The spatiotemporal profile of visual attention

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Abstract

The spatial focus of attention has traditionally been envisioned as a simple spatial gradient of enhanced activity, monotonically falling off with increasing distance. Using magnetoencephalographic recordings in humans, the studies reported here demonstrate that the focus of attention is not a simple monotonic gradient but contains an excitatory peak surrounded by a narrow inhibitory region. A visual search paradigm was used throughout all reported experiments which required subjects to focus attention onto a color pop-out target among eight distractor items arranged as a quarter-circular search array in the lower right visual field. The target position randomly varied relative to the position of a task-irrelevant probe-stimulus whose electromagnetic field response was analyzed. This response was enhanced when the probe appeared at the target's location, was suppressed in a narrow zone surrounding it, and recovered at more distant locations, thus, giving rise to an activity pattern that resembles the shape of a Mexican hat. Withdrawing attention from the pop-out target by engaging observers in a demanding foveal task eliminated the Mexican hat profile, which confirms a truly attention-driven effect. The profile turned out to be very similar across different target-defining features, different levels of task-difficulty, and did not depend on whether distracters were present or not. This is taken to suggest that the Mexican hat profile represents a more elementary routine-like attentional operation, that is less dependent on direct volitional aspects of attentional focusing. Source localization results revealed that the enhancement in the center of the attentional focus and the surrounding inhibition are generated within early-to-intermediate visual cortex. With a peak maximum around 250 ms, the Mexican hat profile evolved comparably late after search frame onset, consistent with feedback processing as underlying activity, and roughly in line with psychophysical estimates of the time it takes to focus attention. Finally it should be noted, that the methodological approach followed in the present thesis rules out a number of important confounds that hampered previous research. It thus provides the first convincing functional neuroimaging evidence for such a profile in humans.

Zusammenfassung

Unser visuelles System ist ständig einer Flut von sensorischen Informationen ausgesetzt, die nicht alle auf einmal mit einem so hohen Grad an Genauigkeit wahrgenommen werden können, wie er für bewußte Wahrnehmung mitunter nötig ist. Visuelle Aufmerksamkeit umfaßt Prozesse, die dafür sorgen, dass diese Verarbeitungsgenauigkeit zumindest für einen Teil der Information erreicht werden kann, indem die Verarbeitung dieses Teils im Vergleich zu anderen Aspekten verstärkt wird. Traditionelle Befunde haben etabliert, dass Aufmerksamkeit hierzu im Raum bewegt werden kann, wobei die Verarbeitung in ihrem Fokus im Vergleich zu seiner Umgebung verbessert ist. Ob diese Verbesserung auf einer Verstärkung der relevanten oder einer Suppression der irrelevanten Information beruht, ist bisher nicht letztlich geklärt. Eine weitere Möglichkeit ist die räumlich koordinierte Zusammenarbeit zwischen beiden Mechanismen. Dies wird beispielsweise von komputationalen Modellen vorgeschlagen, die ein attentionales Profil annehmen, das einem Mexikaner-Hut ähnelt: eine zentrale Zone der relativen Signalverstärkung wird von einer Zone aktiver Suppression umschlossen, welche an weiter entfernten Positionen wieder abklingt. Dies erscheint vor allem vor dem Hintergrund neuronaler Konvergenz im visuellen System sinnvoll, die dazu führt, dass beim Durchlaufen der visuellen Hierarchie die Kodierung eines Objektes zunehmend durch den Einfluß umliegender Objekte gestört wird. Dieser Einfluß ist für direkt benachbarte Objekte maximal, weswegen eine Suppression gerade dieser Einflüsse, wie es in einem Mexikaner-Hut-Profil der Fall wäre, das Signal des attendierten Objektes besonders verbessern würde. Das bekannteste Beispiel für ein komputationales Modell, das ein Mexikaner-Hut-Profil annimmt, ist das „Selective-Tuning“ Modell von Tsotsos und Mitarbeitern, das die vorliegende Arbeit inspiriert hat. Es beruht auf einer Komplexitätsanalyse visueller Suchaufgaben, aus der das Mexikaner-Hut-Profil als emergentes Prinzip hervorging. Bisher hat diese Ansicht allerdings relativ wenig Unterstützung durch experimentelle Befunde erfahren, die im Allgemeinen lediglich ein monotones

Abfallen des Profils vom Zentrum des Aufmerksamkeitsfokus weg beschrieben haben.

Allerdings wurden im Laufe der letzten Jahre immer häufiger Ergebnisse berichtet, die mit einem Mexikaner-Hut-Profil vereinbar sind. Diese stammen vor allem aus dem Bereich der Psychophysik, wohingegen aus der funktionellen Bildgebung beim Menschen bisher lediglich zwei Studien vorliegen. Diese Bildgebungsstudien sind allerdings in ihrer Aussagekraft stark eingeschränkt, so dass sich einigermaßen gesicherte Evidenz beim Menschen bisher auf den Bereich der Psychophysik beschränkt. Untersuchungen aus dem Bereich der funktionellen Bildgebung wären aber insofern wichtig, als dass sie viel genauere Einblicke in die dem Profil unterliegenden Prozesse erlauben könnten. Außerdem ist hier eine viel direktere Messung möglich, so dass Ergebnisse aus diesem Bereich auch sicherere Evidenz dafür darstellen würden, dass der Aufmerksamkeitsfokus tatsächlich in der Form eines Mexikaner-Huts gestaltet ist, als es der Psychophysik möglich ist. Diese Dissertation berichtet sechs magnetoenzephalograpische Experimente, die diese Lücke schließen. Das grundlegende Paradigma dieser Studien ist eine visuelle Suchaufgabe, die dazu diente, die Aufmerksamkeit der Probanden auf jeweils eine von neun Positionen zu lenken. Um die mittlere Position wurde dann in der Hälfte der Durchgänge nach 250 Millisekunden ein heller, für die Aufgabe irrelevanter Kreis eingeblendet, so dass die Aufmerksamkeit der Probanden in fünf verschiedenen Abständen zu diesem Stimulus fokussiert sein konnte (gleiche Position bis maximal vier Positionen Abstand). Durch die Subtraktion von identischen Durchgängen mit und ohne Präsentation des Kreises, wurde die reine kortikale Exzitabilität (operationalisiert als die durch diesen Stimulus evozierte magnetische Aktivität) in Abhängigkeit vom Abstand zum Aufmerksamkeitsfokus ermittelt, was jeglichen rein sensorisch begründbaren Unterschied im evozierten Magnetfeld aus den Daten entfernt.

Über die verschiedenen Bedingungen der unterschiedlichen Studien hinweg zeigte sich, dass das Profil des Aufmerksamkeitsfokus tatsächlich einem Mexikaner-Hut ähnelt, also eine zentrale Zone der attentionalen Exzitation von einer räumlich eng umschriebenen Zone der Suppression umgeben ist, die an weiter entfernten Positionen wieder abebbt. Der attentionale Ursprung dieses Profils wurde in einem Kontroll-Experiment zusätzlich untermauert, in dem die Aufmerksamkeit der Probanden bei identischer Stimulation von der Suchaufgabe abgelenkt wurde. Hierbei resultierte ein über die verschiedenen Abstände zwischen Aufmerksamkeit und evozierendem Reiz undifferenziertes Profil. Die hier vorgelegten Studien können als erste verläßliche funktionell-bildgebenden Untersuchungen beim Menschen angesehen werden, die zeigen, dass der attentionale Fokus ein Mexikaner-Hut-Profil hat.

In einem weiteren Experiment wurde die Aufgabenschwierigkeit erhöht, indem die Unterscheidung des Zielobjektes erschwert wurde. Hier ergab sich ein Mexikaner-Hut-Profil sowohl für einfache als auch für schwierige Durchgänge. Die diesem Profil unterliegenden Prozesse scheinen somit nicht abhängig von der Aufgabenschwierigkeit zu sein. Mexikaner-Hut-Profile wurden auch unter weiteren Bedingungen robust ausgelöst. So wurden die Zielobjekte durch verschiedene Merkmale definiert, sowie die Zielobjekte in Abwesenheit von Distraktoren präsentiert, was jedoch beides nicht zu bedeutenden Veränderungen im resultierenden Profil führte. Weiterhin wurde gezeigt, dass die Etablierung dieses Profils ungefähr 250 Millisekunden benötigt. Davor liegt ein noch undifferenziertes Profil vor, wohingegen zu späteren Zeitpunkten die inhibitorische Zone um den Aufmerksamkeitsfokus verschwindet, welcher wiederum eine weitere Verstärkung erfährt. Zusammengenommen stellen diese Studien einen sehr wichtigen Beitrag zum Verständnis der Verarbeitung im Aufmerksamkeitsfokus dar. Sie sind die erste verläßliche Demonstration dafür, dass er, entgegen der aktuell vorherrschenden Ansicht eines monotonen Abfalls zu seinen Seiten hin, aus einer räumlich koordinierten Kooperation von relativer Exzitation und Inhibition besteht. Diese Arbeit schließt somit eine Lücke zwischen komputationalen Modellen, die ein solches Modell schon lange annehmen, und experimenteller Forschung, die bisher wenig Evidenz erbracht hatte, die diese Annahme stützt.

