

VU Research Portal

Spatial Attention in Early Visual Cortex

Munneke, J.

2010

document version

Publisher's PDF, also known as Version of record

[Link to publication in VU Research Portal](#)

citation for published version (APA)

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

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

E-mail address:

vuresearchportal.ub@vu.nl

Chapter 1

Neural mechanisms of spatial attention

Selective Attention

Every moment our surroundings introduce a vast amount of information to our sensory cortex. Opening our eyes initiates a large influx of information being relayed from the retina to the visual cortex in posterior parts of the brain. The amount of information traveling down this pathway is estimated to be approximately 10^8 bits per second (Itti & Koch, 2000). However, because of capacity-limitations, our brain is not equipped to deal with this overload of information (Neisser, 1967; Schneider & Shiffrin, 1977). Even though it appears as if we perceive everything that falls on our retina, at any moment in time we do in fact only process a small amount of the information around us.

This situation creates the need for an attentive mechanism by which we select a subset of the simultaneously available information either by enhancing processing of visual objects or locations and/or suppressing other sources of information (Johnston & Dark, 1986). This suggests that selective attention can operate in a push-pull manner, facilitating processing of information relevant for ongoing behaviour and future goals, while at the same time suppressing the influence of irrelevant information that may disrupt our ongoing behaviour. In this way visual selective attention regulates the inflow of information from our senses to parts of the brain required for further processing (Hillyard & Mangun, 1987).

Attention can be oriented towards a location in the visual field either through endogenous (top-down) or exogenous (bottom-up) control (for an overview of these mechanisms, see Theeuwes, Belopolsky, & Olivers, in press; Van der Stigchel, et al., 2009). Endogenous attentional orienting is voluntary and goal-driven allowing attention to be moved around the visual field consistent with our top-down goals (e.g. Van der Stigchel & Theeuwes, 2007). Exogenous attention on the other hand is more or less reflexive and occurs in an involuntary, stimulus-driven fashion. One often speaks of exogenous orienting when, irrespective of top-down intentions, attention is captured by the salient physical characteristics of the stimuli present in the visual field such as an object presented abruptly (Schreij, Owens, & Theeuwes, 2008; Theeuwes, 1991, 1994) or an object with a unique colour popping-out from the background (Theeuwes, 1992). Endogenous and exogenous orienting are hypothesized to be mediated by separate neural networks

(Corbetta & Shulman, 2002; Hahn, Ross, & Stein, 2006; but see Peelen, Heslenfeld, & Theeuwes, 2004).

The present review only focuses on voluntary, top-down spatial attentional selection in vision and the effects of this top-down covert orienting on subsequent processing of information. In other words, the review addresses the processes involved in selectively attending to a specific location and the consequences of this top-down preparation on subsequent visual cognition. There is a focus on the consequences of attentional selection in the presence of irrelevant information. As it is still a major debate in the literature, the discussion converges on the neural locus of spatial attention, i.e., whether spatial attentional selection alters the processing already in primary visual cortex (V1), or whether it only affects processing in extrastriate areas.

Top-down control of spatial attention

Spatial selective attention is the mechanism that allows the visual system's processing resources to focus onto a spatial location of the incoming information (Luck, 1995). Classic definitions have characterized attention as a spotlight, a unitary mechanism that selectively enhances contiguous parts of the visual field. Spatial attention has been compared to a spotlight that can be moved around a visual scene (e.g. Posner, 1980; Remington & Pierce, 1984), or a zoom lens (e.g. Eriksen & Yeh, 1985; Muller, Bartelt, Donner, Villringer, & Brandt, 2003) or gradient (Laberge & Brown, 1989), distributing limited attentional resources to a subset of the visual field. Despite differences in these analogies of spatial attention, a common underlying concept is that the attentional mechanism can be voluntarily (top-down) deployed within the visual field in order to select locations containing information relevant to the observer. These shifts of attention can occur covertly, without the need for overt eye or head movements.

Shifts of spatial attention can be voluntarily allocated to locations in the visual field prior to the onset of information. Preparatory focusing of attention leads to facilitated processing of information subsequently presented at the attended location (e.g. Munneke, Heslenfeld, & Theeuwes, 2008; Posner, 1980; Theeuwes & Van der Burg, 2007). In line with the zoom lens/gradient model, influential models of attention suggest that attention is a capacity-limited resource distributed over the visual field (Luck, Hillyard, Mouloua, &

Hawkins, 1996). Facilitation of stimulus processing at the attended location is the result of allocating a large part of these limited attentional resources at a subset of the visual field (Eriksen & Yeh, 1985). When attention is not directed towards a particular location, resources are uniformly spread over the visual field.

Allocating attentional resources to a location may lead to suppression of visual processes at unattended locations. Attentional resources that are transferred to the attended locations are removed from unattended locations, resulting in a reduction in resources available for processing of these unattended locations. According to Johnston and Dark (1986), information presented at unattended locations gets suppressed. Attenuating interference effects from unattended locations adds to the facilitated selection of relevant information and its subsequent processing. Top-down spatial attention may therefore act as a push-pull mechanism, attenuating and facilitating information processes at unattended and attended locations respectively (Pinsk, Doniger, & Kastner, 2004; Somers, Dale, Seiffert, & Tootell, 1999).

The utilization of spatial attention is thought to entail three distinct processes: *Disengaging* from a location, *shifting* towards a new location and *engaging* at the attended location (Posner, Walker, Friedrich, & Rafal, 1984). The first two of these processes, disengaging and shifting attention, reflect top-down control of spatial attention, mediated by regions in dorsal fronto-parietal network (Corbetta & Shulman, 2002). Engaging and subsequent modulation of information processing is the result of top-down control of attention, which acts upon neural processes in visual cortex (Desimone & Duncan, 1995; Kastner & Ungerleider, 2000).

Behavioural evidence of spatial attention

A paradigm that has been widely used for investigating the effects of top-down attention on visual processing comes from a series of classic studies by Posner et al. (1978; 1980). In a typical cueing experiment, participants are instructed (cued) where to expect a target stimulus prior to its presentation. Typically, in an endogenous cueing experiment, a symbolic cue is presented at fixation indicating the likely position where the target is going to be presented. Such an endogenous cue usually consists of an arrow (e.g. Munneke, Van der Stigchel, & Theeuwes, 2008; Posner, et al., 1980; Van der Stigchel, Heslenfeld, &

Theeuwes, 2006; Van der Stigchel & Theeuwes, 2007), but sometimes other symbolic cues are used such as a written or spoken attention directing word (e.g. 'left' or 'right'; Bressler, Tang, Sylvester, Shulman, & Corbetta, 2008; Vecera & Rizzo, 2004) or a number reflecting positions on an imaginary clock (Munneke, Heslenfeld, et al., 2008; Theeuwes & Van der Burg, 2007). These spatial cueing studies show that cueing the location of an upcoming stimulus facilitates its detection and/or discrimination when the target is presented at the cued location.

The voluntary nature of top-down attention becomes apparent when looking at the effects of cue predictability (i.e. a measure indicating how often the cue correctly predicts the target location). In order to invoke top-down control of attention, cue predictability has to be well above chance level, motivating participants to shift attention towards the cued location. Indeed, stimuli are responded to faster and with higher accuracy when the cue is valid compared to the condition in which a cue provides false (invalid) or no (neutral) information as to where the upcoming target stimulus will be presented (e.g. Luck, et al., 1994; Posner, 1980; Posner, et al., 1978; Posner, et al., 1980). Moreover, studies have shown that with increased cue predictability, behavioural performance increases as well (Riggio & Kirsner, 1997; Vossel, Thiel, & Fink, 2006). These results reflect enhanced or facilitated processing of stimuli presented at the cued location as a direct effect of attentional processes.

Critical to the observation of spatial cueing effects (i.e. improved behavioural performance on valid trials compared to invalid trials) is the time between the onset of a cue and the onset of the subsequent target (known as stimulus onset asynchrony or SOA). During this interval the participant is assumed to identify the central cue (e.g., an arrow or a word) and use this information to disengage attention from the central fixation point and shift it to the location in the periphery indicated by the central cue. For example, when an arrow is pointing to the left side, participants are assumed to direct their attention to the left side of the visual field where they expect the target to subsequently arrive. Moreover, it is assumed that these processes occur immediately following cue presentation. Upon the presentation of the central cue, participants immediately identify, disengage and shift their attention to the appropriate location. Variation of the SOA can tell how long these endogenous processes take. In a classic study, Müller and Rabbitt (1989) showed that an SOA of 100 ms or less between a centrally presented cue and a

peripheral target hardly improved discrimination of the target stimulus. A steady increase in performance was obtained by increasing the SOA up to 400ms. SOAs longer than 400 ms did not result in improving the performance anymore (see also Cheal, Lyon, & Gottlob, 1994).

