLD response between expected distractor presence compared to expected distractor absence at regions of the visual cortex contralateral to the indicated distractor location. These preparatory increases were observed in early and midlevel regions of the visual cortex (Brodmann's area (BA) 17, 18 and 19). Under these conditions no additional modulation reflecting target preparation was observed in regions of the visual cortex contralateral to the cued target location. These data clearly show that participants were able to utilize a cue that informed them about distractor-related properties (i.e. location).

Further evidence for top-down control over the suppressive mechanism of attention is found in a behavioural study by Munneke et al. (2008). In this study, a target and a distractor were presented above, below, left or right of the central fixation. On half the trials, a cue indicated the likely position of an upcoming distractor. When the cue was present, a distractor would appear at the cued location on 50% of the trials. In the other half of the trials only a cue would be present, not followed by a distractor. When the cue was absent, a distractor could still appear on 50% of the trials. The results of this study showed that cueing the location of a distractor lead to faster responses to the target compared to an uncued distractor. This effect was only observed when a distractor was actually present. When no distractor was present, no effect of the cue was observed. These results suggest that the behavioural effects are not caused by enhancement of target stimuli but rather by suppressing the interference of the distractor item. This is in line with Serences et al. (2004) and Awh et al. (2003) who showed that the knowledge of distractor properties only influences responses to the target when distractors are actually presented.

The current study investigates how preparing for distractors changes the hemodynamic responses in early visual cortex prior to the onset of the target display. Similar to Serences et al. we used a paradigm in which a target was surrounded by distractors in close proximity. However, the current study differs from the study by Serences et al. (2004) in three important ways. First, Serences et al. investigated how neural activity at the attended target location changed as a result of distractor likelihood. The study did not investigate neural activity at the distractor locations. Therefore, the study by Serences et al. can only infer about how target-related neural processes are changed by the likelihood of upcoming distractors. In the current study we used a design in which the visual area stimulated during distractor trials was similar to target-only trials (see Figure 1). That is, we used a design in which the cued location always had the same size whether distractors were present or not. This allowed us to study the cue-evoked neural modulation at the location where targets and distractors were expected. Second, we employed an endogenous spatial cueing paradigm, instructing participants to voluntarily shift attention towards the cued location. Serences et al. used a peripheral cueing procedure, which involuntarily draws spatial attention towards the cued location. Facilitating and suppressing effects of spatial attention are likely to act differently in

conditions of voluntary (top-down) as opposed to involuntary (bottom-up) attention. Third, Serences et al. always cued two target locations in the visual field, requiring divided attention in order to observe both targets. We cued a single target location in order to investigate the classic effects of spatial attention to a location.

Method

Participants

Twelve paid volunteers participated in the experiment (mean age: 27.2 years, 8 males). All participants were healthy, had normal or corrected-to-normal vision and were right handed. The protocol was approved by the human subject review board of the University of Davis, California. All participants gave written informed consent prior to the start of the experiment.

Stimuli and Task

Participants performed a spatial cueing task in which the location and likelihood of distractors were cued. Figure 1 shows a typical experimental trial. At the start of a trial, participants fixated a centrally presented fixation point until the cue was presented. The arrow cue (subtending a visual angle of 0.6×1.0 degrees) informed the participant about two properties of the upcoming target display. First, the arrow pointed towards the location of the upcoming target, which (when displayed) was always present at the cued location (100% valid). Second, the color of the arrow (blue or red - counterbalanced over participants) informed the participants whether the target would be surrounded by distractors or whether a target would be presented alone. The cue was presented for 1000 ms followed by a blank screen for 800ms. Subsequently, the target screen was presented which remained onscreen for 1500ms. After target offset, the fixation screen would reappear until the next cue was presented 2100ms later. Onset of the cue was synchronized with the onset of a new scanning volume.