Abbreviations

BOLD	Blood-oxygenation level dependent effect
BCM	Biased-competition Model
EEG	Electroencephalography
EOG	Electrooculogram
EPSP	Excitatory postsynaptic potential
ERMF	Event-related magnetic field
ERP	Event-related potential
FEF	Frontal eye field
FIT	Feature Integration Theory
FMRI	Functional magnetic resonance imaging
FO	Frame-only trial
FP	Frame-plus-probe trial
IPSP	Inhibitory postsynaptic potential
ISI	Interstimulus interval
MEG	Magnetoencephalography
PD	Probe-distance
PET	Positron emission tomography
PLM	Perceptual-Load Model
rANOVA	Repeated-measures analysis of variance
ROI	Region of interest
RSVP	Rapid serial visual presentation
RT	Reaction time
SDE	Current source density estimate
SOA	Stimulus onset asynchrony
STM	Selective Tuning Model
WTA	Winner-takes-all

1 General Introduction

Attentional focusing is the key to help us navigate through what appears to be a stream of an almost unmanageable amount of visual information. Relevant information has to be extracted at the cost of irrelevant information - a necessity which arises from our limited capability to process all aspects of a given visual scene with equal degree of scrutiny (Broadbent, 1958; Shiffrin and Gardner, 1972; Tsotsos, 1990). Visual processing outside the focus of attention is very limited and conscious perception, even of seemingly salient stimuli, can be impeded under many circumstances. Notable examples are phenomena called inattentional blindness and change blindness. To induce inattentional blindness, subjects are engaged in a demanding task that requires tight focusing. The occurrence of a salient stimulus often goes unnoticed even in close vicinity of the focus of attention (Mack and Rock, 1998; Most et al., 2001). Change blindness denotes a related phenomenon. Here a significant change in a visual scene is not noticed by subjects, when slow fading-in or a bright stimulus mask in between the change prevents a simple detection of the transients associated with the change (Rensink, 1997; Rensink, 2002; Simons and Rensink, 2005).

In accord with these findings it has been proposed, that there are at least two levels of perception: one rather global level, that is based on a “first-shot” signal, very coarsely coded, and not necessarily depending on attentional resources, while another more detailed level serves to scrutinize parts of the scene at the price of disadvantaging other parts (e.g., Hochstein and Ahissar, 2002). With respect to the latter level of operation, numerous psychophysical studies have demonstrated that attending to a particular location in space can facilitate sensory processing at the cost of degraded processing at other locations. (Colegate et al., 1973; Eriksen and Hoffman, 1973; Posner et al., 1980). Attention can, thus, enhance sensory processing at a restricted region in space, which has given rise to the (metaphorical) notion of a spotlight (Posner, 1980). The precise spatio-temporal profile of this spotlight is the object of investigation of this work.

1.1 Key-concepts of current research on attention

1.1.1 Subdivisions of attention

A recent review by Raz and Buhle proposes the following general classification of attention: *alerting*, *orienting*, and *executive* functions (Raz and Buhle, 2006). *Alerting* describes the ability to maintain (and increase, if needed) response readiness for the task at hand. The definition of this function is therefore roughly overlapping with notions like vigilance, sustained attention, alertness, and arousal, and is usually operationalized as an increment in performance gained through a temporal cue. The underlying neural system comprises the reticular formation (Kinomura et al., 1996) among other areas. *Orienting,* in Raz and Buhle's terms, denotes the ability to select relevant information from a larger pool of data. As opposed to alerting, one classic test is the presentation of a spatial cue, that promotes the processing of stimuli appearing at the cued location (Posner, 1980). One key structure of the underlying neural network seems to be the parietal cortex, as indicated by severe deficits of orienting attention (hemi-neglect) after parietal stroke (Bisiach and Luzzatti, 1978; Halligan et al., 2003). *Executive* attention, in the terminology of Raz and Buhle, involves aspects of cognitive control, like error-monitoring, decision making and conflict resolution. A typical measure is the difference in behavioral variables like congruent versus incongruent responses during conflict processing and resolution (e.g., a Stroop-task (Stroop, 1935)). Neural structures usually associated with executive functions are the anterior cingulate cortex and the dorsolateral prefrontal cortex (Botvinick et al., 2004; Kerns et al., 2004; Egner and Hirsch, 2005). While many aspects of attention can be classified in this system, it provides a rather coarse subdivision. It is particularly coarse regarding a sufficiently detailed conceptualization of the actual neural implementation of attentional processing in the visual system.

Visual attention may be further subdivided regarding different reference frames of operation. For example, the classical finding that perceptual processing benefits from a spatial pre-cue has fostered the notion that space provides the prime reference frame for attention. Indeed, effects of *spatial* attention have been demonstrated in a vast number of psychophysical, neurophysiological and human imaging studies (e.g., Posner, 1980; Moran and Desimone, 1985; Heinze et al., 1994). Space, however, does not seem to be the only reference frame for attention to operate. A large body of evidence has accumulated, showing that attention can also influence neural processing at the level of features and objects independent of space (e.g., Duncan, 1984; Corbetta et al., 1991; Egly et al., 1994; Beauchamp et al., 1997; Valdes-Sosa et al., 1998; O'Craven et al., 1999; Treue and Martinez Trujillo, 1999; Saenz et al., 2002; Muller and Kleinschmidt, 2003; Schoenfeld et al., 2003). Despite clear evidence for all three types of attentional operation, it is frequently assumed that spatial attention ranks highest in priority (Tsal and Lavie, 1988; Cave and Pashler, 1995; Lavie and Driver, 1996; Hillyard and Anllo-Vento, 1998).

A further way of subdividing attention may be based on the neural locus of its modulatory impact on information processing. For example, the question where in the system resource limitations arise during attentional processing (sensory versus response selection) has been a matter of intense debate over decades (Broadbent, 1958; Deutsch and Deutsch, 1963). Important insights for resolving this issue has been provided by event-related potential (ERP) recordings, which revealed gain amplification effects of sensory ERP components due to attention as early as 90 ms after stimulus onset (Mangun, 1995; Hillyard et al., 1998; see also section 1.2.2.1). Late ERP components reflecting response selection processes were also found to be influenced by attention (e.g., Vogel et al., 1998). ERP research, thus, revealed that there may be no simple decision between early or late selection accounts. Relatively early modulations appear to affect sensory processing, while later ones seem to be response-related (reviewed in Luck et al., 2000).

Concerning early visual processing, attentional modulations in striate and extrastriate cortex have been shown to follow the retinotopical organization in the visual system (Tootell et al., 1998; Brefczynski and DeYoe, 1999). Areas higher in the processing hierarchy generally appear to be modulated more strongly (Tootell et al., 1998; Cook and Maunsell, 2002), and the attentional modulations have an earlier onset there as compared with lower-level areas (Luck et al., 1997a; Martinez et al., 1999; Mehta et al., 2000a; Noesselt et al., 2002). This “reversed” timing of attentional modulations in the visual cortex has been taken to suggest that attention influences the processing in low-level visual areas through recurrent (feedback) activity (Martinez et al., 1999; Lamme and Roelfsema, 2000; Noesselt et al., 2002). Finally, although the visual system displays effects of attention at all hierarchical levels (reviewed in (Kastner and Ungerleider, 2000; Kastner and Pinsk, 2004; Reynolds and Chelazzi, 2004), the first feedforward sweep of processing appears to be generally unaffected at earliest levels (Lamme and Roelfsema, 2000).