Partly as a result of this work, most subsequent endogenous spatial cueing studies have used SOAs between 300ms and 1000ms (e.g. Luck, et al., 1996; Posner, et al., 1980), but benefits of spatial cueing have also been observed for SOAs ranging from 1550ms (Theeuwes & Van der Burg, 2007) up to over 5 seconds (Corbetta, Kincade, Ollinger, McAvooy, & Shulman, 2000). The observation that with longer SOAs spatial cueing benefits may turn into costs (see Klein, 2000) is usually not observed when an endogenous cueing procedure is used (as opposed to exogenous/peripheral cueing). However, it is not immediately clear whether during very long intervals attention remains focused at that location during the entire interval. It is possible when using a long interval, that attention is shifted to the cued location just before the target stimulus is expected to arrive. Also, under particular circumstances it seems that endogenous attention can result in IOR. For example, Rafal et al. (1989) observed IOR after an endogenous cue, but only after preparation or execution of a voluntary saccade (but see Chica, Klein, Rafal, & Hopfinger, under review).

Spatial cueing improves when placeholders are present in the periphery indicating the possible target locations relative to conditions in which no exact information is provided where in the periphery the target will appear. These placeholders provide the participant with an anchor at which attention can be focused (e.g. Corbetta, et al., 2000; Luck, et al., 1994). Employing placeholders should lead to attentional benefits as attentional resources can be allocated to the exact target location compared to when no placeholders are present (e.g. Ling & Carrasco, 2006; Munneke, Van der Stigchel, et al., 2008). In the latter case attention is shifted towards the approximate location of the target and attentional resources will be smeared out over a larger part of the visual field. Therefore, exact knowledge of target locations facilitates attentional engaging.

Classical cueing experiments have shown that cueing a target location facilitates target processing, even when the target is the only item present in the visual field. For example, Posner (1980) showed reduced response times to the detection of a target at validly cued locations, compared to invalid locations. Because in this experiment the

target was the only element present in the visual field attention can facilitate the processing of a target element even when no competing stimuli are present. Similar effects have been obtained by a number of studies showing higher accuracy, lower response times and improved sensitivity (d') to validly cued targets compared to invalid or neutrally cued targets in the absence of other elements (Kincade, Abrams, Astafiev, Shulman, & Corbetta, 2005; Ling & Carrasco, 2006).

Some studies have suggested, however, that the facilitatory potential of spatial cueing is maximized when the cued target is surrounded by distractors. For example, Shiu and Pashler (1994) showed that endogenously cueing a target location resulted in a large spatial cueing effect when multiple items were present in the display. When the target was presented without distractors, no validity effect was observed. The difference in spatial cueing effect between "target only" and "target + distractors" displays was caused by decreased performance on invalid "target + distractor" displays compared to invalid trials in the single item display. Performance on valid trials did not differ between the two display types. These data suggest that spatial cueing reduces the effect of interfering information. When no interfering information was present, spatial cueing did not lead to facilitated target selection.

A similar argument was put forward by Awh et al. (2003) who showed larger spatial cueing effects when a target was surrounded by distractors, compared to when targets were presented alone. Moreover, they showed that when participants expected distractors and these distractors were present, spatial cueing effects were larger compared to when distractors were presented unexpectedly. When no distractors were present, expectancy of distractors had no effect on the size of the spatial cueing effect. This shows that the expectancy of distractors does not lead to enhanced processing at the target locations, but suggests that spatial cueing effects are the result of distractor suppression at non-target locations. Furthermore, this study shows that participants have top-down control over the degree to which target processing is protected from interfering information. This study was later replicated by Serences et al. (2004).

To further investigate top-down control over the suppressive mechanism of attention, Munneke et al. (2008) used a paradigm in which instead of the target location, the distractor location was cued. The results showed that cueing the location of a distractor resulted in a faster detection of the target than when the distractor location

was not cued. This effect was only observed when the cue was followed by a distractor. When the cue was present, but a distractor was absent, no facilitation in target selection was observed, showing that facilitation of target selection was caused by distractor suppression as opposed to target enhancement.

These and other studies (e.g. Lu & Doshier, 2000; Ruff & Driver, 2006) indicate that spatial attention may exert its influence by suppressing irrelevant information thereby reducing interfering effects on target processing. A mechanism of distractor suppression seems likely when considering what happens when only one target item is presented. If a spatial cue facilitates target selection, some ambiguity should exist as to which item the target is. When only one target is presented, providing a cue which should facilitate selection seems superfluous as the only item that is presented will be the target and will therefore be selected anyhow. Nevertheless, if a spatial cue results in allocating additional resources to the cued location, no distractors are required to find facilitated target selection. Despite increased spatial cueing effects under distractor-present conditions, a model of "uncertainty-reduction" cannot be the only mechanism that leads to facilitated target selection. Many spatial cueing studies have shown spatial cueing effects in the absence of distracting information (e.g. Henderson, 1996; Luck, et al., 1994). For instance, Luck et al. showed that luminance detection accuracy was better at validly cued locations, compared to invalidly cued locations when only one target was displayed. Therefore it seems that multiple attentional mechanisms of spatial attention may act independently of each other, leading to seemingly identical results, namely facilitated target selection.

As noted, the spatial cueing paradigm allows us to disentangle the processes involved in preparing for the upcoming stimulus from the consequences of attentional orienting on subsequent processing. When a cue is presented, observers start to prepare for an upcoming target by shifting attention towards the cued location. Typically neither the target nor the distractors are present yet, so no sensory modulation of these stimuli can take place during this stage of processing. However, foreknowledge of a target location leads to enhanced processing of stimuli at the attended location. This suggests that the attentional system already biases the location of the upcoming target, either through modulating the cued location or through suppressing the uncued locations. Once the target appears, preparatory attention biases processing of stimuli at the attended location. This results in faster and better detection or discrimination of the presented

stimuli. Behavioural studies cannot discriminate whether observed results are caused by preparatory effects of attention, the subsequent modulation of visual information or both. However, electroencephalography (EEG) and neuroimaging studies have teased apart these separate processes, providing insight into how spatial attention facilitates target processing.

Theories of spatial attention

Different theories explaining the role of spatial attention on visual selection have emerged over the past decades. An important distinction between the emerged theories focuses on the manner in which irrelevant information in the visual field is processed (if at all). A further distinction is made based on the stage of visual processing during which attention exerts its influence (e.g. before or after stimulus presentation). Below we discuss the various models that explain the effects of spatial orienting. This list is by no means exhaustive nor are the models discussed mutually exclusive.

Sensory gain control

Studies of spatial attention have led to the hypothesis that attention functions as a mechanism of sensory gain control (see Hillyard, Vogel, & Luck, 1998). Sensory gain or "amplification" entails that attention amplifies the neural response in visual cortex when a visual stimulus is presented at the attended location. This amplification mechanism operates by increasing the signal-to-noise ratio of attended stimuli compared to unattended stimuli. Effects of sensory gain control have been reported in spatial cueing studies in which EEG was measured. In these experiments, the effects of sensory gain are illustrated by amplifications of two early visual components of the visual evoked event-related potential (ERP) known as the P1 and N1 (Eimer, 1997; Heslenfeld, Kenemans, Kok, & Molenaar, 1997; Mangun & Hillyard, 1995; Mangun, Hillyard, & Luck, 1993). The increased amplitude of these components reflects the gain effect of spatial attention on visual processing. The N1 and P1 are generated in extrastriate cortex, which adds to notion that visual attention acts upon this part of the visual cortex (Clark & Hillyard, 1996; Heinze, et al., 1994).

Recently, the P1 elicited by invalidly cued targets has been observed to decrease below baseline levels, suggesting that attention acts to reduce gain at irrelevant locations in the visual field in addition to amplifying gain at attended locations (Luck, et al., 1994; Talsma, Slagter, Nieuwenhuis, Hage, & Kok, 2005). Effects of sensory gain control have been observed in single-cell studies in monkeys, showing increased neural firing rates in visual cortex, when an effective stimulus is presented at the attended location (e.g. Luck, Chelazzi, Hillyard, & Desimone, 1997).

Consistent with these ERP results, results from neuroimaging have demonstrated that neural activity in regions of visual cortex coding a specific location in the visual field increases when attention is focused on this location. This increased neural activity most likely reflects enhanced processing of stimuli presented at the attended location as a direct result of sensory gain control. Increased patterns of cortical activation evoked by stimuli presented at the attended location, compared to stimuli presented at an unattended location have been observed with PET (Heinze, et al., 1994; Mangun, Hopfinger, Kussmaul, Fletcher, & Heinze, 1997; Woldorff, et al., 1997) and fMRI (Di Russo, Martinez, & Hillyard, 2003; Hopfinger, Buonocore, & Mangun, 2000; Martinez, et al., 1999).

However, amplified neural signals observed with PET or fMRI do not necessarily reflect a mechanism of sensory gain control. A different explanation comes from single-cell studies showing that attending a location (or other features of the visual stimulus) may result in a bias signal from higher-order attentional areas. This bias signal may lead to a sustained neural response in visual areas coding the attended location (Desimone & Duncan, 1995; Luck, Chelazzi, et al., 1997). Luck et al. (1997) showed that this bias signal could enhance neural responses prior to the onset of visual stimuli, which is not readily explained by a mechanism of sensory gain control as the source of the enhanced neural response. According to sensory gain control, it is the stimulus-evoked response, not the baseline neural firing rate that is enhanced by spatial attention. It has to be noted that these bias signals do not rule out mechanisms of sensory gain control by itself. Because the temporal resolution of PET and fMRI is generally low, it is not always possible to distinguish between increased sensory gain and a sustained bias signal as the underlying mechanism of increased neural responses to visual stimuli presented in visual cortex. Although increased baseline signals occur prior to the presentation of information, it may

very well be that sensory gain control reflects the effects of baseline changes on processing of visual information.

