Spatial Attention in Early Visual Cortex

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Chapter 6

Summary and conclusions:
Dynamics of spatial attention

Introduction

This thesis deals with effects of top-down spatial attention in early visual cortex. We specifically focus on the role of primary visual cortex since a considerable debate remains whether, when and under what circumstances this region is modulated by attention (Posner & Gilbert, 1999). Top-down spatial attention facilitates processing of information presented at the attended location by modulating neural processes in visual cortex that code the location to which attention is directed (Posner & Petersen, 1990). This effect is observed in many parts of early cortex, including V1 (Gandhi, et al., 1999; Somers, et al., 1999). Claiming that attention facilitates target processing at the attended location does not reflect the flexible and dynamical nature of the attentional mechanism per se. Rather, it portrays spatial attention as a uniform all-or-nothing mechanism that is only employed after a specific instruction to attend to a predefined location. However, the degree to which attention modulates early visual cortex depends on a number of properties related to ongoing task demands. For example, the presence or absence of distractors has been deemed important for attentional effects to be observed in V1 (Motter, 1993). Furthermore, task difficulty and attentional demands may correlate with the neural attentional response in primary visual cortex (Chen, et al., 2008).

The idea that V1 is merely a passive node in the pathway of visual information processing seems incorrect. For example, we have shown that primary visual cortex is modulated by working memory related processes (Munneke, Heslenfeld, & Theeuwes, in press). Other research has shown that V1 is important for cross-modal integration (Falchier, Clavagnier, Barone, & Kennedy, 2002). Also, V1 in rats is directly influenced by the timing of an expected reward (Shuler & Bear, 2006). It should be noted however that higher cognitive processes such as spatial working memory may not by themselves act on visual cortex. Instead these higher processes act through the attentional mechanism to tailor to the demands of a certain task. For example, storing location information in working memory may be accomplished through shifts of attention towards the remembered location.

Based on the analysis above, two conclusions can be drawn concerning attentional modulation in early visual cortex. 1) (Spatial) attention is a highly dynamic mechanism not only employed in order to facilitate the selection of relevant information. 2) Primary visual cortex is more than a passive processing node, and supports a large array of higher cognitive functions. The remainder of this chapter will focus on the results and conclusions of experiments described in this thesis as well as a theoretical background underlying these conclusions.

A facilitatory mechanism

Chapter 2 deals with effects of attention in primary visual cortex prior to target presentation. In this study participants had to focus their attention on a low-contrast stimulus embedded in an array of distractors. The findings of this study show that attending a location in the visual field lead to spatially specific preparatory effects of attention in regions of early visual cortex, including V1. Cueing the location of an upcoming target resulted in a higher perceptual sensitivity at this location as shown by an increased *d'* for target detection compared to when the target location was not cued in advance. Based on theories regarding spatial attention, it is assumed that deploying spatial attention prior to the onset of the target results in increased neural processes in retinotopically specific visual cortex. The subsequent presentation of a target stimulus at the attended location results in facilitated processing of this stimulus. A number of separate mechanisms may explain the role of attention in facilitated target detection.

First, according to a model of biased competition, preparatory effects of attention may act on the location of the to be attended target thereby biasing this stimulus over surrounding distractors (Desimone & Duncan, 1995; Moran & Desimone, 1985). Facilitated target selection is accomplished by attenuating the suppressive influence the distractors have on target processing. At a neural level this means that neurons coding the attended part of the visual field are no longer or at least to a lesser extent modulated by properties of the distractor stimuli. Second, preparatory effects of attention may also result in sensory gain of items presented at the target location irrespective of distractor presence. Increased sensory gain leads to an improved signal-to-noise ratio of the neural signal coding the target (Hillyard, et al., 1998). Third, a model of uncertainty reduction could explain the results described in Chapter 2 (Shiu & Pashler, 1994). Because the target was surrounded by distractors on every trial, it is not unlikely that the preparatory effects observed reflect a mechanism that prepares for suppressing irrelevant information.

