Spatial Attention in Early Visual Cortex

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English Summary

This thesis deals with the neural mechanisms of visual spatial attentional selection. Visual spatial attention is the mechanism that selectively enhances processing of potentially relevant visual information in the environment while at the same time suppressing irrelevant and interfering information. Although attention can be involuntarily captured by highly salient information in the environment such as a bright flash or a deviant colour relative to its background (bottom-up attention), this thesis will focus mainly on voluntary deployment of visual spatial attention irrespective of the physical properties of objects in the environment (top-down attention). Top-down control of attention entails that attention can be voluntarily shifted towards locations in the environment prior to the onset of visual information. This allows investigation in how the brain prepares for upcoming information. A large part of this thesis deals with these preparatory effects of attention.

In Chapter 1 an overview of studies and theories related to visual spatial attention is provided. This overview focuses on a number of different aspects related to visual spatial attention. First, different theories are discussed that explain how attentional selection may occur. Second, the neural correlates of selective attention are discussed, primarily focusing on the role of a frontal-parietal network in top-down control of attention and on how this network influences the visual cortex. It is assumed that the frontal-parietal network sends signals towards spatially specific locations in visual cortex, thereby preparing parts of the visual cortex responsible for coding the attended location of the visual field. This mechanism allows facilitated processing of visual information by selectively biasing information presented at attended locations over information present at other locations. A third important topic of Chapter 1 is concerned with how attentional mechanisms deal with irrelevant and possibly interfering information in the visual environment. It is speculated that the presence or absence of irrelevant information has an impact on neural processes in early visual cortex.

In Chapter 2 an fMRI study is discussed that investigated whether and to what extent striate and extrastriate cortex are modulated by preparatory spatial attention. On a trial-by-trial basis, the location of an upcoming target was cued prior to its onset, allowing participants to shift their attention towards the cued location. A few seconds after cue offset the target display would appear and participants had to indicate whether a line segment presented at the cued location either had horizontal or vertical orientation. Due to the long delay between cue and target presentation, cue induced preparatory effects of attention were studied in the absence of visual information. It was observed that the endogenous cue elicited spatially specific neural responses in all studied regions (V1, V2 and V3) of early visual cortex in the absence of visual stimulation. This is taken as evidence that attention can modulate visual cortex at early stages of visual processing.

In Chapter 3 changes in BOLD responses elicited by a spatial working memory task were compared to changes in BOLD responses elicited by a spatial attention task. In this fMRI study two perceptually similar tasks were presented to the participants. In the spatial working memory task, participants had to remember the exact location of one of four coloured circles over a brief period of time (5s) during which

no visual information was presented. Four new white circles were presented after the delay period and participants had to indicate whether one of the new circles was presented at the same location as the remembered coloured circle or slightly deviated away from this location. In the spatial attention task, participants used the coloured circle as a cue for an upcoming target. Similar to the spatial working memory task, four new circles were presented after a period of 5 seconds and participants had to indicate whether the circle presented at the cued location contained an opening on the left or right side. Due to the perceptual similarity between the two tasks, any observed differences in BOLD signal could be attributed to differences in the underlying functional processes between the two tasks. The study showed that maintaining a location in spatial working memory resulted in a spatially specific increase in BOLD signal in early visual cortex. A very similar pattern of activation was observed for the spatial attention task. The strong overlap in BOLD changes between the two tasks is in line with theories that claim that maintenance processes in spatial working memory are accomplished by shifts of attention towards the remembered location. Therefore, it was concluded that although spatial working memory and spatial attention are two distinct functional concepts, the mechanism underlying spatial working memory may be attentional in nature.

In Chapter 4, a behavioural study is discussed that investigated whether cueing the location of a distractor facilitates target selection. In two experiments, a central cue indicated the location of an upcoming distractor stimulus, whereas the location of the target was never cued. Indeed, Experiment 1 showed that cueing the location of a distractor resulted in facilitated selection of the target stimulus (as shown by faster response times). In addition, cueing the location of a distractor only facilitated target selection when the distractor was presented, ruling out more general effects such as alerting or shifting attention away from the cued location. A second experiment confirmed the finding of Experiment 1, showing that compatibility effects induced by flanker like stimuli were reduced when the distractor location was cued. This study showed that prior knowledge of the location of distracting information can facilitate target selection. This facilitation is not accomplished by enhancing the response to the target, but is caused by actively inhibiting the effects of distractors present in the visual field.

In Chapter 5 an fMRI study is discussed that investigated the neural correlates of preparation for upcoming distractors. In the experiment participants were cued the location of a target and they were informed whether the target would be accompanied by distractors or not. Participants had to indicate whether a target Gabor-patch was tilted towards the left or the right. When distractors were present, they always fully surrounded the target. The cue was 100% valid, therefore participants were always aware if and where target and distractors would be presented. Because filtering out irrelevant information is an active process, it was assumed that this condition would lead to larger BOLD responses compared to when no distractors would be present. The results of this study showed that early visual cortex was modulated by spatial attention in V1, V2 and V3. However, an influence of distractor presence versus distractor absence was observed in V3 only, showing increased BOLD responses in the region coding the upcoming target and distractors location. This indicates that extrastriate cortex is the first region in visual cortex that is modulated by the expectancy of distractors. An explanation for this finding may be that in V3 the receptive field sizes of neurons are large enough to encompass both target and distractors. Therefore, this region prepares to deal with information coming from both target and distractors. Receptive field sizes in V1 and V2 are smaller and may only code information coming from either target or distractor but not both. Therefore, there is no need to resolve competition between these items. Had smaller stimuli been used at close proximity of each other, preparation for distractors may have modulated regions in V1 and V2 as well.

Chapter 6 provides a summary of the empirical studies and elaborates on theoretical implications of the findings reported in this thesis. The main conclusions indicate that preparatory effects of attention can act in early visual cortex including V1. Furthermore, attentional modulation in visual cortex may be dependent on the presence or absence of distractors and whether they will be present in the same receptive field of neurons coding the target stimulus. Selective attention seems to be able to operate in a push-pull manner, facilitating target related processes and suppressing distractor related influences. In conclusion, primary visual cortex supports a number of higher cognitive functions such as attention and spatial working memory and should therefore be considered as more than a simple processing node for visual information.