Importantly, mechanisms of sensory gain control do not rely on the presence of distractors in the visual field to enhance target processing. Although sensory gain at attended locations can lead to suppression at unattended locations, this latter effect seems to be an emergent effect as a result of enhanced neural processing at attended locations. This is in line with theories that consider attention as a limited resource that is allocated over the visual field (Eriksen & Yeh, 1985; Laberge & Brown, 1989; Luck, et al., 1996).

Biased competition and ambiguity resolution

Desimone and Duncan (1995) proposed a “biased competition” account of attention. This model suggests that enhanced processing of visual information due to spatial attention should be viewed in terms of a mechanism that resolves competition for neural representation in visual cortex (for an overview, see Kastner & Ungerleider, 2000, 2001). The biased competition account of selective attention suggests that the neural amplification effect of attention can be understood in terms of multiple stimuli vying for available resources in order to control behaviour (Desimone, 1998; Desimone & Duncan, 1995; Kastner, De Weerd, Desimone, & Ungerleider, 1998; Kastner, et al., 2001; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999).

Early evidence for competitive interactions in visual cortex came from electrophysiological work with monkeys. These studies showed that the neural response elicited when two stimuli are presented in the receptive field (RF) of a neuron was equal to the weighted average of the responses to each of the stimuli presented in isolation (Reynolds, Chelazzi, & Desimone, 1999). These results suggest that when more than one stimulus is presented in a neuron's receptive field, they are not processed independently, but rather compete for neural representation. The competition between multiple items can be influenced by focusing spatial attention on a stimulus that falls in the RF of a neuron. It is suggested that attention biases the competition between competing items by reducing the suppressive effects of the unattended items in the receptive field (Moran & Desimone, 1985; Reynolds, et al., 1999; Reynolds & Desimone, 2003). Moran and

Desimone (1985) have shown that a neuron's response is primarily dependent on the focus of attention when an effective and an ineffective stimulus are presented in the RF of a neuron. The neuron will respond to the physical properties of the effective stimulus irrespective of whether it is attended or not. However, when the ineffective stimulus is attended the neuron representing the effective stimulus will stop firing. This finding shows that a neuron's response is influenced by the focus of attention.

Although most pioneering work on biased competition has been done with animals, recently effects of attention on biased competition have been observed with fMRI (Kastner, et al., 1998; Kastner, et al., 2001; Kastner, et al., 1999). For example, Kastner et al. (1998) showed that four complex stimuli presented simultaneously and close together showed mutually suppressing interactions between the items, but that the suppressing interactions were attenuated when spatial attention was focused on one of the stimuli. These findings suggest that in human visual cortex, attention biases the outcome of the competition between multiple stimuli by enhancing the attended locations and suppressing effects of stimuli presented at unattended locations. Although competition between multiple items is resolved in visual cortex, the attentional signal is hypothesized to derive from higher-order areas in fronto-parietal cortex. This signal is thought to prime (bias) the attended locations, resulting in an enhanced neural response to stimuli presented at that location biasing the competition in favor of the attended stimulus (Kastner & Ungerleider, 2000, 2001). As shown in single cell studies (Luck, Chelazzi, et al., 1997), biasing signals appear to start modulating visual cortex prior to the onset of relevant stimuli. Under these conditions, the competition between two stimuli can be quickly resolved once the target and distractors are presented.

A theory that is closely related to the biased competition model of attention is the "ambiguity resolution theory" of Luck et al. (Luck & Ford, 1998; Luck, Girelli, McDermott, & Ford, 1997). When multiple items are presented in the receptive field of a neuron, the response of the neuron is ambiguous as it is not clear which item is responsible for the neuron's response. Features of stimuli such as their location, colour or orientation are coded in different parts of the brain and the question remains how the brain 'binds' these features into a single coherent percept. Luck et al. propose that part of the solution to the binding problem can be found in utilizing spatial selective attention (see also Treisman & Gelade, 1980). The binding problem arises when multiple items are presented in the visual

field. It may therefore be beneficial to selectively focus spatial attention on one item at the time. This way the response of clusters of neurons merely reflects stimulus properties of the attended object, allowing identification of that particular object. After identification of an object, attention is shifted to the next object, resulting in a change in neural firing patterns, now representing the newly attended stimulus. This way, spatial attention allows unambiguous responses caused by the separate items in the visual field, facilitating target selection. Luck et al. showed that effects of attention were larger in conjunction discrimination tasks, as the combined features of the target would lead to the binding problem. In contrast, in feature detection tasks attention was not required as the detection of single features did not lead to a binding problem. Consistent with the ambiguity resolution theory, Luck and Ford (1998) showed that for detecting a target feature spatial attention was not necessary, as there was no ambiguity with respect to the coding of the feature (but see Theeuwes, Van Der Burg, & Belopolsky, 2008).

Uncertainty reduction

Based on previous studies, it has been proposed that attention is a limited resource (Luck, et al., 1996). Cueing a target location results in transference of resources from unattended to attended locations, leading to an increased or decreased perceptual sensitivity at cued and uncued locations respectively (Bashinski & Bacharach, 1980). When no location is cued, it is hypothesized that attention is uniformly distributed over the entire visual field. The classic pattern of spatial cueing effects (facilitated processing at validly cued locations compared to invalidly cued locations) can be explained by this limited resource model. When a target is presented at the cued location, it has access to a large amount of attentional resources leading to enhanced detection or discrimination, compared to when a target is presented at an invalid location from where attentional resources have been removed. Neutral cueing leads to intermediate detection or discrimination as some resources will still be available at the target location.

A different account was proposed by Shiu and Pashler (1994) explaining spatial cueing effects independent of capacity limitations. They claimed that attentional effects were not the result of limited resource allocation, but instead that cueing a location removed uncertainty as to which item in a display functioned as a target. Presenting

multiple items in a display results in a larger statistical likelihood that the wrong element is selected as a target, especially when target-distractor confusability is high. However, by cueing the target location, the likelihood of selecting the wrong element is decreased. This leads to a reduction in the amount of noise (i.e. the uncertainty is reduced), as a number of unlikely target stimuli get excluded in the selection process. Shiu and Pashler showed that spatial cueing effects were only observed under conditions in which multiple items were presented. When only one item was presented, there was no option of choosing the wrong element and no elements could be excluded based on a location cue. Lack of distractor noise therefore lead to the absence of a spatial cueing effect. Thus, similar to biased competition, the proposed model of uncertainty reduction as a means of selection facilitation is dependent on the presence of distractors accompanying the target.

The results presented by Shiu and Pashler (1994) were critically refuted by Luck et al. (Luck, et al., 1996), who showed substantial cueing effects in displays containing only the target element. Luck et al. concluded that the results observed by Shiu and Pashler were most likely caused by narrow experimental constraints such as using SOAs too short to shift attention towards the cued location.

Neural correlates of spatial attention

The role of spatial attention in visual perception has been studied using a diverse array of techniques such as single-cell recording, EEG, PET and fMRI. Compared to behavioural and psychophysical studies, these techniques provide additional information concerning the brain areas involved in visual spatial attention and the time course of attentional processes. Importantly, when investigating the effects of top-down attention on visual processing, a distinction has to be made between preparatory (biasing) effects of attention and the subsequent attentional modulation of visual stimuli. When looking at the neural correlates of attention this distinction has to be maintained in order to separate brain structures involved in top-down control of attention and the brain regions that are directly influenced as a result of this top-down control of attention. Distinct regions of cortex are involved in top-down control processes of attention and the modulation resulting from these top-down control processes (for reviews see Corbetta & Shulman, 2002; Kanwisher & Wojciulik, 2000; Kastner & Ungerleider, 2000; Posner &

Petersen, 1990). The distinction between top-down processes and sensory modulation can be clearly differentiated when using a cueing paradigm. This type of paradigm typically contains an attention-directing cue and a to-be-responded-to target separated in time. With this type of experimental paradigm one can investigate the neural effects specific to top-down control (as elicited by an attention-directing cue) and the effects of top-down attention on the visual system. Figure 1 provides a schematic lay-out of the different structures in early visual cortex that may be modulated by spatial attention.