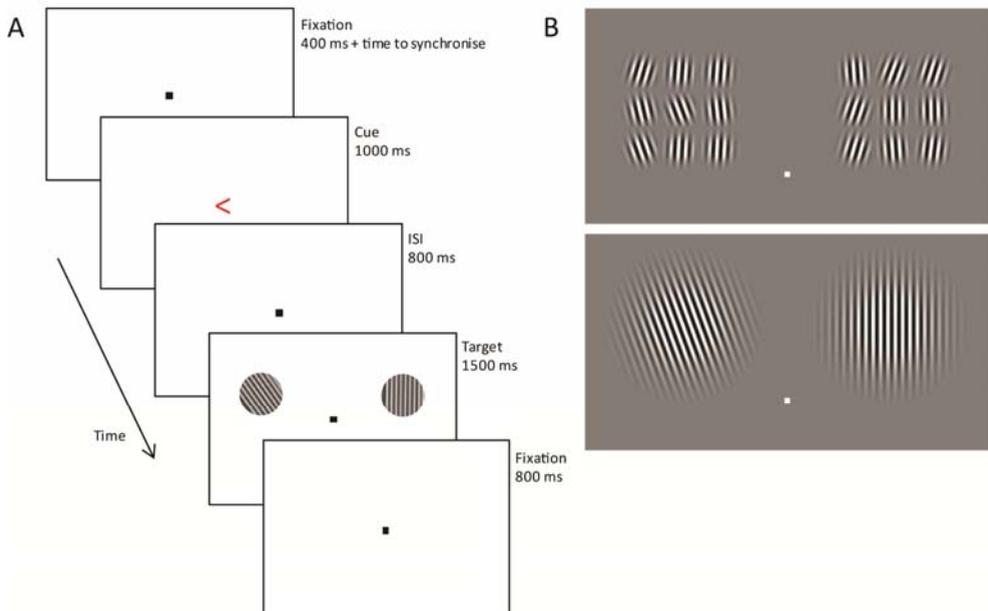


Figure 1. A) The cueing task. Participants focused on a central fixation point until a cue appeared. The cue indicated on which side of the visual field the target would appear and whether or not this target would be surrounded by distractors. Participants responded to the orientation of the indicated Gabor patch. B) Examples of actual target and distractor displays. The top-panel shows target and distractors, the target always being the middle patch on the indicated side (here left). The bottom panel shows the target display when no distractors were present.

When no distractors were present, the target consisting of a tilted black and white Gabor patch (subtending a visual angle of 3.5 degrees in diameter) was presented above the horizontal meridian (1.75 degrees to the center of the patch). The Gabor was placed with its center at a distance of 2.9 visual degrees from the fixation marker. A non-target (not tilted) patch of the same size was presented at the corresponding location in the opposite hemifield. When distractors were present, the target was a small Gabor patch, surrounded by eight patches of equal size (0.8 degrees per patch) and was placed at the same distance from fixation compared to the large target patch (see Figure 1B). At the same time nine small non-target/distractor patches were placed at the corresponding location in the opposite hemifield. All Gabor patches had a spatial frequency of 6.3 cycles per degree. The patches could be tilted either to the left or the right, the angle of orientation depending on the performance of the participant. Participants responded to the orientation of the

target patch by pressing a button with the right or left hand. Participants were instructed to respond as accurately as possible.

In order to obtain clear cue-related BOLD signals, 41% of all trials consisted only of the presentation of a cue, not followed by a target display. Furthermore, 18% of the trials were blank in which neither cue nor target was presented. This allowed the BOLD signals to return back to baseline. In total, 384 trials were presented to each participant, divided over 6 blocks. The order of different trial-types was semi-random and was designed using a genetic algorithm to optimize independency between the event-related signals. This implicated that the order of trial presentation was fixed over participants. Stimulus presentation and response collection were controlled using E-Prime 2.0. (Psychology Software Tools).

Staircase procedure

Because presenting targets with or without distractors may lead to differences in task difficulty between these two types of trials, a staircase procedure was developed to equate differences in task difficulty. Changes in task-difficulty were accomplished by adjusting the angle of orientation of the target stimuli based on the performance of the participant. A moving average calculated the participants' average performance over the last 4 trials separately for both trial-types. If performance on the last 4 trials dropped below 75% correct responses, the angle of orientation was increased by 1 degree in relation to a perfectly vertical orientation (90 degrees), increasing discriminability of the target resulting in an easier task. When the participants' performance rose above 75% the angle of orientation was decreased by 1 degree (getting closer to a vertical orientation), making the task harder. When the angle of orientation deviated 1 degree from a perfect vertical orientation (i.e. 89 or 91 degrees), increments of 0.1 degree were used to increase or decrease task difficulty. Separate performance levels were calculated for target and distractor trials which should result in an average performance of both trials of approximately 75% correct responses.