1.1.2 Attention and eye-movements

Most evidence for attention effects in the visual system described so far, was gathered during experiments where subjects did not move their eyes. In a typical experiment the eyes remain fixed on a fixation point and only the “mind’s eye” is allowed to move. This situation is referred to as covert attentional focusing (Posner, 1980) in contrast to a situation where the eyes are allowed to move freely (overt attention). While overt attention differs from covert attention in this respect, many studies revealed that both, nonetheless, share important features. For example, Sheliga and colleagues found that the trajectories of saccades systematically deviated in relation to a position covertly attended (Sheliga et al., 1994; Sheliga et al., 1995). Hoffmann and Subramaniam demonstrated, that target detection was best at positions that subjects were just preparing to saccade to (Hoffman and Subramaniam, 1995). These insights led Rizzolatti and colleagues to propose that covert attention and saccade programming rely on a common neural circuitry (pre-motor theory of attention; Rizzolatti et al., 1987). Neurophysiological evidence has only partly supported this notion, as there is experimental evidence that the two systems may not be fully overlapping (Corbetta, 1998; Thompson et al., 2005).

1.1.3 Necessity for attention

In addition to coding problems the overwhelming flood of sensory input poses at any given moment, the way information is processed in the brain causes further problems that necessitate attentional resolution. For the visual system, two architectural principles cause these intricacies, mainly due to massive parallel processing of different features in different modules. In addition, with increasing hierarchical levels there is a considerable increase of the size of receptive fields (neuronal convergence) and a concomitant increase of the complexity of the conveyed information (Gattass et al., 1981; Desimone et al., 1984; Desimone et al., 1985; Saito et al., 1986; Desimone and Schein, 1987; Maunsell and Newsome, 1987; Gattass et al., 1988; Corbetta et al., 1990; Schein and Desimone, 1990; Felleman and Van Essen, 1991; Zeki et al., 1991; Sereno et al., 1995). As long as an isolated object requires processing (i.e., within the receptive field of a given neuron) this convergent architecture does not face coding problems. Coding may become ambiguous, however, in the case of multi-item presentations. Furthermore, ambiguities may arise at the level of feature encoding. For example, assigning a particular attribute to a specific object may be complicated when multiple objects are present. Fig. 1 illustrates this coding problem using four hypothetical neurons that are all responsive to a similar region in the visual field but are specialized for different attributes (color, orientation). Two cells signal the presence of a color (green vs. red), while the other two cells respond to orientation (horizontal vs. vertical). As long as only one object is present in the receptive field (for example a red horizontal bar; Fig. 1a) the net activity of the four neurons unambiguously identifies the object. If another object is added (e.g., a green vertical bar; Fig. 1b), all cells signal the presence of the attribute they are tuned for, and the overall activity becomes ambiguous as to which attribute belongs to which object. The fact that the outcome of these calculations has to be disambiguated in order to allocate the existing features to the correct objects, represents the so called feature conjunction problem – one instance of the so-called *binding problem*.

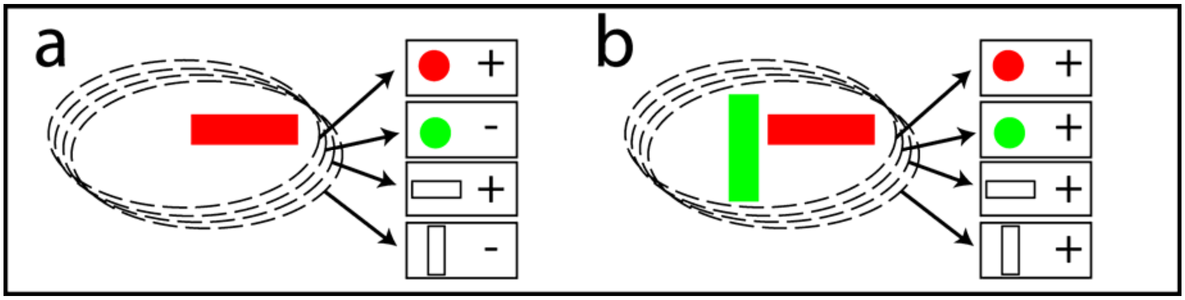

Fig. 1: *Illustration of the feature conjunction problem.* The broken ellipses represent the receptive fields of four hypothetical neurons, while the boxes illustrate the feature they preferentially respond to and their respective response. **(a)** one object is unambiguously coded, while **(b)** two objects lead to ambiguous coding, because an assignment of the different feature values to the two objects is not possible (adapted from Luck and Vecera, 2002).

A theoretical framework, that has offered a solution for the binding problem is the Feature Integration Theory (FIT). FIT mainly capitalizes on observations from visual search tasks (Treisman and Gelade, 1980; Treisman, 1988). Specifically, FIT assumes that different features are processed within specialized modules in parallel, but that a combination of the signals from different modules requires spatial attention in a serial manner. This notion is inferred from the finding, that the addition of distractors to a search array leads to a linear increase in reaction times when feature encoding is ambiguous as illustrated in Fig.1 (conjunction search; Treisman and Gelade, 1980; Treisman, 1988; Treisman and Gormican, 1988). Although there are demonstrations of conjunction searches where this increase is not large enough to support the sequential deployment of an attentional focus (Nakayama and Silverman, 1986; Wolfe et al., 1989; Treisman and Sato, 1990), the general principle still holds.

While FIT makes a good case to emphasize the key role of sequential deployments of attention during conjunction search, it is unclear as to how the fundamental coding ambiguities resulting from the massive convergence of the visual system are actually solved by attention. Various models propose that this is accomplished by biasing neural activity towards the attributes of the attended object (biased competition theory (BCM); e.g., Desimone and Duncan, 1995). These proposals are based on a large body of evidence, showing that (1) attention preferably modulates the activity of neurons with receptive fields that “see” multiple objects (see section 1.2.1), and (2) attention changes neuronal activity as if the attended stimulus would be alone in the receptive field (Reynolds and Desimone, 1999). In other words, attention operate by shrinking the receptive field around the attended item (Moran and Desimone, 1985). In principal, there are two ways this can be accomplished: (1) the information of the attended object could be enhanced, or (2) the information related to the unattended object could be suppressed. The following section will review evidence for both alternatives.

1.2 Basic mechanisms of visual attention

1.2.1 Neurophysiological Studies in Animals

Attention has been shown to cause enhancements of cell-firing in the monkey. In early studies the exploration of covert attentional focusing was linked to saccade preparation (Wurtz and Mohler, 1976; Robinson et al., 1980; Bushnell et al., 1981), or the behavioral relevance of a stimulus (Haenny and Schiller, 1988), and enhancement effects were observed throughout the visual cortex. More recent studies have attempted to clarify the quantitative relationship between firing effects and attention more thoroughly (e.g., Treue and Martinez Trujillo, 1999). These studies demonstrated that, although attention enhances firing rates, the tuning curve of visual neurons does not change qualitatively (feature similarity gain model; (Treue, 2001; but see Womelsdorf et al., 2006). Moreover, attention effects on cell firing appear to scale with stimulus contrast, with maximal effects seen at contrasts-levels that just fail to elicit a robust response in the absence of attention, while the signaling is mostly unchanged for very low- or high-contrast stimuli (Reynolds et al., 2000). As already mentioned above, cell-recording studies established that attention exerts largest effects on cell-firing when multiple items compete for processing (e.g., Motter, 1993; Luck et al., 1997a).

A first convincing demonstration of neuronal inhibition serving as a key mechanism during attentional selection was provided by Moran and Desimone two decades ago (Moran and Desimone, 1985). Moran and Desimone investigated effects of location and feature selection on the firing of single neurons in areas V2, V4 and IT. In their experiments effective and ineffective stimuli were simultaneously presented in the receptive field, while the monkey attended to only one of them. Their key observation was that the response of the neuron was highly dependent on which stimulus was being attended. Despite identical physical stimulation, a strong response was elicited, when the effective stimulus was attended, while the response was significantly reduced when the ineffective stimulus was attended. Attention, thus appeared to constrict the receptive field around the attended stimulus. In a different experimental condition, the effective stimulus was placed within the receptive field of the cell, whereas the ineffective stimulus was presented at a position outside of it. In this constellation the cells gave a strong response no matter whether the monkey attended inside or outside the cell’s receptive field. Moran and Desimone concluded that attention may impact the cell’s response only if more than one stimulus was present in its receptive field, that is, under conditions that render stimulus coding ambiguous (see section 1.1.3). Moreover, as the size of the firing-response to the effective stimulus was similar, whether or not it was attended, attention was assumed to exert its modulatory effects mainly through the attenuation of irrelevant information, and not so much via enhancement of relevant information.