Uncertainty reduction is different from a biased competition model of attention, because uncertainty reduction does neither require sensory interaction between target and distractors, nor do these stimuli have to be presented in the receptive field of the same neuron.

The experiment contained a number of catch-trials (cues without subsequent target presentation). These trials were inserted in order to decorrelate cue and target related processes, and to obtain pure cue evoked neural signals. Although an effect of attention was observed during catch trials, during these unexpected events a strong deactivation in BOLD signal was found. This deactivation appeared to result from the absence of a target that was expected. It has been claimed that during such events, the negative BOLD response represents an increased visual threshold which may reflect suppression of visual processing. This is plausible as no relevant visual stimuli were present that had to be coded in the visual cortex. Because an effect of spatial attention was still obtained despite suppression of visual processing, it means that even when visual processing gets suppressed attention may still exert an influence on early visual cortex. This adds to the observation that attention can act completely independent of visual processing as indicated by studies that show increased baseline effects in visual cortex in the absence of visual stimulation (e.g. Kastner, et al., 1999; Ress, et al., 2000).

A role in spatial working memory

Chapter 3 investigated the direct link between spatial working memory and spatial attention. Attention based models of working memory have been proposed before (Awh, et al., 1998; Awh, et al., 1999; Mayer, et al., 2007; Postle, et al., 2004). In the study described in Chapter 3, the role of (primary) visual cortex in spatial working memory was investigated. This study showed that maintaining a location in working memory lead to retinotopically specific modulation in visual cortex contralateral to the remembered location. The pattern of activation was highly similar to that found in a second task in which participants were required to shift attention to the same location. These effects were observed in all studied regions, including V1. Because the task only differed in instruction to either remember or attend, any difference observed in the neural response could not be attributed to differences is sensory processing. Two important conclusions could be drawn from this study. 1) Spatial working memory maintenance may be accomplished by shifts of spatial attention towards the remembered location, confirming the rehearsal mechanism by Awh et al. (Awh, Anllo-Vento, & Hillyard, 2000; Awh, et al., 1998; Awh, et al., 1999). 2.) Spatial working memory maintenance processes elicit increased baseline levels of neural activation in early visual cortex. These increased neural signals most likely reflect preparatory attentional activity.

Furthermore, increased activity in contralateral compared to ipsilateral visual cortex was observed only between the attended and unattended target locations and not between the non-target location in the attended quadrant and the non-target locations in the unattended quadrant. This suggests that attentional modulation in V1 is retinotopic in nature. In addition, some of the effects in V1 were not caused by facilitated target processing, but resulted from reduced processing at the target location ipsilateral to the region of interest. This latter result once again emphasizes the importance of attentional suppression of irrelevant information. Hypothetically, the reason for suppression of the unattended target location may be strategic. As the non-target locations in this experiment never functioned as target locations, it would never be the case that a target would suddenly appear here. However, the irrelevant target location did function as a target location on other trials; therefore interference from this location might be more probable than from non-target locations. As a result, additional suppressing mechanisms may act specifically upon the unattended target location.

Considering that spatial attention is the underlying mechanism of spatial working memory, the result of both trial types may be explained by facilitated target processing (sensory gain) and suppression of irrelevant information (uncertainty reduction). Once again, this suggests that multiple mechanisms of spatial attention act concurrently in a push-pull manner.

The role of distractors

Chapter 4 and 5 directly deal with top-down control of a suppressive mechanism of spatial attention. In the experiments described in both chapters, participants were provided with knowledge concerning properties of the distractor. In Chapter 4, the location of the distractor was cued, whereas in Chapter 5, the likelihood of distractor presence was cued.

The experiment in Chapter 4 showed that prior knowledge of the distractor location can result in facilitated selection of the target. A spatial cueing paradigm was used to indicate the upcoming location of a distractor, whereas an uncued target would always appear at a different location on the screen. Cueing the distractor location only had an influence when an actual distractor was presented after cue presentation. Therefore, the mere presence of a cue did not enhance processing at the remaining target locations or resulted in overall higher arousal facilitating target processing.