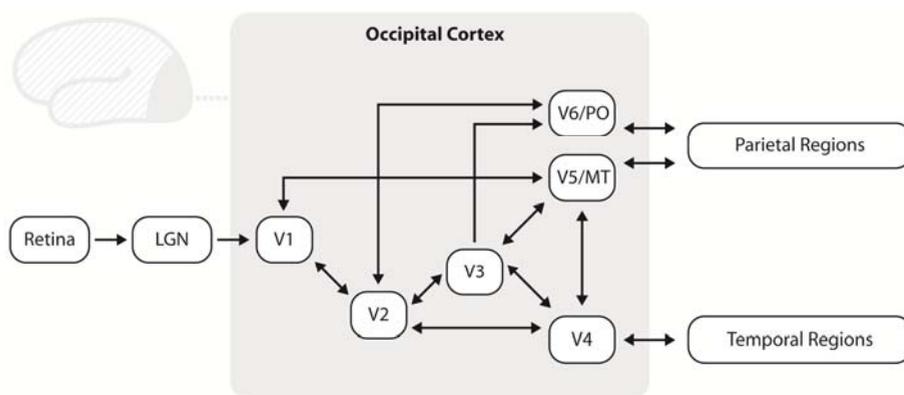


Figure 1. Overview of information processing pathways in visual cortex. Attentional modulation in visual cortex is evoked by top-down signals from fronto-parietal cortex projecting to occipital sites responsible for processing of visual input (Picture adapted from Luck, S.J. in: *Cognitive Neuroscience: The Biology of the Mind*. Gazzaniga, Ivry and Mangun, 1998).

The remainder of this chapter describes the involvement of the fronto-parietal network in spatial attention and how areas within this network influence neural responses in visual cortex. It is assumed that specific regions in fronto-parietal cortex, such as the frontal eye fields (FEF) and the intraparietal sulcus (IPS) send signals towards regions in early visual cortex in a spatially specific manner. These top-down signals result in enhanced processing of visual information presented at the attended location. Thus, spatial cueing effects are the result of direct interactions between frontal, parietal and occipital cortices. Whereas activity in frontal and parietal cortex reflect the control of attention (*disengaging, shifting and engaging of attention*), attentional modulation in visual cortex represents the effects of spatially directed attention.

The fronto-parietal network

Covert voluntary orienting to specific spatial locations has been associated with a large-scale dorsal fronto-parietal network consisting of superior frontal regions including the human homologue of the (monkey) frontal eye fields and parietal regions along the intraparietal sulcus (Corbetta, et al., 1998; Corbetta, et al., 2005; Giesbrecht, Woldorff, Song, & Mangun, 2003; Hopfinger, et al., 2000; Kincade, et al., 2005; Slagter, et al., 2007). The fronto-parietal network has often been suggested as the source of attentional modulation in visual cortex relaying top-down signals to occipital sites responsible for processing of visual input (Corbetta & Shulman, 2002; Kanwisher & Wojciulik, 2000; Kastner & Ungerleider, 2000). Distinctions can be made concerning the underlying functions of unique regions within the fronto-parietal network. For example, it appears that regions in the frontal lobe are associated with voluntary shifts of attention (de Fockert, Rees, Frith, & Lavie, 2004), whereas structures in the parietal lobe appear to be more involved in bottom-up attentional capture (Hodsoll, Mevorach, & Humphreys, 2009). Furthermore, the fronto-parietal cortex has also been associated with attention based models of working memory encoding, showing that selective attention plays a crucial role in working memory maintenance (Awh & Jonides, 1998, 2001; Mayer, et al., 2007; Postle, Awh, Jonides, Smith, & D'Esposito, 2004).

Hopfinger et al. (2000) examined the role of the fronto-parietal network in top-down control of attention by using a spatial cueing task while measuring changes in the BOLD response. In this study, participants were endogenously cued towards a location in either the left or the right hemifield. Subsequently, black and white checkerboard patterns were presented bilaterally. On some trials the checkerboard patterns could contain a number of grey checks at the cued location. Participants had to detect these grey checks and respond to their presence or absence. The design of the experiment was such that cue-related neural activity could be separated from target related neural activity, allowing a separation of the top-down control processes from the subsequent attentional modulations. The results showed that presenting a cue resulted in increased neural responses in regions in frontal and parietal cortex compared to neural activity obtained during passive viewing conditions. Bilateral regions showing cue-induced neural activity irrespective of cue direction were observed in the inferior parietal lobule (IPL), most

notably in the lateral intraparietal sulcus, the superior parietal lobule (SPL) and the posterior cingulate cortex (PCC). Furthermore, regions in the lateral and medial frontal lobe, including the frontal eye fields were bilaterally active (somewhat more pronounced in the left hemisphere) after cue presentation. Furthermore, the cue elicited stronger patterns of activation in extrastriate cortex contralateral to the cued location compared to ipsilateral regions, prior to the onset of the target.

Target presentation yielded distinct activated regions in fronto-parietal cortex not observed after presentation of attention-directing cues. Neural activation was observed bilaterally in the supplementary motor area (SMA), areas surrounding the central sulcus and ventrolateral prefrontal cortex (PFC). Only the SPL was found to be active after both cue and target presentation. Furthermore, target presentation elicited contralateral neural activation in regions of extrastriate visual cortex. Prior to target onset, an increase in neural response was observed in occipital regions V2 - V4.

In line with previous studies, the authors suggested that the neural responses in the parietal regions were involved in control processes of attention, such as shifting the focus of attention (Corbetta, et al., 1998; Gitelman, et al., 1999; Yantis, et al., 2002). The superior parietal lobule, which is thought to be involved in attentional orienting was also found to be active after target presentation, suggesting a more general and less critical role in attentional orienting than the inferior regions of the parietal cortex (Friedrich, Egly, Rafal, & Beck, 1998). Previous studies have shown a role for the frontal eye fields in covert attention (Corbetta, et al., 1998; Kastner, et al., 1999).

In conclusion, this study isolated a fronto-parietal network involved in top-down control of attention evoked by an attention directing cue and a network that responded largely to the presentation of a subsequent target. These results provide converging evidence for the existence of separate networks of attentional control and subsequent modulation of sensory processes as a result of top-down control. Although a network of frontal and parietal regions was activated during voluntary orienting of attention, Hopfinger et al. (2000) do not distinguish between the different functions of regions in this network.

A study by Corbetta et al. (2000) further investigated the underlying functions of the different regions in the parietal cortex associated with attention. More specifically, the researchers examined the role of the IPS and the temporo-parietal junction (TPJ) in visual

selective attention. The design of the study employed a standard Posner cueing task. An arrow cue pointed towards the location of a target with a high validity, ensuring attentional orienting towards the cued location. Placeholders were provided throughout the trial to ensure that participants were able to focus at the correct location. Furthermore, invalid trials, cue-only trials and noise trials (cue trials in which no target was presented but with the same duration as a cue + target trial) were included in the design. The design was set up so that separate cue and target related neural activity could be distinguished. Contrary to Hopfinger et al. (2000), IPS was found to be active after cue and target presentation, whereas Hopfinger et al. only found modulation of IPS after cue presentation. The authors concluded that IPS activity reflects voluntary allocation to, and maintenance of attentional focus at the cued location in the visual field, independent of processes related to target detection. Therefore, a hypothesized role of this region appears to be the source of the spatial biasing mechanism underlying mechanisms such as biased competition.

A region that showed increased activity after target presentation was the right temporo-parietal junction. This region was most active when the target appeared at an invalidly cued location. Based on these results and on results of patient studies with damage to the right temporo-parietal cortex (Posner, et al., 1984), the authors conclude that activity in this region in parietal cortex was responsible for reorienting of attention. The observation that participants showed the largest modulation of this area during invalid trials supports this notion, because only during these trials did participants have to reorient their attention to the opposite hemifield. The cue evoked bilateral responses in the SPL and regions in the occipital cortex, similar to Hopfinger et al. (2000). Both cue and target elicited responses in a number of extrastriate regions, but not in striate cortex. Only after target presentation did regions in visual cortex show activity in regions contralateral to the cued location. This suggests that attention acts upon visual cortex in a spatially specific fashion.

In conclusion, this study shows different functional processes in distinct parts of parietal cortex, suggesting that cue-based activity in IPS may function as the source of top-down attentional signals that biases regions of visual cortex in order to facilitate processing of upcoming stimuli. On the other hand, TPJ may support a mechanism

responsible for the reorienting of attention to a previously unattended location in order to detect a target.

Neurophysiological studies using Transcranial Magnetic Stimulation (TMS) have provided additional evidence for frontal and parietal involvement in top-down control. Ruff et al. (2006) combined TMS with fMRI to directly investigate the effects of TMS stimulation of the frontal eye fields (FEF) on information processing in visual cortex. The aim of this study was to show a functional connection between FEF and the visual cortex. Although this study did not include an attentional manipulation, the results of the study showed that stimulating FEF during passive viewing conditions (either with or without the presence of visual stimuli), lead to a substantial increase in neural activity in regions of visual cortex ranging from V1 to V4. Retinotopic differences were observed, showing more activity in regions of the visual cortex coding the visual field surrounding fixation when TMS intensity was low, whereas a higher TMS intensity induced neural responses in parts of the visual cortex coding more peripheral locations. FEF is a region often found to be active during tasks of covert spatial attention (e.g. Corbetta, et al., 1998; Kastner, et al., 1999). Because this region is thought to influence processing in visual cortex, evidence of a causal connection between FEF and neural responses in the visual cortex supports the notion of FEF being one of the sources of top-down modulation of visual cortex by attention.