Subsequent studies by Chelazzi and co-workers used the memory-guided visual search paradigm while pursuing the same general approach of having an effective and an ineffective stimulus in the receptive field of a single cell (Chelazzi et al., 1993; Chelazzi et al., 1998). At the start of each trial, the effective or ineffective item was cued to be identified (target saccade) on a subsequent search frame. On this frame both stimuli were placed at random locations within the same receptive field. The results indicated that the initial response to the search array was identical no matter which stimulus was the saccade target. After approximately 160 ms, however, the cells’ response was dramatically attenuated when the attended stimulus was the ineffective one. On the other hand, the cell continued to fire when the effective stimulus was attended. These observations were taken to further emphasize the notion put forward by Moran and Desimone that attention acts preferably via neural inhibition. While the studies detailed so far recorded from cells within the ventral processing stream, analogous results have been reported for the dorsal stream of visual processing (Treue and Maunsell, 1996; Recanzone et al., 1997).

Cell-recordings from V1 were not able to provide reliable evidence, because the receptive field size is too small with respect to typical eye-movements. Using a different methodological approach (double-label deoxyglucose technique in monkeys), Vanduffel and colleagues were able to provide evidence for attentional suppression in V1 (Vanduffel et al., 2000). Specifically, they found evidence for attention-related suppression (reduced energy consumption) in a zone of V1 that surrounded the representation of the attended location, while no indication of elevated energy consumption in the focus of attention was found.

The evidence from studies in the monkey taken together suggests that attention can influence sensory processing through both, relative enhancement and suppression of neuronal activity. It is noteworthy that attentional enhancement is typically demonstrated in the absence of distractors, while attentional suppression is a prominent feature when distractors are present. This suggests (and is in line with the psychophysical data, reviewed in chapter 1.4.2) that stimulus configuration represents an important determinant of the particular selection mechanism involved.

1.2.2 Studies in Humans

1.2.2.1 ERP studies

The majority of ERP studies has emphasized that attention enhances early sensory ERP components. This general observation facilitated the conclusion that attention operates via gain amplification in visual sensory areas (Eason, 1981; Harter et al., 1982; Hillyard and Münte, 1984; Hillyard and Mangun, 1987; Luck et al., 1994; Mangun, 1995; Hillyard et al., 1998). This notion is mainly based on the observation that ERP components reflecting early sensory processing (P1- and N1-components) are enhanced in amplitude when elicited by attended stimuli, for example in a Posner paradigm. The components that undergo modulation represent the first major positive and negative deflections in the canonical ERP around 90 to 150 ms after stimulus presentation, and have been shown to index activity in early visual cortex areas (Regan, 1989). A further important paradigmatic approach revealing sensory enhancement effects was the passive probe paradigm. For example, presenting an irrelevant probe at the target location shortly after the onset of a search array elicits a stronger response relative to a probe location in the opposite visual hemifield (Heinze et al., 1990; Luck et al., 1993; Luck and Hillyard, 1995). Remarkably, some studies also reported that the amplitude of these components was reduced for unattended stimuli (Luck et al., 1994; Luck and Hillyard, 1995). Altogether, the so far reviewed ERP data clearly indicate that attention acts through modulating the inflow of sensory information. These modulations appear as amplitude enhancements without significant changes in onset latency and scalp topography, which was taken to suggest sensory gain amplification as an underlying mechanism (see sensory gain control account (Hillyard and Mangun, 1987; Hillyard et al., 1998)).

Besides gain amplification, ERP research into visual attention has also revealed ERP correlates of sensory suppression. For example, the so called N2pc component has been shown to reflect the filtering of unwanted information during visual search (Luck and Hillyard, 1994a; Luck et al., 1997b) via suppression. The N2pc is an enhanced negativity between approximately 180 and 300 ms over the scalp contralateral to the attended location (Luck and Hillyard, 1994a, 1994b). It has been linked to the suppression of information from unattended items for several reasons. The N2pc is the larger the more distractor items are present in the search array (Luck and Hillyard, 1994a), and it is larger for feature-conjunction targets than for pop-out targets (Luck et al., 1997b). The N2pc has been likened to parallel cell-firing effects reflecting distractor suppression in ventral extrastriate areas of the monkey (Luck et al., 1997b). It should be noted, however, that an overly parallelism between ERP studies in humans and cell-recordings in the monkey should be taken with caution as single-cell recordings might miss some general coding characteristic present at the population level, which may in turn be more directly reflected by ERP recordings.

In sum, in line with observations from single-cell recordings in animals, ERP research has revealed evidence for both, sensory enhancement and suppression. Courtesy of its excellent temporal resolution, the ERP permits an examination of the relative timing of these effects, which highlights enhancement during an early time-window, whereas effects related to suppression of information appear to succeed.

1.2.2.2 PET and fMRI studies

Functional brain imaging methods (PET, fMRI) provide another approach to investigate the impact of attention on neural processing in the visual system. A typical observation has been an increase of the BOLD-signal (blood oxygenation-level dependent effect in fMRI) or an intensified cerebral blood flow (PET) following attended versus unattended stimuli. Because of their excellent spatial resolution, these methods revealed detailed and reliable information about the particular visual cortical areas that are subject to attentional modulations (Corbetta et al., 1990, 1991; Beauchamp et al., 1997; O'Craven et al., 1997; Buchel et al., 1998). A seminal finding has been that signal-increases due to spatial attention arise in cortical areas that are retinotopically consistent with the attended part of the visual field (Woldorff et al., 1997; Tootell et al., 1998; Brefczynski and DeYoe, 1999). Other studies have focused on fMRI and PET correlates of feature-based attention (e.g., color, motion, form), and observed that attention enhances neural activity in cortical regions specialized for the attended feature domain. Corbetta and co-workers, report increases in local blood-flow in regions coding for relevant features as compared to passive viewing, which was not modulated in regions coding task-irrelevant regions (Corbetta et al., 1990, 1991). Similar results have been obtained in cortical areas of the ventral processing stream that show high-level feature specializations for faces and houses (Wojciulik et al., 1998; O'Craven et al., 1999; see also Haxby et al., 1994). Attention to faces led to increased signals in the region known to be specialized for the processing of faces (Kanwisher et al., 1997), whereas no modulation was found in the area specialized for houses (Epstein and Kanwisher, 1998) and vice versa. This clearly argues in favor of the notion, that attention enhances the processing of the attended object class, as opposed to a potential down-regulation of the unattended category. An fMRI study by Kastner and colleagues argues in favor of the notion, that the modulations found in the former studies, at least in part, represent changes in baseline activity (Kastner et al., 1999). Specifically, this study could demonstrate that activity in visual cortex was enhanced in the absence of any stimulation, while subjects expected a stimulus to come up. As this enhancement was retinotopically consistent with the attended location, this has been taken as further evidence for attentional enhancement.

The bulk of imaging studies on attention effects in the visual system emphasize signal-enhancement as a mechanism of attention. Nevertheless, there are a number of studies suggesting that suppressive mechanisms may be as important. For example, an fMRI experiment demonstrating a retinotopically specific signal-enhancement in the focus of attention observed a concomitant signal reduction outside the attended area (Tootell et al., 1998; see also Somers et al., 1999). Smith et al. demonstrated that directing attention to a specific location leads to widespread activity reduction throughout the remaining visual field (Smith et al., 2000; see Drevets et al., 1995, for similar results in the somatosensory cortex).

The amount of signal suppression devoted to irrelevant input appears to be load-dependent. That is, the signal representing task-irrelevant distractors (irrelevant moving dots in the background of a task requiring either to discriminate the appearance or the structure of a word) was attenuated under the high-load condition while a strong response was measured under low load (Rees et al., 1997). Moreover, Serences and co-workers found that preparatory activity in visual cortex can also be linked to distractor suppression. In their experiments enhanced preparatory activity was observed when interference from distractors was probable (Serences et al., 2004).

Thus, analogous to the ERP/MEG observations reviewed above, PET and fMRI studies provide evidence for both, attentional enhancement and suppression of sensory activity to play an important role during attentional focusing. In fact, recent evidence in humans points to a tight link between both. Pinsk and co-workers demonstrate that attention enhanced the BOLD-response in retinotopically organized visual areas representing the contralateral target visual field but attenuated the BOLD-response on the ipsilateral side (Pinsk et al., 2004). While this effect was independent of task-difficulty in V1 and V2, task-difficulty had an effect in higher-level cortical areas. In V4 and TEO the BOLD-response was more strongly enhanced in the target visual field and more strongly attenuated in the opposite non-target visual field. Pinsk and colleagues concluded that enhancement and suppression cooperate in a push-pull like manner to mediate attentional selection across hemispheres. The present work will demonstrate that neural enhancement and suppression cooperate at an even finer spatial scale.