Scan Acquisition

Imaging sessions took place on a 3T Siemens TRIO scanner (Siemens Medical Systems, Erlangen, Germany) at the UC Davis imaging research center. Participants viewed the stimuli through a mirror attached at 45 degree angle to the head coil. The experiment was back-projected on a semi-transparent screen placed outside the bore, using a 75Hz Digital Projection Mercury 5000HD projector. Eye movements were measured with an ASL Long Range Optic 6000 eye tracker. All subsequent analysis of fMRI data were done with BrainVoyager 2.0 (Brain Innovation, Maastricht, The Netherlands).

Scanning acquisition parameters for the main experimental task were: TR = 1800 ms, TE = 25 ms, flip angle = 80°, slice thickness = 3.6 mm, slice gap = 0 mm (no gap), acquisition matrix = 64 x 64, in-plane resolution = 3.2 x 3.2 mm. Functional data were collected using a gradient recalled EPI sequence scanning the whole brain in 33 near-axial slices. A 3-D anatomical scan was made at the end of the session, using a T1-weighted MP-Rage sequence. Scanning parameters were: TR = 1660 ms, TE = 2.17, TI = 1100 ms, flip angle = 8°, sagittal slice thickness = 1 mm, acquisition matrix = 256 x 256 pixels, in-plane resolution = 1 x 1 mm.

Retinotopic mapping of visual areas

Mapping the borders of early visual areas (V1 - V3) was accomplished by presenting a slowly rotating bifield checkerboard wedge pattern (see Slotnick & Yantis, 2003). The wedges, with a width of 30 degrees, completed eight full rotations (meaning that both hemifields were fully stimulated twice on each rotation; i.e. 16 times), each rotation lasting 48.5 seconds (24 TRs, each TR 2020 ms). The checkerboard pattern flickered at 9 Hz.

An additional task was employed to locate target locations within regions of early visual cortex. Circular checkerboard patterns (9 Hz) with a diameter of 3.5 degrees were presented at the two target locations. The checkerboard patterns had the same size as the single target Gabor patches in the main experiment. Each pattern was presented with a duration of 2020ms (1TR) after which a blank screen with a duration of either 4040ms (2TR) or 6060 (3TR) was presented before the next pattern would appear. Checkerboard patterns were presented at the target locations in a semi-random order as defined by a

genetic algorithm. This task combined with the double wedge task pinpointed the projections of target and distractor locations in early visual areas.

MRI Data Analysis

The first two volumes of each block were omitted in order to avoid differences in T1 saturation. The preprocessing of the remaining functional volumes consisted of motion correction, slice scan-time correction, high-pass filtering (0.01 Hz), slight spatial smoothing (3mm FWHM Gaussian kernel), but no temporal smoothing.

After preprocessing, all functional scans of each participant were manually co-registered to the anatomical scan of that participant. Both functional and anatomical data were subsequently converted to Talairach space (Talairach & Tournoux, 1988). Converting functional data to Talairach space resulted in 4D functional data sets (e.g. Goebel, et al., 2001). Anatomical data was automatically and where necessary manually segmented in order to separate the different tissues of the brain. Based on the observed gray and white matter boundary, a model of the cortical mantle of each hemisphere was created. This model was subsequently inflated resulting in a smooth reconstruction of the cortical surface on which cortical gyri and sulci were displayed. Regions of interest (ROIs) derived from visual mapping experiments were defined for each of the 24 hemispheres in ventral visual areas V1v, V2v and V3v/VP (henceforth called V1, V2 and V3).

In order to investigate cue-related neural activity, BOLD responses were estimated to all cues, independent of whether they were followed by a target or not. A deconvolution GLM was employed using predictors for cues and (if present) targets, thereby separating cue-related activity from BOLD changes due to subsequent target presentation. A regressor was assigned to each of 8 volumes following the onset of target displays as well as all leftward and rightward pointing cues, separately for cues that indicated the presence of distractors and cues that indicated that no distractors would be presented. These analyses were performed separately for each participant and ROI, and the resulting time-series of response estimates for the cues were averaged over hemispheres for each ROI and condition. These cue-evoked response estimates were further investigated in two ways. First, we investigated whether attention modulated visual cortex in a spatially specific way by comparing cue-evoked activity in the hemisphere contralateral to the cued

location to the evoked activity in the hemisphere ipsilateral to the cued location. Second, in order to investigate preparatory effects of distractor expectation, the response estimates evoked by cues indicating the presence or absence of distractors were compared. Differences between these conditions were expected to be maximal when the magnitude of the BOLD signal was largest. Therefore all further analyses will focus on the time period reflecting this part of the BOLD response, which in the current experiment is between 5.4 and 10.8 seconds after cue onset (see Figure 2).