In a second study employing the same behavioural paradigm (Ruff, et al., 2008), TMS was applied to right IPS, a region involved in visual selective attention (Corbetta, et al., 1998; Corbetta, et al., 2000; Gitelman, et al., 1999). Stimulating right IPS led to qualitatively different results in visual cortex than stimulating FEF, suggesting separate roles for frontal and parietal structures in visual attention. This agrees with recent studies showing that frontal cortex seems more involved in top-down aspects of attention, whereas parietal regions appear to reflect bottom-up processes (de Fockert, et al., 2004; Hodsoll, et al., 2009). Applying TMS over right IPS elicited responses in visual cortex. The nature of these responses depended on the presence or absence of stimuli (as opposed to FEF). In area V1 – V4 increased activity was observed only in the absence of visual stimulation and was not retinotopically specific, whereas in V5/MT+ a significant difference in activation was observed only when moving stimuli were presented. The observed differences between FEF and IPS stimulation fit models that suggest a

differential role for frontal and parietal cortex in attention (Kastner, et al., 1999; Shulman, et al., 2003).

A recent study by Bressler et al. (2008), employing granger causality methodology, investigated the directionality of neural responses in FEF, IPS and visual cortex prior to the onset of a target. Participants performed a visual-spatial attention task. Each trial started with a preparatory attention-directing cue (spoken words 'left' or 'right'). After a stimulus-onset asynchrony, bilateral targets were presented consisting of tilted Gabor patches. A report cue, consisting of the spoken words 'left' or 'right' was presented at the same time as the targets, indicating the location of the Gabor patch that required a response. Trials were valid when the sides indicated by the preparatory cue and the report cue matched (75% of the trials) and invalid when a mismatch between preparatory cued side and report cued side existed (25% of the trials). Participants responded significantly more accurately to valid trials compared to invalid trials.

This study showed that prior to the onset of a target, visual cortex received modulatory input from FEF and IPS. The directionality of these effects was such that observed BOLD responses in visual cortex could be predicted based on BOLD responses in FEF and IPS, but not the other way around. A similar effect was observed between FEF and IPS showing that activity in IPS could be predicted based on BOLD responses in FEF, but not vice versa, suggesting that FEF modulates IPS much more. These results suggest that neural information representing top-down attentional processes flows from frontal cortex towards parietal cortex and then to visual cortex (see also Grent 't Jong & Woldorff, 2007). Critically, this study observed that modulations in regions V4 and VP could be predicted better than modulations in V1 and V2 by FEF and IPS activity, suggesting that processing of visual information in those areas are the primary areas to be modulated by attention. A final important result of this study showed a larger causality between frontal and occipital regions and parietal and occipital regions (with the exception of right IPS) before a correctly responded-to trial compared to an incorrectly responded-to trial. This suggests that increased connectivity between these regions affects attentional processing which results in better task performance.

To conclude, this study showed directional involvement of top-down attentional processes evoked in fronto-parietal cortex on subsequent attentional processes in visual cortex. These directional effects were strongest from FEF to IPS and from both IPS and FEF

to regions in extrastriate cortex and correctly predicted behaviour of the participant, reflecting the attentional mechanism.

The abovementioned studies provide strong support for the involvement of a fronto-parietal network in top-down control of attentional modulation and as the source of a biasing signal leading to preparatory effects of attention in visual cortex. This preparatory signal, in turn, may facilitate selection by biasing upcoming target locations over upcoming distractor locations, which adds to resolving competition between these items. Similarly, a biasing signal can act by allocating resources to the upcoming target location prior to the onset of the target stimulus. Most notably, FEF, IPS and SPL seem crucial brain structures for top-down control of attention. The role of the frontal eye fields has been coined as one of the sources of top-down attentional signals emanating towards visual cortex (Corbetta, et al., 2005; Kastner, et al., 2004; Kastner, et al., 1999; Pinsk, et al., 2004; Slagter, et al., 2007). Furthermore, FEF has been implicated to play a role in the maintenance of top-down attention (Corbetta & Shulman, 2002), and has been observed to be active during voluntary search through non-targets, but not when the target was found and processed (Shulman, et al., 2003). Additionally, responses in FEF are found to be larger when evoked by voluntary shifts of attention, compared to stimulus-driven effects of attention (Kincade, et al., 2005).

Compared to FEF functionality, previous studies have ascribed similar functions to IPS. It has been suggested that IPS is involved in sustained top-down effects of attention (Corbetta, et al., 2000; Corbetta & Shulman, 2002; Yantis, et al., 2002; Yantis & Serences, 2003). Furthermore, IPS is implicated in voluntary search through non-targets and subsequent target processing (Shulman, et al., 2003) and shifts of spatial attention (Serences & Yantis, 2007). Similar to FEF, IPS activity was larger during voluntary shifts of attention compared to stimulus-driven shifts of attention (Kincade, et al., 2005). Silver et al. (2005) further showed that ventral IPS can be modulated in a spatially specific manner, showing that topographic maps exist in regions of parietal cortex.

Activity in the superior parietal lobule has been observed during shifts of attention (Yantis, et al., 2002; Yantis & Serences, 2003). SPL has also been hypothesized as one of the structures involved in top-down control of attention (Giesbrecht, et al., 2003; Kastner, et al., 1999; Pinsk, et al., 2004). These studies have provided converging evidence of an

attentional network in fronto-parietal cortex comprising FEF, IPS and SPL. For a more extensive overview see Kastner et al. (2000) and Kanwisher et al. (2000).

Preparatory effects of attention in early visual cortex

As noted, in a spatial cueing paradigm during the interval between the presentation of the cue and that of the target, participants are assumed to prepare for the upcoming target by disengaging attention from the central fixation location followed by shifting attention to the location indicated by the cue. It is assumed that attention remains focused at the cued location until the target is presented. Preparatory shifts of attention, prior to the onset of a target stimulus, yields a number of distinct components in the ERP: An early directing-attention negativity (EDAN), observed over contralateral occipital cortex, 200-300 ms after cue presentation. This component is thought to reflect encoding of the spatial cue and the subsequent shift of attention (Harter, Miller, Price, LaLonde, & Keyes, 1989; Van der Stigchel, et al., 2006). Furthermore, an anterior directing-attention negativity (ADAN) observed 300-500 ms post cue over frontal areas, which is hypothesized to reflect control of allocating spatial attention towards an upcoming target location (Eimer, van Velzen, & Driver, 2002). And finally, a late directing-attention positivity (LDAP) observed approximately 500 ms post-cue contralaterally over occipital regions. It has been suggested that the LDAP reflects cue evoked preparatory effects of attention observed in visual cortex. Even though its locus has not been defined precisely, some indirect evidence provides information concerning the initial locus of this preparatory component. For instance, Hopf and Mangun (2000) observed that the topography of the LDAP component was highly similar to the topography of the P1 component, suggesting that the LDAP originates in extrastriate cortex similar to the P1. This overlap in topography suggests that the LDAP reflects preparatory modulation in parts of visual cortex that at a later stage will facilitate the processing of the target resulting in a P1. No preparatory components of the ERP have been found to originate in striate cortex (V1), but neither has striate cortex been discarded as potentially part of the overall structure that creates these components.

Contrary to ERP studies, an increase in baseline activity has been observed in primary visual cortex under conditions of covertly directed attention with fMRI (Jack, Shulman, Snyder, McAvoy, & Corbetta, 2006; Kastner, et al., 1999; Munneke, Heslenfeld, et al.,

2008; Ress, Backus, & Heeger, 2000; Serences, et al., 2004; Silver, Ress, & Heeger, 2007). This suggests that top-down feedback projections from fronto-parietal cortex may influence attentional processing in primary visual cortex in order to selectively bias information that is processed in this region.

Some of the earliest fMRI evidence of attentional preparatory modulation in V1 in the absence of visual stimulation comes from a study by Kastner et al. (1999). Four complex coloured stimuli were presented in the upper right quadrant of the visual field either simultaneously or sequentially. Conditions in which stimuli were presented simultaneously allowed the investigation of mutually suppressive influences evoked by stimuli presented together. When stimuli were presented sequentially no suppressive interactions were expected because conditions in which more than one stimulus was present in the RF of a neuron did not occur. Furthermore, participants were either instructed to attend one of the locations of the stimuli (always the one closest to central fixation) or remain focused at the central fixation point. In order to investigate preparatory effects of spatially directed attention, participants were instructed to attend to the cued location 10 seconds prior to target onset. During the preparatory period, in the absence of visual stimulation, increased BOLD responses (baseline shifts) were observed in areas V1, V2, V4 and TEO. This was only observed in parts of visual cortex coding the location of the stimuli, suggesting that the modulation reflected the deployment of attention to that particular location. According to the authors, baseline increases evoked by spatially directed attention should be interpreted in the framework of biased competition, resolving the competition between target and distractors once presented. However, no differences in baseline increases were observed between sequential and simultaneous presentation of stimuli. This suggests the possibility that the baseline signal did not reflect processes related to biased competition, but rather the allocation of resources to the cued location. Increases in baseline firing rates were also observed in regions in fronto-parietal cortex such as the frontal eye fields (FEF), superior parietal lobule (SPL) and supplementary eye fields (SEF). These findings fit with other studies that suggest that the fronto-parietal network serves as the source of top-down feedback signals biasing responses in visual.