1.2.3 Methodological considerations

At a first glance, it appears easy to decide whether attention operates by exerting inhibitory or excitatory influences on neural processing. However, all reviewed methods are limited as to their ability of disentangling the two. In particular, a general problem faced by most methodologies is the fact that a lack of enhancement (relative to some baseline condition) may be indistinguishable from true suppression and vice versa. Such ambiguity poses particular interpretive problems in studies, that missed to include a neutral baseline condition. So for most cases, it is more parsimonious to refer to relative expressions of enhancement or suppression. Throughout the following sections, the terms enhancement (or excitation, which is used synonymously) and suppression (or inhibition) are used in this relative sense.

The ambiguity concerning neural enhancement and suppression also arises from interpretive problems inherent in the experimental measures. Psychophysical studies are hampered by their indirect measure, as only the final output of a behavioral task can be portrayed, whereas intermediate steps are quasi “invisible”, and hence indirectly inferred. FMRI studies conversely suffer from their poor temporal resolution as well as the indirect link to neuronal activity. Notwithstanding the large progress in understanding the BOLD effect (Logothetis et al., 2001; Logothetis, 2003; Shmuel et al., 2006), both neuronal enhancement and suppression are energy-consuming mechanisms, possibly producing similar BOLD effects.

Fortunately, electroencephalographic and magnetoencephalographic (EEG/MEG) measures provide more direct measures of underlying neuronal activity. It appears that the signal is dominated by EPSPs (excitatory postsynaptical potentials) and IPSPs (inhibitory postsynaptical potentials) generated in the pyramidal cells of the cortex (Nunez, 1981). Thus, the link to neuronal activity is very direct. Nevertheless, EEG/MEG measures remain ambiguous as to the direct linkage of enhancement and suppression of a component to the underlying EPSPs and IPSPs. For example, take a component that is a summation of two (or even more) subcomponents, one of positive, one of negative polarity (note that the polarity of an EEG/MEG-component has nothing to do with enhancement or suppression). Let us assume that the positive subcomponent has a larger amplitude, so that the overall component will be positive. If the effect of attention is to enhance the negative subcomponent, the net effect will be a reduction of the component - a pattern that could erroneously be taken as evidence for suppression, although the underlying process was an enhancement (for a more detailed discussion of this issue see Luck, 2004). This shortcoming is much less pronounced for MEG than with EEG, as the superior spatial resolution of MEG allows for the separation of more subcomponents. It thus appears, that among noninvasive electrophysiological methods, MEG is best suited to enlighten the processes of neuronal enhancement and suppression.

1.3 Computational Modeling of Visual Attention

Another way to investigate the potential roles of neural enhancement and suppression during attentional focusing, is to examine the issue within a computational framework that uses realistic assumptions about the neural implementation. Such framework has been developed, for example, with the selective tuning model (STM) of Tsotsos and co-workers (Tsotsos et al., 1995; Tsotsos, 1999; Tsotsos et al., 2001; Tsotsos, 2005) – a model that will be reviewed in detail below. Other models will only be mentioned with respect to their predictions concerning the profile of attention.

STM is based on a complexity analysis of the problem of visual focusing, and proposes computational principles that are in accord with general aspects of the neuroanatomical organization of the visual system (Tsotsos, 1990; Tsotsos et al., 1995). These principles contain a considerable degree of parallelism, a massive bottom-up and top-down convergence between hierarchical levels, as well as modulatory units implemented as winner-takes-all (WTA) processes. As outlined in section 1.1.3 the many-to-one convergence in the visual hierarchy produces ambiguities of feature and object coding during signal processing. In a computational frame-work, this problem is called the routing problem (Anderson and Van Essen, 1987; Olshausen et al., 1993). The analysis underlying STM argues in favor of the notion, that suppressing irrelevant information provides the best solution for this problem, while it also constitutes an effective way to reduce the complexity of the task (e.g., visual search; Tsotsos, 1990, 1999).

STM assumes three main processing stages (see Fig. 2): 1) a feedforward sweep of information flow ascending the hierarchy mainly reflecting the cells' particular selectivities (and potentially a preset bias). 2) a hierarchical top-down propagating WTA process that prunes away activity in connections representing the unattended input. This hierarchical WTA process starts at the top-layer, and the winner at this level again, activates a WTA process over its direct input, thereby pruning away input from other objects. Connections conveying information about the attended object remain active. As this process propagates down through the hierarchical levels, a pass-zone for relevant information is formed while information outside the pass-zone is suppressed. Importantly, this wave of top-down propagation produces an inhibitory annulus directly surrounding the zone of unaffected signaling, which tapers off again towards the more distant surround. The outer extent of this inhibitory annulus corresponds to the size of the receptive field of the winning unit in the top-layer, so that active suppression is restricted to its input, whereas the signaling of more distal items is unaffected. 3) the selected input repropagates through the system in feedforward direction, refining the coding of the attended object.

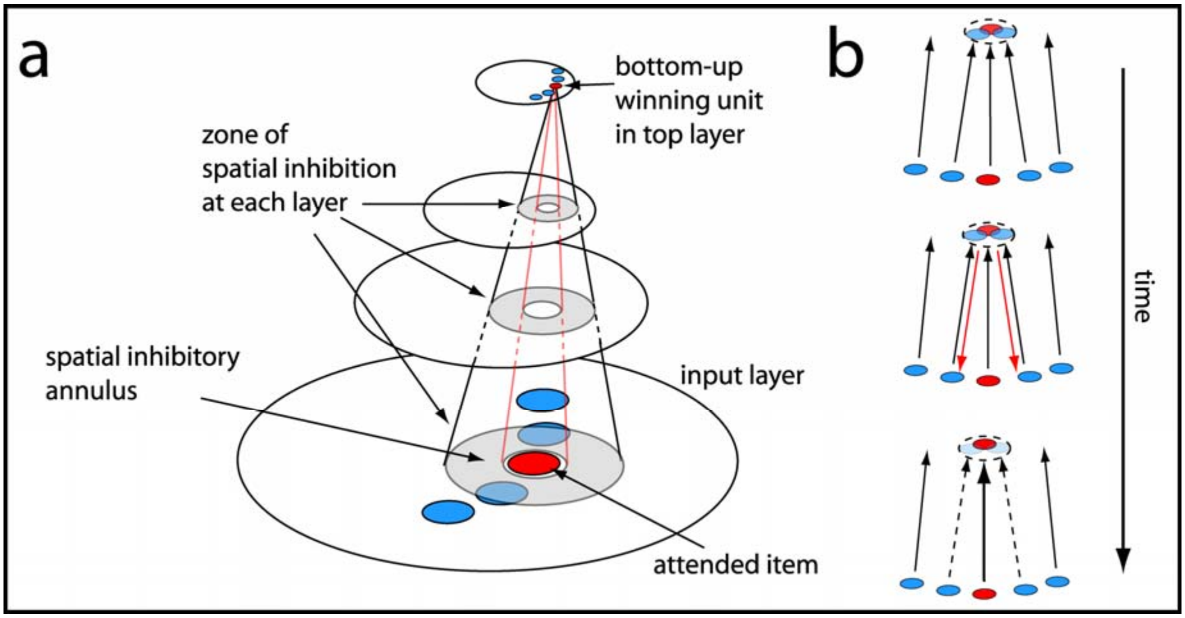

Fig. 2: *Illustration of the Selective Tuning Model.* **(a)** a four-layer pyramid is illustrated. After the initial traversal, the system calculates the winning unit in the top layer, which initiates a downward cascade of WTA processes, that leads to the formation of an inhibitory annulus, which surrounds a pass-zone of unaffected signaling. **(b)** the temporal succession (from top to bottom) of the model steps begins with an initial bottom-up traversal. A WTA process first calculates the global winner in the top layer, and then activates a downward cascade of WTA processes over its direct inputs, thereby pruning away the signals from the unattended stimuli (red arrows). In a last step, the signal repropagates refining the value of the winner.

Taken together, STM provides a powerful model of visual attention and a solution for the complexity problem of feature and object coding in vision that has also proven to be beneficial for computer vision. It is widely consistent with the experimental evidence to date, and advances a number of testable predictions. Among these are the predictions that the latency of attentional modulations should increase from higher to lower areas in the visual hierarchy, and that the focus of attention is surrounded by a spatially confined inhibitory annulus. The first prediction has lately gained empirical support (Martinez et al., 1999; Mehta et al., 2000a; Noesselt et al., 2002). Similarly, empirical evidence for the second prediction starts to accumulate (see section 1.4.2), and this thesis is aimed to add to it. Throughout the main section of this thesis, STM will be frequently referred to when discussing the observations.