Additional evidence that distractors were suppressed based on location cueing was observed in a second experiment in which distractors were presented as typical "flankers". From classic studies on the flanker effect, it is known that when the identity of a distractor is such that it can also function as a target at times, interference is automatic and large. By cueing the location of these distractors, there was less interference of the flanker-like distractors. This shows that the attentional mechanism directly acts upon the cued distractor locations and not on the target locations. Based on these experiments we concluded that the suppressive mechanism of attention is under top-down control. The data in this experiment are in line with a model of uncertainty reduction, indicating that target selection is facilitated by suppressing the influence of distractors. When no distractors were present (Chapter 4, exp 1) facilitation of target processing was found to be less pronounced. This experiment was not designed to investigate whether target selection was facilitated by sensory gain control, as the target was never cued. Therefore, resources (assuming that sensory gain is a resource model) could not be allocated to an upcoming target location as this location was never known on any trial.

In Chapter 5, the neural correlates of preparation for distractors were investigated by employing a spatial cueing paradigm that provided information concerning the upcoming target location and whether or not this target was surrounded by distractors. This study replicated the effects described in Chapter 2, indicating that preparatory effects of attention could be observed in V1 as well as V2 and V3. Furthermore, this study showed that the magnitude of the neural response was dependent on knowledge of distractor presence. However, this effect was only observed in mid-level regions of visual cortex (area V3). No effects of distractor modulation were observed in V1. In line with the biased competition model of attention, these results may be explained by considering the size of the receptive fields in different visual regions. V3 may very well be the first region within the visual processing pathway in which target and distractors are presented within the same RF of a neuron. Therefore, V3 may be the first region in which information from distractors interferes with target processing and a suppressive mechanism may act upon this area in order to reduce these effects. As all observed effects were preparatory in nature, this may suggest that a suppressive mechanism of attention is deployed prior to distractor onset.

Attention and V1

Throughout this thesis, the claim has been made that preparatory attentional modulation can be observed in V1. The experiments described in Chapters 2, 3 and 5 support this claim, and based on these chapters and other literature (Jack, et al., 2006; Kastner, et al., 1999; Silver, et al., 2007) it seems irrefutable that attention does indeed modulate the earliest regions of visual cortex in a preparatory way. However, an issue concerning the time course of attentional modulation in V1 remains. A number of studies have suggested that sensory processes in V1 are not modulated by attention during the first feedforward sweep of information (Di Russo, et al., 2003; Martinez, et al., 1999; Martinez, et al., 2001). Nevertheless, if preparatory effects of attention can be observed in V1, then the question arises why effects of attention on sensory processing do not take place during the initial sweep. Recently, this issue may have been resolved by showing that V1 is in fact modulated by attention during the earliest stages of visual processing (Kelly, et al., 2008). Kelly et al. showed that by carefully mapping neural generators of sensory processing in V1, attentional modulation could be observed at the location of these neural generators. Although only one study has so far has obtained these early effects of attention in V1, this study provides conclusive evidence that attention indeed influences information processing from the moment information from the retina arrives in primary visual cortex.

Concluding remarks

The studies in this thesis have investigated properties and constraints of spatial attention in early visual cortex prior to the onset of information. From these studies it can be concluded that participants can prepare for different kinds of upcoming information. Participants show benefits in attentional processing based on prior knowledge concerning both target and distractor information. This shows that top-down control of attention does not necessarily resemble a spotlight moving around the visual field. Moreover, the mechanism that is under top-down control can both enhance as well as inhibit the neural response of incoming information based on the nature of this information. Furthermore, attentional processes reflecting suppression and facilitation may act concurrently and are not necessarily mediated by one single unitary mechanism. Although, there is more evidence that suggest that attention can function in a push-pull like fashion, further research is needed to determine the circumstances under which facilitation and/or suppression takes place.