Even though Kastner et al. (1999) showed increased baseline shifts in striate and extrastriate cortex, the increase in BOLD contrast has not been linked to behavioural

performance. If preparatory attention reflects an attentional biasing mechanism, this should be reflected in a correlation between behavioural data and the preparatory biasing signal. Ress et al. (2000) investigated the relationship between behavioural performance and baseline BOLD responses in V1. During fMRI scanning sessions, participants were focusing on a fixation point presented on a grey background. Every 20 seconds an auditory tone would indicate that a new trial had started and participants had to judge whether a low-contrast annulus presented in the periphery surrounding the central fixation point was present or absent in the display. On half the trials, the annulus was present. The experiment was designed such that on average individual performance approximated 75% correct responses. This experiment was not designed to study orienting of attention to a predefined location in the visual field, but was designed to investigate whether visual cortex would be modulated by attention in the absence of a visual stimulation and how the magnitude of the baseline response would relate to behaviour. The fMRI data showed a large baseline response in areas V1, V2 and V3 independent of the presence or absence of the actual annulus. The fMRI patterns were assumed to reflect attentional processes because 1) the effects were retinotopically specific and 2) the effects were dependent on task difficulty (when the task was made easier, the baseline response disappeared). It was concluded that the observed response reflected preparatory effects of attention. These results have been replicated and elaborated on by Jack et al. (2006), using a similar paradigm. Jack et al. provided evidence that the observed attentional modulation in V1 was time-locked to the presentation of the low-contrast annulus. Furthermore, by using multiple peripheral eccentricities surrounding fixation Jack et al. showed that attentional modulation in V1 was retinotopic in nature and dependent on the attended location. Importantly, Ress et al. (2000) showed that the magnitude of the fMRI response predicted behavioural performance. A strong, significant correlation was observed between d' (measure of detection sensitivity) and the average fMRI response when data was binned based on increasing MRI-signal magnitude. This indicated that behavioural performance could be predicted based on the preparatory attentional modulation of primary visual cortex. Ress et al. hypothesized that baseline signals reflected top-down modulation that may lead to enhancement in the stimulus-evoked response, possibly by bringing neurons into a more sensitive segment of the operating range improving signal-to-noise ratio during sensory processes.

The study by Ress et al. (2000) elegantly showed a relationship between baseline activity in visual cortex, spatial attention and behavioural performance. However, in the study by Ress et al. cue onset (signaling the start of a trial) and target onset (whether the annulus was present or absent) were only separated by 1 second on every trial. This interval was too short to investigate preparatory effects of attention, prior to the onset of a possible target. Silver et al. (2007) investigated the time course of baseline shifts in early visual cortex (V1, V2 and V3) by employing a visual detection task with a variable cue-target delay period. While changes in blood oxygen level dependent (BOLD) signals were measured, participants were presented with an auditory tone indicating the start of a new trial. Following the tone, a delay period of 2 to 16 seconds was presented after which a low-contrast annulus was presented on approximately half the trials. After target presentation, a second auditory tone would sound, indicating that participants had to respond to the presence or absence of the target stimulus. As the duration of the delay period was determined randomly, participants had to maintain attentional focus during the entire delay period. The results of the study showed a sustained baseline shift of neural activity in retinotopic specific areas in V1, V2 and V3. Even though the onsets of the time courses of the fMRI responses were similar for all delay-periods, the later parts of the time course showed sustained cortical activity that was highly (positively) correlated with the length of the delay period in striate and extrastriate cortex. Furthermore, in peripheral unattended locations in V1, V2 and V3, a sustained decrease in activation was observed, showing a similar time course as the baseline shifts at the attended locations. Decreases in activation near the focus of attention have been observed before and have been attributed to center-surround inhibition surrounding the attended location (Muller & Kleinschmidt, 2004; Pihlaja, Henriksson, James, & Vanni, 2008; Slotnick, Schwarzbach, & Yantis, 2003). The results of this study provide evidence that the time course of preparatory attention parallels the time course of the attentional demands of a task. Furthermore, it showed that baseline shifts of attention can be sustained for a longer period of time and that irrelevant locations can be selectively inhibited or deactivated. The results are in line with the sustained effects observed by Kastner et al. (1999) and the patterns of baseline increases observed by Ress et al. (2000) and Jack et al. (2006).

The above studies have all shown that attention can modulate neural activity in primary visual cortex in the absence of visual stimulation (Jack, et al., 2006; Kastner, et al.,

1999; Ress, et al., 2000; Silver, et al., 2007). Even though the observed modulation was retinotopic in nature, a major criticism of these studies is that only one fixed target location was used over blocks of trials. Therefore, participants could maintain attentional fixation at a single location, instead of deploying spatial attention towards different locations dynamically on a trial-by-trial basis. In contrast, Munneke et al. (2008) investigated whether baseline shifts could be observed in primary visual cortex in a variant of Posner's classic orienting task. In this task, participants were required to direct attention to a location in space on a trial-by-trial basis, minimizing inter-trial priming effects. On each trial participants were cued towards the location of a possible target which was either a horizontal or vertical line surrounded by random diagonal lines functioning as distractors. Cue and target were separated over time in such a way that fMRI responses to the cues could be separated from responses to the target. Furthermore, in order to obtain a purely cue-evoked neural response, catch trials were inserted in which only a cue but no target was presented. Behavioural data showed that performance on the discrimination task was better when the location of the target was cued correctly. This indicates that preparatory attention was deployed towards the target location on a trial-by-trial basis, and not to other locations. The fMRI data of this study showed an increase in baseline response in visual cortex. The baseline shifts were observed at parts of the visual cortex coding for the attended location in the contralateral hemifield in V1, V2 and V3. This study shows that even when attention is deployed flexibly across the visual field, preparatory effects of attention still bias the location of the upcoming target.

A second important observation of this study was that on catch trials, after the presentation of a cue, the observed BOLD response dropped below baseline level resulting in a negative bold response (NBR). This drop below baseline level was observed at the interval during which on cue + target trials the search display would have been presented. It was suggested that the NBR was the result of the expectation of a stimulus to appear, when such event would not take place. Importantly, an effect of attention was still observed between NBRs elicited contralateral to the cued location compared to the BOLD response ipsilateral to the cued location. A recent study showed that NBRs in early visual cortex are associated with local decreases in neural activity (Shmuel, Augath, Oeltermann, & Logothetis, 2006). Functionally, NBRs have been associated with increased perceptual

thresholds (Kastrup, et al., 2008), which may reflect suppression of ongoing visual information processing (Kaas, Weigelt, Roebroek, Kohler, & Muckli, 2010). Suppression of visual information processing is in line with the visual demands of the task. Once it was clear to the participant that no target would be presented, less processing was required in visual cortex and the pathway towards higher visual areas may be suppressed.

In order to investigate whether the possibility of distractor presence influenced neural responses in early visual cortex, Serences et al. (2004) cued a target location and the likelihood that the targets would be surrounded by distractors. Preparatory activity in visual cortex was investigated by measuring cue evoked signal changes with fMRI. The fMRI data showed that cue-induced responses were larger for attended relative to unattended locations and that these effects were primarily evoked when distractor likelihood was high. The effects were observed in areas V1, V2, VP and V4v in the ventral part of the visual cortex. This study shows that cue-evoked preparatory activity in visual cortex operates at least partially through a mechanism of distractor suppression. Moreover, attentional control settings are influenced by distractor likelihood and the effects of distractor likelihood act directly upon early visual cortex.

In conclusion, a number of studies have shown that attention can modulate neural responses in the absence of visual stimulation in regions of visual cortex as early as V1. Attentional modulation in V1 appears to be dependent on task properties as it was observed that these modulatory effects were retinotopic in nature and dependent on task difficulty. Furthermore, preparatory modulation of visual cortex was sustained during the entire cue-target interval. The observed preparatory effects most likely reflect the result of attentional top-down signals from fronto-parietal cortex, facilitating upcoming target selection.

Effects of attention on visual processing in early visual cortex

This section discusses the effects of spatial attention. In other words, how does spatial attention directed to a location in space change the processing of stimuli presented at attended and unattended locations? Previous studies have shown that certain components of the visual event-related potential (ERP) are enhanced by spatial attention. Typical findings show increased amplitude of the P1 (80 - 130 ms after target onset) and

N1 (140 - 190 ms after target onset) for attended locations compared to unattended locations, without changes in the time course or scalp topography (Eimer, 1997; Mangun & Hillyard, 1995; Mangun, et al., 1993; Talsma, Mulckhuyse, Slagter, & Theeuwes, 2007). P1 and N1 are thought to reflect sensory processing in extrastriate cortex (Clark & Hillyard, 1996; Johannes, Munte, Heinze, & Mangun, 1995; Mangun, et al., 1993). Attention modulates only the magnitude of the P1 and N1 response, but not the time course or the scalp topography of these components. This suggests that attention acts at the same moment and upon the same neurons that elicit these visually evoked components.