1.3.1 Model Predictions concerning the spatial profile of attention

One key feature of STM is that it predicts a spatially restricted zone of suppression surrounding the focus of attention. While the predictions of other models are compatible with an inhibitory surround in an explicit or implicit form (like the Biased Competition Model by Desimone and colleagues (Desimone and Duncan, 1995), Ambiguity Resolution Theory by Luck and co-workers (Luck et al., 1997b), the FeatureGate Model by Cave (Cave, 1999), and different versions of the Adaptive Resonance Theory by Grossberg and colleagues (Grossberg, 1999; Raizada and Grossberg, 2003)) the structured center-surround profile does not directly arise as an emergent property of the computations involved in these models. Notwithstanding the fact that different computational conceptualizations of visual attention have (explicitly or implicitly) converged on the view that the focus of attention may be surrounded by a spatially confined inhibitory zone, there is very little experimental evidence, in support of this notion thus far. The next section will review the currently available evidence compatible with an inhibitory annulus around the focus of attention, and will pit this evidence against data suggesting a simple gradient model.

1.4 The spatial profile of the focus of attention

The classic conception of the focus of attention has been that of a spotlight, that is fixed in size (Posner, 1980; Posner et al., 1980), and can be moved through the scene with a certain speed (Tsal, 1983). While it has already been outlined that different accounts prefer to conceive of the focus of attention as an aperture (Navon, 1990), evidence has accumulated to question the general validity of the original spotlight metaphor. For example, estimates of the size of the attentional spotlight yielded very diverse results (ranging from approximately 1° (Eriksen and Hoffman, 1973) to over 10° of visual angle (Hughes and Zimba, 1985)), suggesting that the size of the focus may not be fixed (e.g., LaBerge, 1983). The spatial focus of attention has, thus, been likened to a zoom-lens whose size can be changed to adapt to task demands. This zoom-lens model (Eriksen and James, 1986) proposed a tradeoff between its width and the degree to which processing can benefit from attention, resulting from an approximately constant amount of resources to be distributed (i.e., getting flatter with expansion (Castiello and Umilta, 1990)). Evidence supporting such adaptable size of the attentional focus has recently been provided using fMRI with human observers (Muller et al., 2003b). Furthermore, there is data compatible with the possibility, that the focus of attention can be split into disjunctive areas (reviewed in Juola et al., 1991; Muller and Hubner, 2002; Cavanagh and Alvarez, 2005).

To summarize the major notions about the spatial profile of attention: there are (1) the classical accounts in form of a spotlight or zoom-lens, which assumed that the attentional profile resembles an even distribution with sharp edges. (2) gradient models challenged this view by demonstrating that there is an interrelation of attentional measures and the distance from the very focus of attention, resulting in a graded profile. (3) models that assume a center-surround profile. That is, the focus of attention encompasses a gradient of relatively enhanced sensory processing, that is encircled by a suppressive annulus of markedly reduced processing that recovers again at further distances. This profile resembles a “Mexican hat”, with the “tip” of the distribution being encircled by a “brim” of suppression and a rebound to a level intermediate between the two.

1.4.1 Evidence in favor of a monotonic gradient

Most evidence favoring the conception of the focus of attention as a monotonic gradient stems from psychophysical experiments. For example, with their classic flanker task Eriksen and Hoffman demonstrated a gradual fall-off of flanker interference with distance to the target (Eriksen and Hoffman, 1973). Analogous effects have been observed in other investigations (Eriksen and James, 1986; Miller, 1991; Andersen and Kramer, 1993), and similar results have been reported for adapted versions of the Stroop interference task (e.g., Kahneman and Chajczyk, 1983).

Downing and Pinker used a location-cuing paradigm to show that reaction times to a target increased with increasing cue-target distances (Downing and Pinker, 1985) - a result that has been frequently replicated (Shulman et al., 1985; Shulman et al., 1986; Rizzolatti et al., 1987; Downing, 1988; Henderson and Macquistan, 1993; Handy et al., 1996). The simple gradient notion was also supported by studies that relied on detecting two targets that appeared in rapid succession at different distances from each other, a situation where reaction times to the second target have been found to increase with distance between the two stimuli (LaBerge, 1983; LaBerge and Brown, 1989).

The gradient model has furthermore experienced support from ERP studies. For example, Mangun and Hillyard report a progressive decline in amplitude of the occipital P1 and N1 components for targets with increasing distance from a cued location (Mangun and Hillyard, 1987, 1988; see also Eimer, 1997). Finally, neurophysiological observations based on single-unit recordings in monkeys provided support for the gradient model of the attentional distribution. For example, Connor and colleagues reported that the response of a V4 neuron to an irrelevant stimulus passing through its receptive field became gradually stronger, the closer it came to the actual focus of attention inside, and outside the receptive field (Connor et al., 1996).

1.4.2 Evidence in favor of a Mexican hat profile

Psychophysical studies have piled evidence suggesting that both enhancement and suppression play important roles during attentional selection. As already mentioned, one milestone finding was the observation that location pre-cuing facilitates the discrimination of a target item at this location (faster reaction times, lower detection thresholds, etc.) relative to other locations where target discrimination deteriorated (Colegate et al., 1973; Eriksen and Hoffman, 1973; Posner et al., 1980).

The mechanisms underlying attention are discussed in the psychophysical literature in roughly three directions: (1) signal enhancement, (2) distractor (noise) exclusion or uncertainty resolution, and (3) ambiguity resolution. The signal enhancement hypothesis primarily emphasizes sensory facilitation in the absence of interfering information (Henderson, 1996; Carrasco et al., 2000; Cameron et al., 2002; Carrasco et al., 2002). Distractor exclusion or uncertainty resolution is assumed to dominate attentional selection under high-noise conditions. Ambiguity resolution becomes essential when sensory coding or response selection processes produce ambiguous representations or response tendencies, respectively. That these mechanism might rely on suppression of distractor information is illustrated by the example of negative priming. Here, a stimulus that serves as a distractor in a response-competition paradigm, becomes a response target in a subsequent task. This causes reaction times to this item to slow down relative to a situation where this item did not serve as a competing distractor in one of the preceding tasks (Tipper, 1985; Tipper and Cranston, 1985). A growing number of psychophysical studies have indicated that attentional enhancement and suppression might cooperate in a spatially coordinated way (see section 1.4.2.1), that is, by enhancing the information in the focus of attention and suppressing the information surrounding it.

1.4.2.1 Psychophysical evidence

Several studies provide evidence for an enhancement at the center of attentional focusing encompassed by suppression, whereas no rebound to neutral is demonstrated. While these studies are compatible with a Mexican hat profile in general, they do not provide evidence for such profile in a strict sense. One example of such a study was provided by Steinman and colleagues, who investigated attention effects on the line-motion illusion (Steinman et al., 1995). In this illusion, a cue preceding a bar at a position later occupied by that bar leads to the perception of the bar moving away from the cue. The illusion has been suggested to reflect attentional enhancement, that speeds the processing of the bar at the cued position relative to other positions (Hikosaka et al., 1993; but see Jancke et al., 2004). Steinman and colleagues found that an additional cue could enhance the illusion the closer it was presented to the bar, but would reduce the illusion if presented very distally. This was taken to reflect a central zone of graded enhancement surrounded by an inhibitory zone encircling the rest of the display.

While there have been casual observations suggesting that the spatial profile of attention might be more complex than a simple gradient (Skelton and Eriksen, 1976; Krose and Julesz, 1989; Eriksen et al., 1993), a more systematic investigation of this possibility was pursued only recently. Cave and Zimmerman report that the detection of a probe presented after the presentation of a search array depended on the distance of this probe to the target in the search array (Cave and Zimmerman, 1997). Response times to that probe were fastest, when it appeared at the position formerly occupied by the target. Probing distractor locations next to the target item produced enhanced reaction times relative to farther away distractor locations - a trend that was intensified with practice when subjects performed the task in numerous sessions.

A more systematic exploration of the spatial profile of attention was attempted by Caputo and Guerra, who used a modified search paradigm, with search frames containing two pop-out items, one on a target feature dimension, and one on a non-target dimension (distractor; Caputo and Guerra, 1998). The latter served as an attention capturing probe. By varying the distance of the distractor relative to the target pop-out item, Caputo and Guerra could show that performance (line length discrimination) was worst for the distractor appearing next to the target, but improved for distractor locations farther away from the target. Importantly, no such profile of distractor influence on target discrimination was seen when the target’s location was specified in advance, which presumably rendered the distractor less relevant.