Results

Behavioural results

Accuracy was measured separately for distractor trials and target-only trials. The task was designed in such a way that no differences in difficulty should be able to explain observed neural responses. Indeed behavioural data indicated that performance on both trial types was equal (distractor trials 75,2% correct, target-only trials 74,8% correct). A paired samples t-test indicated no differences between these trial types ($t(11) = 0.407, p = 0.692$). Therefore, any observed difference in neural response cannot be attributed to task difficulty, but has to be attributed to the presence or absence of distractors.

Task difficulty was adjusted by increasing or decreasing the angle of the target patch relative to a perfectly vertical lay-out of the patches (90 degrees). Behavioural data showed that on average the angles deviated 8 degrees and 2 degrees from a perfectly vertical orientation respectively for distractor present and distractor absent trials.

fMRI Data

By means of a deconvolution analysis, changes in the hemodynamic response as a result of attention-directing cues were calculated separately for the attended (contralateral) and unattended (ipsilateral) location and for distractor present and distractor absent cues. These analyses were performed separately for each participant and ROI. Figure 2a shows the evoked time-courses for V1, V2 and V3 for the four trial types averaged over participants and hemispheres. The differences between these time courses were statistically tested for TR 3 to TR 5 (5.4 - 10.8s after cue onset) reflecting the maximal amplitude of the BOLD signal (see Figure 2B).