Importantly, up to now there is only one study that has shown attentional modulation of the earliest component in the visual ERP, the NP80 or C1, which is thought to originate in primary visual cortex (Kelly, Gomez-Ramirez, & Foxe, 2008). Kelly et al. showed that the C1 component was modulated in conditions in which for each participant the optimal spatial locations for C1 generation were used. Using individually defined target and distractor locations severely reduces variability in the visual evoked potential. This variability is normally caused by anatomical differences in properties of the primary visual cortex such as its orientation and size. Subsequently, these optimal locations were then used to present cued target and distractors and resulted in very early attentional modulations. However, contrary to the effects observed by Kelly et al., older combined fMRI-EEG studies found modulation of attention in V1 in the absence of C1 modulation (Di Russo, et al., 2003; Martinez, et al., 1999; Martinez, et al., 2001; Noesselt, et al., 2002) and claim that attentional modulation in V1 observed with fMRI reflects reentrant feedback processes from higher-order extrastriate or parietal regions. This indicates that visual information processes are not modulated by attention in V1 during the first sweep of feedforward information but that information is modulated in V1 during later stages of processing.

Similar to fMRI studies on preparatory attention, a number of influential studies have shown effects of spatial attention on subsequent target processing and that attentional modulation in striate cortex may not be functionally different from modulation in extrastriate cortex. Attentional modulation in extrastriate cortex as observed with fMRI most likely reflects the same underlying processes as attentional modulation of the P1 and N1 component in the ERP. Similarly, modulation in primary visual cortex may reflect the

same process as modulation of the C1 response. Thus, attention facilitates neural processes in visual cortex by increasing the neural response to a visual stimulus.

Brefczynski and DeYoe (1999) investigated the neural correlates of the ability to precisely focus attention towards a location in the visual field. During an fMRI experiment, participants were instructed to shift attention towards a cued location in a circular display. The circular display was divided into elements by using different eccentricities and polar angles, resulting in four small segments per sector. During every two seconds the conjunction of a coloured and striped pattern could change in the small segments within a sector. Participants were instructed to detect certain predefined conjunctions at the cued location. Participants made five conjunction judgments per segment at two second intervals, before shifting attention to the next more eccentric segment. This way, spatial attention was systematically varied and focused on different but adjacent regions in the visual field. This allowed the researchers to investigate whether the effects of spatial attention in occipital cortex followed patterns similar to the retinotopic lay-out of visual cortex.

The key finding of this study was that shifts of attention to relevant locations at increasing eccentricities lead to enhanced responses that were spatially specific in striate and extrastriate cortex. When attention shifted to greater eccentricities (from perifoveal to peripheral locations), the locus of the effect moved away from the posterior occipital pole towards more anterior locations modulating neural activity in V1, V2, V3, VP, V4v and cortex anterior to area V4v. The strongest modulation was observed in the ventral pathway, which is known to be sensitive to colour and pattern discrimination. This study clearly demonstrated that spatial attention follows the retinotopic mapping of visual cortex and supported the idea that spatial attention enhances the same cortical neurons involved in processing of visual information. Although this study elegantly shows that moving the “spotlight” of attention results in spatially specific modulation of regions in visual cortex, an issue remains whether the observed neural patterns reflect processing benefits at the attended location. Though possible, the observed neural response does not necessarily reflect enhanced processing of the attended conjunction stimulus. The study provides no evidence that the neural correlates of the spotlight of attention reflect an increased sensory response. What this study shows is that attention modulates visual cortex in a spatially specific manner. However, it does not provide additional insight in

how attended visual information benefits from attentional processes. Based on the results of this study, one cannot distinguish between enhanced sensory responses or an effect similar to preparatory effects of attention.

Similar to the study by Brefczynski and DeYoe (1999), Gandhi et al. (1999) investigated whether attentional modulation could be observed in primary visual cortex. In the study by Gandhi et al., participants were endogenously cued towards the location of the target. A trial consisted of two consecutive presentations of two moving gratings presented left and right of the fixation point. A speeded response was required from the participants indicating in which of the two consecutive presentations the grating moved with a higher speed at the cued location. The fMRI data showed strong attentional modulation in V1 and MT contralateral to the cued target side. Furthermore, the pattern of neural activation moved with the attended location in the visual field, showing enhanced modulation in primary visual cortex of the right hemisphere when attention was cued to the left and vice versa. These results are in line with the results obtained by Brefczynski and DeYoe (1999), showing strong effects of spatial attention on target processing in V1.

Provided that spatial attention modulates primary visual cortex (Brefczynski & DeYoe, 1999; Gandhi, et al., 1999; Somers, et al., 1999), a question that remains concerns the functional role of attention in V1. As V1 codes low-level features of visual stimuli such as spatial frequency and orientation, Kelly et al. (2008), who show modulation of the C1 component of the ERP signal, suggested that attentional modulation may act upon primary visual cortex when targets and non-targets are defined by low-level features. In the task by Kelly et al., participants had to make a present - absent decision concerning the presence of a low-contrast stimulus embedded in a higher contrast stimulus. Crucial information concerning the low-contrast target presence may possibly be coded in V1 during the initial sweep of feedforward processing. Moreover, detecting a low-contrast stimulus embedded in a uniform high-contrast stimulus (as was the case in the study by Kelly et al.) requires processes similar to figure-ground segregation which are known to be highly dependent on V1. In addition, figure-ground segregation may at least partially depend on mechanisms of biased competition. The edges of a figure are coded by the same neuron as the directly adjacent parts of the background. Perhaps attention resolves the competition between figure and background representations in the RF. As figure-

background processes are dependent on V1, attentional modulation is most likely to take place in this region as well. fMRI studies that show preparatory effects of attention in V1 are often studies in which a target is surrounded by distractors (Kastner, et al., 1999; Munneke, Heslenfeld, et al., 2008), whereas studies that do not show these preparatory effects in V1 often only display only one target stimulus (e.g., Corbetta, et al., 2000). Competition among multiple items in the visual field therefore may be a necessary requirement for attentional modulation in V1.

Single-cell studies have provided further evidence for attentional modulation in V1. Motter et al. (1993) had monkeys perform an orientation discrimination task. A strong effect of attention on the response of V1 (and V2, V4) cells was observed, but only when the target stimulus was surrounded by competing distractors in the visual field. Similar to the ERP study by Kelly et al. (2008), modulation of V1 was observed when the target was defined by a low-level feature (orientation) that is coded in V1. Motter emphasized that the effects observed in V1 may very well represent suppression of the interfering stimuli.

Luck et al. (Luck, Chelazzi, et al., 1997) did not observe attention-related responses in V1 in a task that had monkeys detect the presence of a black target square. They suggested that attentional modulation in V1 may occur in much the same way as modulation in V2 and V4 but that the small receptive field sizes in this brain area meant that it was impossible to present two stimuli in the RF of a single V1 neuron. Consistent with the biased competition account of attention they reasoned that only when at least two stimuli are present at the same time within a RF one should see effects of attention.

In conclusion, attentional modulation in V1 may be dependent on two task-related properties. First, the target stimulus has to be surrounded by distractors in order to require attention to resolve competition. Second, in order to obtain modulation of V1 during the initial sweep of feedforward information, the target stimulus has to be defined by low-level features which are known to be coded in V1 (Harter & Aine, 1984; Heslenfeld, et al., 1997). Attentional modulation of V1 at a later point in time (Di Russo, et al., 2003; Martinez, et al., 2001; Noesselt, et al., 2002) may be dependent not on features of the attended target, but on other task-related processes such as task difficulty.

The role of LGN and the Pulvinar

There is some literature suggesting that attention may modulate neural processing in the lateral geniculate nucleus of the thalamus (LGN) during the first sweep of information from the retina to the visual cortex. McAlonan et al. (2008) measured neural responses in LGN and the thalamic reticular nucleus (TRN) of three monkeys while the monkeys were instructed to attend one of two stimuli. One of the stimuli was presented in the RF of an LGN neuron, whereas the other stimulus was placed outside the RF. The results showed that attention modulated the firing rate of the cell within the RF of the neuron within less than 50 ms after target presentation. When attention was focused inside the RF compared to when attention was focused outside of it, a higher neuronal firing rate was observed. The increase in LGN neural firing rate was accompanied by a decrease in activity of the TRN. According to the authors and in accordance with Crick (1984), TRN most likely inhibits LGN thereby regulating the flow of information from the retina to the cortex. A decrease in activation in TRN most likely reflects less inhibition in LGN and therefore a larger inflow of information to the visual cortex. A second modulation was observed in LGN in the absence of TRN modulation. The authors hypothesize that this may reflect goal-directed attentional modulation effects reaching the LGN through top-down connections from visual cortex.