A similar experimental approach has been adopted by Mounts (Mounts, 2000a). He presented circular search arrays containing a salient distractor singleton together with a briefly delayed change of one other search item, rendering it the search target. Close proximity of the target and the distractor singleton degraded target discrimination performance, irrespective of whether the singleton required a response or not. Mounts could demonstrate that this degradation effect gets larger with increasing stimulus onset asynchrony (SOA; from 0, to 40, to 80 ms) between the singleton and the target. He also observed that the effect depends on spatial distance between the singleton and the target, but not on the number of distractors separating the two items. Target detectability was unaffected from this distance, arguing against a sensory explanation of the effect. Applying similar approaches, three additional studies replicated this general pattern (Mounts, 2000b; Turatto and Galfano, 2001; Kristjansson and Nakayama, 2002).

Bahcall and Kowler, pre-cued two positions before presenting an array of stimuli, and subjects had to discriminate the stimuli at both positions (Bahcall and Kowler, 1999). The general observation of several experiments was a decrease in overall performance with decreasing distance between the two targets. Possible alternative explanations in terms of perceptual interactions or a hemispheric lateralization confound could be ruled out. As in the experiments of Mounts, varying the SOA between the cue- and search-frame onset (100, 200, 300 ms) revealed that the effect increases with time, being larger for the two longer SOAs than for the 100 ms SOA. In a similar experimental setup, Mounts and Gavett cued two locations of a circular array, while only one contained the target to be discriminated (Mounts and Gavett, 2004). This replicated the general pattern of stronger suppressive interactions at small distances.

Cutzu and Tsotsos provided further evidence in favor of a Mexican hat profile of attention (Cutzu and Tsotsos, 2003). In their experiments, subjects were required to perform a same-different discrimination at two cued positions in a circular array. Varying the distance between the cued locations revealed a strong detrimental influence on task performance when decreasing the distance. Additionally, they reported that this effect got asymptotic at some distance. In an additional experiment, they varied their paradigm and cued only one position, so that they could estimate the influence of attention on item discrimination on every position of the search array independently. Best performance was seen at the cued location, while performance was worst at the positions directly adjacent to it. With these observations Cutzu and Tsotsos provide a complete description of an attentional Mexican hat profile including the “tip” and an independent estimation of the “brim”. Finally, they demonstrated that their effects were truly attention-driven by showing that an omission of the cues yielded very uniform results over the different distances. Another study using a similar approach replicated this general profile (McCarley et al., 2004).

Muller and co-workers, used a modified flanker paradigm (Eriksen and Hoffman, 1973) to investigate the profile of attention (Muller et al., 2005). Subjects focused on a pre-defined item location, while response-compatible, -incompatible, or neutral flankers were presented at varying distances. Incompatible and neutral flankers yielded the strongest interference at the position next to the focused item. No interference was found for these flanker types at two position away. Incompatible stimuli, however, had a slightly interfering influence at positions further away. The evaluation of these findings requires some commenting: A large performance difference between compatible and neutral flankers suggests a strong processing of the flanker, a small difference argues for a small amount of resources allocated to the flanker. The authors argue that the large difference between compatible and neutral flankers at the position next to the target reflects a residual attentional enhancement near the peak of the attentional profile, while the lacking difference at two positions away from the target signals the presence of an inhibitory surround, that in turn vanishes at positions further away. Thus, this interpretation of the findings is compatible with a Mexican hat profile of attention. Finally, hints at the existence of such center-surround profile for attention to features (orientation space) have been provided recently (Tombu and Tsotsos, 2005).

It is important to acknowledge that all the above reviewed psychophysical demonstrations of a Mexican hat profile do not provide perfect evidence for this notion. For example, studies requiring the identification of a second target at an uncued location may force a strategy that deemphasizes the vicinity of the primary target to start the search for the secondary target from. Studies cuing more than one position may rather stress the ability to split attentional resources, than to focus them. Furthermore, many studies have confounded spatial distance with a presentation in different hemifields. A relative improvement in performance at more distant positions may simply result from the fact that the two hemispheres are partially independent regarding their attentional resources. Although all experiments suffer from some shortcomings, and the psychophysical measures appear to provide an indirect measure of attentional functioning, all studies together provide substantial evidence that attentional resources are not distributed in form of a continuous simple gradient, but rather in the shape of a Mexican hat.

1.4.2.2 Neurophysiological and functional imaging evidence

Neurophysiological support for a center-surround structure of the attentional focus was provided by single-cell recordings in the frontal eye field (FEF) in monkeys (Schall and Hanes, 1993; Schall et al., 1995; Schall et al., 2004). Schall and co-workers recorded from FEF-neurons while monkeys performed a visual search task that required monkeys to make an eye-movement towards a pre-specified target. While the signaling of the cell specified the target location before the actual execution of an eye-movement, Schall and colleagues could demonstrate maximal distractor suppression for potential saccade targets in the direct vicinity of the attended stimulus.

In humans, there have been some physiological indications in favor of a Mexican hat profile, although evidence so far is sparse and not entirely convincing. In one of these studies ERPs were recorded from subjects focusing on one of three different locations (one central, one on the left, one on the right), while locations at varying distance from the attended positions were probed by irrelevant checkerboards presented as an m-sequence of multi-stimulus presentation (Slotnick et al., 2002). The analysis (based on a complex dipole modeling approach) revealed a central zone of enhanced dipole strength at the focus of attention surrounded by a relative reduction of dipole strength, that recovered to neutral further away. Slotnick and co-workers inferred that this center-surround profile arises from the primary visual cortex (V1), because the authors found their probe-paradigm to elicit most robust responses in V1 (Slotnick et al., 2001). Unfortunately, the interpretive power of these results is limited in some critical respects. (1) focusing attention onto a location in one hemifield may not be a good baseline condition for attending the corresponding location in the opposite hemifield (only separated by 5°), as homologue areas in the two hemifields are connected via the corpus callosum (Bosking et al., 2000) and competition between homologous regions may be different from competition between non-homologous areas. (2) Subjects were required to focus their attention for over 50 seconds on the same position (of only three possible locations). It remains unclear whether the reported effects also play a role in the ecologically more relevant case of moment-to-moment re-focusing.

Müller and Kleinschmidt used fMRI to investigate the profile of attention following the presentation of a spatial cue and found a distribution compatible with a Mexican hat profile of attention in the primary visual cortex (Muller and Kleinschmidt, 2004). In this study subjects were cued (symbolic cue at fixation) to attend to one out of four potential target locations in the upper visual field. While either one or more positions were cued at a time, only the data of cuing a single position was analyzed. This position was always the same (position 2, when counted from left to right), so that two position (positions 1 and 3) could be referred to as “near”, whereas one position (position 4) constituted the “far” condition. Positions 1 and 2 were presented in the left hemifield, whereas positions 3 and 4 resided in the right one. The preparatory attention-related BOLD signal was quantified in ROIs determined by passively stimulating the four positions of actual stimulus presentation. While areas V2, V4 and VP displayed strong attentional enhancement for the attended position, some residual enhancement was also evident for the “near” condition that was not present in the “far” ROI. By contrast, area V1 displayed strong signal enhancement for the attended position, and some enhancement for the “far” condition. For the “near” positions, a decrease in signal was found, that is taken to reflect attentional suppression. Although the pattern of results obtained by Müller and Kleinschmidt is in agreement with a Mexican hat profile of the focus of attention, their experimental setup suffers from at least one important limitation. The “far” condition is quantified in a ROI in the hemifield opposite to the attended position, while the “near” condition is always quantified from estimates of the near location in the attended hemifield. This raises the problem of a hemispheric confound analogous to the study by Slotnick and colleagues detailed above. Finally, an fMRI study by Schwartz and colleagues, might bear on the issue, as it demonstrates load dependent attentional suppression, that is strongest in the vicinity of the attentional focus, although the lack of a neutral baseline condition hampers its interpretation (Schwartz et al., 2005).