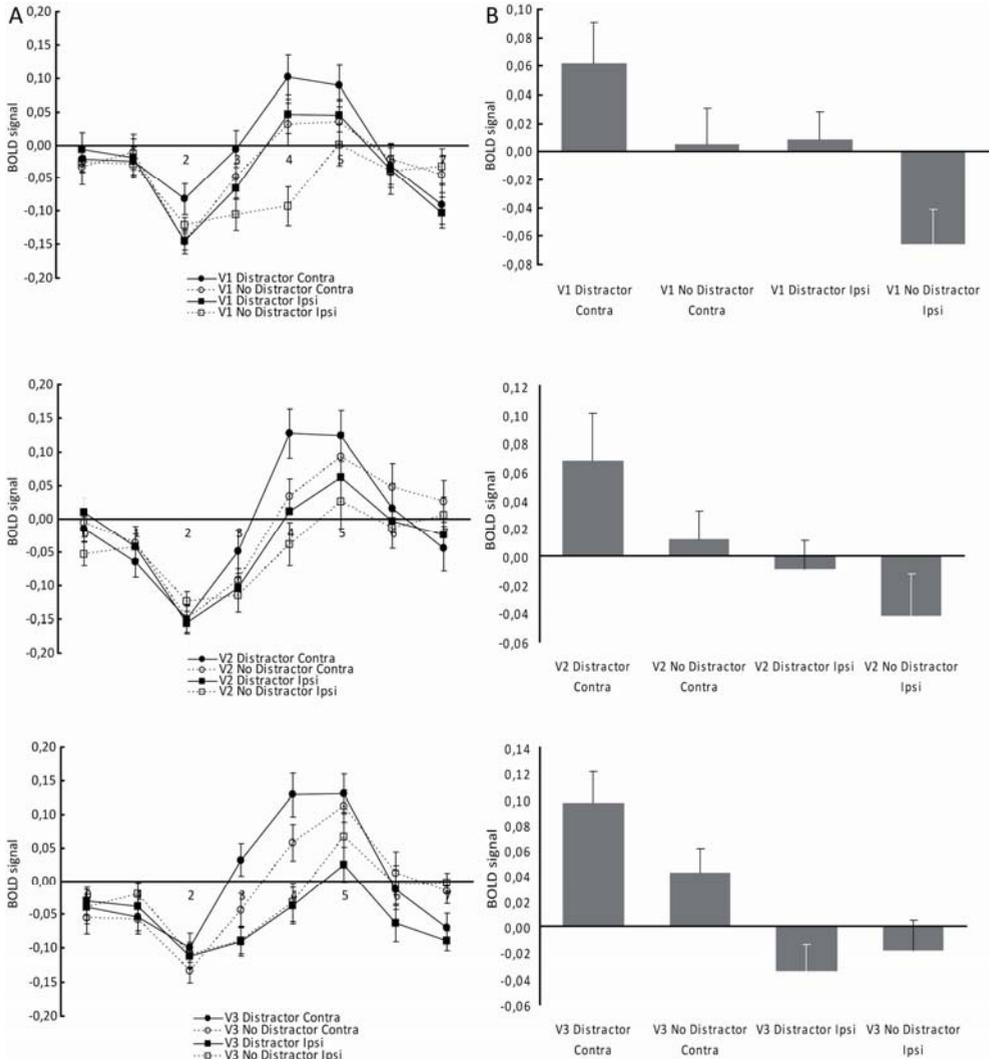


Figure 2. A) Deconvolved time courses of the four trial types measured from cue onset. B) Average signal calculated over the peak of the BOLD response (TR3 – TR5; 1 TR = 1.8 s). Regions contralateral to the cued side showed larger responses compared to ipsilateral regions in all ROIs during this interval. There was no main effect of distractor expectation, but in V3, an interaction between laterality and distractor expectation was observed for this interval, showing that preparation for a distractor had the largest effect at contralateral sites. Error-bars reflect standard-error corrected for the use of a within-subjects design (Loftus & Masson, 1994).

An ANOVA with laterality (contralateral vs. ipsilateral) and distractor expectation (present vs. absent) as within-subject factors was performed investigating the effects of directing

spatial attention and the expectation of distractor presence or absence on the obtained fMRI signals. The results of the ANOVA showed a main effect of laterality, indicating that the magnitude of the BOLD response was larger at contralateral sites compared to ipsilateral sites. This effect was obtained for all ROIs (V1: $F(1,11) = 6.941$, $p = 0.023$; V2: $F(1,11) = 5.703$, $p = 0.036$; V3: $F(1,11) = 17.111$, $p = 0.002$), indicating that spatial attention was deployed towards the indicated location, prior to the onset of visual information.

The effect of distractor expectation was investigated during the same time period in which effects of spatial attention were observed. No main effects of distractor expectation were observed (V1: $F(1,11) = 2.352$, $p = 0.153$; V2: $F < 1$, *ns*; V3: $F < 1$; *ns*). However, a significant interaction between distractor expectation and laterality was observed in V3, showing a larger preparatory BOLD signal when distractors were expected at contralateral sites, compared to the ipsilateral sites ($F(1,11) = 8.641$, $p = 0.013$). No such effect was observed in V1 ($F < 1$, *ns*) and V2 ($F(1,11) = 1.036$, $p = 0.331$), showing that distractor presence only influenced V3, and only at the attended location.

Discussion

The aim of the current study was to investigate whether foreknowledge concerning distractor presence would alter the BOLD responses in visual cortex. In addition, we aimed to replicate studies that showed preparatory effects of spatial attention in early visual cortex. An experimental paradigm was used in which target location and the presence or absence of distractors was indicated by a symbolic cueing procedure, prior to the onset of target and distractors. By measuring changes in BOLD signal in response to the cue, the influence of spatial attention and distractor expectation on preparatory neural processes in visual cortex could be determined.

The results of the current study showed that endogenous cues evoked hemodynamic modulations throughout early visual cortex, including V1, V2 and V3. These increased baseline responses were retinotopic in nature. This confirmed the results of previous studies which showed that preparatory attention acts upon spatially specific regions of early visual cortex (Hopfinger, et al., 2000; Jack, et al., 2006; Kastner, et al., 1999; Munneke, Heslenfeld, et al., 2008; Ress, et al., 2000; Silver, et al., 2007). More importantly, the present study shows that a cue indicating that distractors will be present

induced a larger increase in baseline signal compared to a cue indicating that no distractors would accompany the target. This effect was observed in retinotopically specific regions of V3 contralateral to the cued target location. Since no main effect of distractor presence was observed in any of the ROIs, it can be assumed that neural modulation due to distractor expectation was not the result of more general neural processes such as increased arousal. Rather, the effects were both retinotopic in nature and only observed at the attended location. These results indicate that neural processes in V3 reflecting preparatory attention are not only modulated by prior knowledge concerning the location of upcoming targets, but also by the nature of these targets. That is, foreknowledge of distractor presence results in a larger BOLD response, enhancing the spatial cueing effect.