Similar effects were observed in an fMRI study on humans by O'Connor et al. (O'Connor, Fukui, Pinsk, & Kastner, 2002) investigating the role of LGN in visual selective attention. Participants either focused their attention towards a high or low contrast checkerboard pattern presented peripherally in one of the hemifields or maintained their focus in the middle of the screen while the checkerboard patterns were presented. LGN showed spatially specific enhanced responses when participants attended the checkerboards compared to the unattended condition for both high and low contrast checkerboards. Furthermore, participants showed an increase in baseline signal prior to the onset of a target, showing that attention can modulate responses in LGN in the absence of visual stimulation. Attentional modulation in LGN was larger than in V1, suggesting that cortico-thalamic feedback is not the source of attentional modulation in LGN. Similar to McAlonan et al. (2008) it has been suggested that TRN may play an important role in LGN modulation (Kastner & Pinsk, 2004). TRN is a likely candidate to act

as a gatekeeper on LGN because all thalamo-cortical and cortico-thalamic connections pass through the TRN. Moreover, TRN receives input from extrastriate cortex and the pulvinar due to which the TRN may act as node in which cortical and thalamic influences can interact and exert inhibitory effects through the TRN on the LGN (Guillery, Feig, & Lozsadi, 1998). Due to the low temporal resolution of fMRI it is uncertain whether the modulation in LGN observed in the study by O'Conner et al. is elicited during the initial sweep of information from the retina to the cortex or whether it is the result of feedback connections from higher-order visual regions.

Another part of the thalamus, the pulvinar, may play an important role in visual selection processes (Laberge & Buchsbaum, 1990; Snow, Allen, Rafal, & Humphreys, 2009). Recent PET and fMRI studies have suggested that the pulvinar may be important for attentional selection and filtering of irrelevant information. For example, Snow et al. (2009) showed that patients with damage in the ventral parts of the pulvinar were impaired in discriminating target features, but only when the targets were surrounded by salient distractors. LaBerge et al. (1990) showed that pulvinar activity increased when participants had to detect a target in a cluttered visual display compared to a condition in which no distractors had to be filtered out. Due to its direct connections with regions in fronto-parietal cortex and visual cortex, the pulvinar is assumed to play a central role in how attentional fronto-parietal activity influences the visual system (for an overview, see Shipp, 2004).

Discussion

Neural correlates of attention show that anatomically 'early' regions of visual cortex, including V1, can be modulated by attention during cue-induced preparatory periods and during subsequent sensory processes. However, with the exception of the study by Kelly et al. (2008), a discrepancy between ERP and fMRI can be observed. FMRI studies show preparatory effects of attention in V1 based on location cueing (Kastner, et al., 1999; Munneke, Heslenfeld, et al., 2008). This preparatory effect reflects a biasing signal from a fronto-parietal network and should facilitate sensory processes in the regions upon which this bias signal acts. This means that when a target is presented at a "biased" location, facilitation should be immediate and modulate target processing in the first sweep of

feedforward information. However, most ERP studies failed to report a modulated C1 component (Clark & Hillyard, 1996; Di Russo, et al., 2003; Johannes, et al., 1995; Mangun, et al., 1993; Martinez, et al., 1999; Martinez, et al., 2001; Noesselt, et al., 2002), suggesting that V1 is not modulated by attention during the first sweep of information from striate cortex to higher-order visual regions. Kelly et al. suggested that the lack of C1 modulation may be partly attributed to individual variation in anatomical properties of V1, such as its size and location in occipital cortex. Averaged neural responses elicited in V1 over participants may therefore contain too much variation to obtain robust modulations of the C1 component. Kelly et al. employed a procedure that excluded inter-subject variability and observed large C1 components that were modulated by attention. Additionally, attentional modulation in V1 may be dependent on the nature of targets and non-targets. Attending simple targets defined by low-level features may modulate V1 on the initial sweep of feedforward processing, whereas spatial attention to more complex target stimuli may modulate V1 at a later point in time through reentrant feedback processes. Kelly et al. concluded that striate cortex was modulated by attention during the initial sweep of feedforward information from V1 to higher order visual areas.

Even though the study by Kelly et al. (2008) provides strong evidence of attentional modulation in V1, older fMRI research has often failed to observe either preparatory or sensory modulation in V1 (Corbetta, et al., 2000; Hopfinger, et al., 2000). Some studies have proposed that attentional modulation in V1 may only be observed when sufficient attentional demand is required (Gandhi, et al., 1999; Ress, et al., 2000). This is in line with the results by Ress et al. (2000) who showed that baseline increases in V1 disappeared when the task was made easier (i.e. when attentional demands of the task were reduced). Furthermore, Chen et al. (2008) showed increased firing rates in monkey V1 neurons when monkeys performed an attention demanding spatial cueing task, compared to an easier version of the same task.

Furthermore, it could be argued that studies in which a target is surrounded by distractors require additional perceptual and attentional processing in order to distinguish the target. Surely, this adds to the difficulty and attentional demands of such a task: Finding and interpreting a target among distractors is more difficult than when a target is presented on an empty background. It may very well be that attention only modulates V1 sufficiently when attentional demand is high. This may apply to preparatory effects as well

as subsequent sensory modulation in V1. Concerning preparatory effects, prior knowledge of task difficulty may elicit a stronger biasing signal from fronto-parietal regions resulting in enhanced preparatory attentional modulation in visual regions including V1 (Serences, et al., 2004; but see Munneke, Heslenfeld, Mangun, & Theeuwes, in preparation).

The reason that V1 shows the most pronounced attentional effects as the result of increased attentional demand, may have to do with the order in which early visual cortex is modulated by top-down signals from higher areas. As it appears, top-down attentional biasing signals arrive in 'mid-level' visual regions V3 and V4, where attention first starts modulating sensory processes (Martinez, et al., 1999; Martinez, et al., 2001; Noesselt, et al., 2002). Only later in time is early visual cortex (V1 and V2) modulated by attention (Di Russo, et al., 2003; Noesselt, et al., 2002). If modulation of the visual cortex would follow a path similar to visual sensory processing (from V1 to higher visual areas), effects of attention would most certainly have been observed in primary visual cortex. However, due to an almost reversed order of attentional modulation in early visual cortex (from V4 to V1) it might be that regions with a delayed modulatory onset (V1 and possibly V2) may not be required as attentional demands of the task have already been met by attentional processes in temporally early regions (V3/V4). In addition, the small receptive field size of V1 neurons may result in this area not being modulated by attention, as target and distractors do not easily fall within the same receptive field.

In addition, studies that do show preparatory effects of attention in V1 suggest that enhanced neural responses in primary visual cortex biases visual processing at the attended locations, emphasizing the spatial nature of the observed preparatory effects. Results obtained by Ress et al. (2000) and Jack et al. (2006) in which a low-contrast annulus had to be detected, suggest that attentional modulation in V1 may reflect facilitation of low-level visual processes in order to enhance target detection. From a different line of research it is known that attention can facilitate low-level processes such as contour detection (Ito, Westheimer, & Gilbert, 1998), contrast sensitivity (Carrasco, Penpeci-Talgar, & Eckstein, 2000) and spatial resolution (Yeshurun & Carrasco, 2000). It may well be that preparatory effects of attention bias these processes at the attended location.

In conclusion, spatial attention is a highly dynamic mechanism whose operation depends on the perceptual properties and the demands of the visual task at hand. The

presence of distractors, the ease with which a target is separated from its background and the likelihood of interfering information may all be factors influencing how attention modulates visual cortex. It appears that V1 modulation is strongest when task demands are high, whereas when they are low modulation in V1 may be too small or absent to be registered by current neuroimaging methods.

General Conclusions

Spatial attention can facilitate target selection and target processing in multiple ways. Crucial in most theories of spatial attention is the presence of a top-down biasing signal derived from fronto-parietal cortex. This biasing signal can be evoked by an attention-directing cue and this signal changes cortical excitability in preparation for upcoming target stimuli. The presence or absence of irrelevant and possibly distracting information appears to play a major role in how spatial attention facilitates target processing.

First, when a target is presented in the absence of distractors, enhanced target processing can be explained by a sensory gain control model of attention. It is assumed that the top-down biasing signal leads to increased neural responses in parts of the visual cortex coding the attended location. Once a target is presented at the cued location, facilitated processing will take place as a result of increased neural activity. Theories of uncertainty reduction would not predict facilitated target processing because according to this theory, attention facilitates target processing by reducing the effects of potentially interfering information. In the case where no distractors are present, nothing can be suppressed and ambiguity mechanisms therefore cannot influence target processing.

The presence of distractors may lead to competition for neural representation between the presented items. Top-down attentional signals resolve this competition by biasing the stimuli presented at the attended location over items presented at unattended locations. This way the neural response reflects the properties of the attended stimulus and ambiguity between which of the presented items evokes the neural response is resolved. Both biased competition and ambiguity resolution are mechanisms that employ top-down attention in order to make a distinction between target and distractors when presented simultaneously.

It has been hypothesized that primary visual cortex may only be modulated by attention under increased attentional demand. Models of sensory gain control, biased competition/ambiguity resolution and uncertainty reduction are in line with the hypothesized role of attentional demand as one of the reasons of attentional modulation in early visual cortex. Under conditions of biased competition and uncertainty reduction, criteria for this type of modulation would be met more often due to the presence of distractors. The presence of distractors is therefore not necessary for modulation in V1, but adds to the requirements of task difficulty in order to observe effects of spatial attention in early visual cortex.