Modulation of the preparatory BOLD response evoked by prior knowledge concerning distractor presence was found to be different in V3 compared to V1 and V2. These differences in attentional modulation may be caused by properties of the receptive field size of neurons in these visual areas. Receptive field sizes are known to increase in higher visual regions (Smith, et al., 2001). Furthermore, previous work has shown that when multiple stimuli are presented in the receptive field of a neuron, these stimuli compete for neural representation (i.e. biased competition). It is known that attention resolves this competition between multiple items presented within a neuron's receptive field (Kastner, et al., 1999; Moran & Desimone, 1985; Reynolds, et al., 1999). Competition between multiple items is resolved by focusing attention on the relevant target stimulus, thereby attenuating the interfering effects the irrelevant stimulus has on target processing. Therefore, when multiple items are presented in the visual field, irrelevant items may be suppressed, but only when these items are presented in the same receptive field. Even though the observed effects in the current study reflect cue-based activity, it might be that the attentional mechanism already starts suppressing the distractor locations in order to resolve the upcoming competition.

Area V3 may be the first area in the feedforward stream of visual processing with receptive field sizes large enough to encompass both target and distractors. If the receptive field size of neurons in V1 and V2 are too small to contain both target and distractor, no competition between multiple items takes place and hence the need for suppression is low. Therefore, the results suggest that foreknowledge concerning

distractor information modulates the neural signal evoked by spatial attention only when target and distractors are presented in the same neuronal receptive fields.

The current study shows that distractor suppression is not merely a side effect observed at regions in visual cortex that code unattended locations while attention is deployed elsewhere (Silver, et al., 2007; Somers, et al., 1999). Amplified neural changes were observed in V3 after cue presentation, reflecting additional processes when distractors would be presented. This result shows that attentional control settings can be changed based on an instructive cue informing whether distractors will be presented or not.

Ruff and Driver (2006) cued the presence or absence of a distractor which was always presented in the hemifield opposite to the target. The results by Ruff and Driver are in line with the current study in so far as both studies show top-down control over a distractor suppressing mechanism. The observed preparatory increases in BOLD signal in early and midlevel visual cortex (BA 17, 18 and 19) cannot be explained by competition between the target and the distractor, because receptive field sizes of neurons at these levels of visual cortex do not encompass the entire visual field. A possible explanation put forward by Ruff and Driver, suggests that the increased BOLD response may reflect occipital “predictive coding” of the pattern of expected stimulation in visual cortex (cf. Rao & Ballard, 1999), assuming that neurons in the visual cortex are activated already by an expected pattern of stimulation. Note that this holds for both target and distractor stimuli. However, an explanation in terms of “predictive coding” is unlikely to apply to the current data, as this effect of expectation should have propagated down from V3 to V2 and V1.

An alternative explanation for the effects observed in the current study can be hypothesized without the need for a mechanism of distractor suppression. Attention has been compared to a zoom lens (Eriksen & Yeh, 1985), suggesting that an observer can zoom in on relevant stimuli. When competition arises because multiple stimuli are presented in the receptive field of a neuron, attention may zoom in on the attended location, effectively placing the irrelevant stimulus outside the focus of attention. Because the irrelevant stimulus is no longer attended, the neuron’s response is primarily defined by the attended stimulus. Because the receptive fields in V1 and V2 are too small to contain both target and distractor, there is no competition and hence no need to “zoom

in” on the target stimulus. This could lead to a similar pattern of activation without the need for any suppression of unattended items.

In conclusion, the current study shows an interaction between spatial attention and mechanisms that prepare the visual system for upcoming distractors. Preparation for distractors at the attended location modulates neural processes in mid-level visual cortex. However, early visual areas (V1, V2) only show an effect of spatial attention but no distractor-related modulation. Results of this study may be explained by a biased competition account of attention in which interfering influences of irrelevant information are suppressed. This is only required at cortical levels where neuronal receptive fields are large enough to encompass both targets and distractors.