1.4.2.3 Spatial configuration

This section summarizes the spatial constellation of the studies reporting a Mexican hat distribution (Tab. 1). The study of Cave and Zimmerman was excluded as a result of lacking spatial information (Cave and Zimmerman, 1997). The study of Kristjansson and Nakayama is listed, but the values were generally hard to estimate as a result of pronounced between-subject and between-conditions differences, and will not be considered further in the following section (Kristjansson and Nakayama, 2002). Slotnick and colleagues generally followed a different approach in controlling for eccentricity not by iso-eccentric stimulation but by correcting for cortical magnification (Slotnick et al., 2002). Thus, their results can not be easily fit into the structure of Tab. 1. In their study, the central zone of enhancement subtended approximately 2° (of corresponding visual angle) at a radius of 2.6°, while the surrounding zone of inhibition was approximately 4° wide.

study	radius	sampling	enh.	sup.	asympt.
Bahcall et al. (1999)	4°	15/30/60/120/180°	15°	30°	120°
	2°	15/30/60/120/180°	15°	30°	60-120°
Caputo et al. (1998)	3.3°	51/103/154°	------	51°	103°-154°
Cutzu et al. (2003)	4°	0/30/60/90/120/150/180°	0°	30°	150°-180°
	6°	30/60/90/120/150/180°	------	30°	90°
Kristjansson et al. (2002)[1]	7.5°	0/35/60/85/110/140°	0-35°	35-85°	85-140°
McCarley et al. (2004)	6°	36/72/108/144/180°	------	36°	108°
Mounts et al. (2004)	5.5°	22.5/45/67.5/112.5/180°	------	22.5°	112.5
Mounts (2000a)[2]	4°	0/30/60/90/120/150/180°	0°	30°	90°
Mounts (2000b)	5°	0/45/90/135/180°	0°	45°	135°
Muller et al. (2004)	7.3°	0/45/90°	0°	45°	90°
Muller et al. (2005)	4°	30/60/120/180°	30°	60°	120°
Turatto et al. (2001)	4.5°	0/45/90/135/180°	0°	45°	180°

Tab. 1: *Spatial aspects of the results of different psychophysical investigations.* The first column denotes the respective study (s. above), followed by the radius in which the stimuli were arranged around fixation. In the next column, the different directional angles that were generally sampled by the respective studies are specified. Next, (enh.) denotes the outermost directional angle showing attentional enhancement (if any was reported), (sup.) the directional angle where inhibition was maximal, and (asympt.) the estimated directional angle where the rebound following the inhibitory surround gets asymptotic. Values are mostly eye-balled summarizing different experiments and subjects, depending on the presentation of results, and are to be understood as mere approximations.

[1] The sampled directional distances had to be estimated from a figure and might be imprecise.
[2] The array was not circular and the distances not precisely identical.

Taken together, some general features evolve from this synopsis. First of all, the zone of central enhancement appears to be rather small. Most studies only find it, when the location being measured (0°) is attended, while the study of Bahcall and Kowler finds a small upslope at 15° (4° radius; Bahcall and Kowler, 1999). Apparently broader central enhancement is described in the psychophysical study by Muller and colleagues, at a distance of 30° (4° radius) between the focus of attention and the flanker influencing attentional deployment (Muller et al., 2005), a distance where numerous other studies already report attentional inhibition. The maximal attentional suppression varies between 20 and 60° of directional angle (respective radii 2 - 6°), while the end of this zone of pronounced suppression encircling the focus of attention is estimated very diversely, ranging from 70° to the maximal 180° possible.

1.5 Summary and Hypotheses

As reviewed above, attention has been demonstrated to influence sensory processing both through enhancement and suppression. While both mechanisms appear to reflect contrary operations, reports of a structured cooperation of these two mechanisms have accumulated. A number of models and psychophysical studies have put forward the notion, that the focus of attention might have a “rich” inner structure that resembles the shape of a Mexican hat – a central “tip” of enhanced processing is encompassed by a spatially confined zone of active suppression.

At present, very little direct experimental evidence has been provided in support of this notion. This lack is rather striking outside the area of psychophysical investigations. In fact, a compelling demonstration has only been provided for the frontal eye field of the macaque. Neurophysiological studies directly addressing the question in humans are particularly sparse and – as noted above – respective findings are limited due to several experimental confounds. Specifically, attentional functioning was not investigated under the ecologically relevant case of moment-to-moment refocusing. Furthermore, spatial distance was confounded with presentation in different hemifields, which might lead to misleading results as the two cortical hemispheres have been demonstrated to be partially independent. Psychophysical evidence is more substantial, but of limited significance regarding the underlying neural circuitry. In sum, neurophysiological evidence for the notion of a Mexican hat profile of attention in humans is seriously lacking – a situation this thesis attempts to ameliorate.

To this end, magnetoencephalographic responses were recorded from human observers while they performed a visual search task that was combined with a task-irrelevant probe. The amplitude of the response to that probe was measured under varying distance from the focus of attention, that had to be focused in a trial-by-trial fashion. This bears some important advantages and avoids problems of the aforementioned studies: (1) the trial-by-trial search task requires attentional focusing during its regular functioning mode. (2) the search array was restricted to one visual quadrant, circumventing a potential hemispheric confound. (3) the position of the probe was fixed, whereas the attentional focus was engaged at varying distances from it. Hence, it is possible to extract the passive response to that probe under varying distances from the attentional focus.

The set of experiments reported in this thesis will investigate several features of the spatial profile of attention. To preview, it will be demonstrated that the focus of attention bears a profile resembling the shape of a Mexican hat. Thus, one of the main predictions of the Selective Tuning Model, the model that inspired this work, is supported. In subsequent experiments several further predictions of STM are investigated, including the temporal evolution of the profile as well as the influence of different target-defining features, different levels of task-difficulty, and the presence or absence of distractors in the display.

2 General Methods

This section summarizes basic methodological aspects, that were constant across the different experiments. Details of the paradigm are described in the method-section preceding the results of Experiment 1 (section 3.2), while aspects specific to the subsequent experiments are detailed in the respective method-sections.

2.1 Instrumentation and Acquisition

The MEG and EOG signals were registered simultaneously using a 148-channel Bti Magnes 2500 whole-head magnetometer (Biomagnetic Technologies Inc., San Diego, CA) and a Synamps amplifier (NeuroScan Inc., Herndon, VA). The signals were digitized at a rate of 254 Hz and bandpassed from DC to 50 Hz. Both the horizontal and the vertical EOG were recorded bipolarly, using two electrodes behind the lateral orbital angles for the horizontal EOG, while the vertical EOG was recorded from an electrode below the right orbital limb and one above the right eye. Impedances were kept below 5 kΩ, and an electrode placed at FPZ served as ground. MEG signals were submitted to online and offline noise reduction (Robinson, 1989), and an artifact rejection was applied with peak-to-peak limits of 3 pT for the MEG and 100 µV for the EOG signal. Epochs containing eye-movements, artifacts or incorrect button-presses were excluded from further analysis. To co-register anatomical and functional data, anatomical landmarks (left and right preauricular points, nasion) were digitized using a Polhemus 3Space Fastrak system (Polhemus Inc., Colchester, VT). These landmarks were then brought into reference with magnetic marker fields generated by five spatially distributed coils attached to the subjects head.

2.2 Analysis

2.2.1 Experimental design

The general paradigm consisted of the presentation of nine Cs on an invisible quarter-circle in the lower right quadrant (see Fig. 4). While eight of the Cs were uniformly colored, one was special on a feature dimension (either brighter or of a different color in the respective experiments), rendering it the target. At the middle position, a task-irrelevant probe was presented on half of the trials, while subjects focused their attention on positions with varying distance from this probe-position (ranging from the same position to maximally 4 positions away - probe-distance (PD0 through PD4).

2.2.2 Data analysis

Average ERMF waveforms were computed for each subject, time-locked to probe onset, relative to a 250-ms pre-stimulus baseline interval. Separate averages were computed for each probe-distance condition (PD0 through PD4) for frames with (frame-plus-probe trials - FP) and without a probe (frame-only trials - FO). To isolate the ERMF response elicited by the probe (henceforth referred to as *probe–related response*) from the overlapping response elicited by the search array, FO waveforms were subtracted from FP waveforms (FP-minus-FO difference) of trials with identical target positions. This difference, thus, reflects the differential response to the probe under varying distances from the focus of attention, with search array differences subtracted away. The size of the probe-related response was quantified in each observer as the mean amplitude of the ERMF difference between the efflux- and influx-maximum, relative to the baseline. The choice of relevant sensors was restricted to the posterior half of the sensor array, which usually comprised the globally maximal responses. Sensor sites showing the efflux- and influx-maximum varied between subjects, but were identical for all probe-distances for a given subject (see section 2.2.3). In Experiment 1, the time-range of data analysis was determined by the maximum probe-related response of the different probe-distances. To this end, a “sliding” one-way rANOVA with a factor of probe-target distance (PD0 through PD4) was computed for subsequent time samples from 100 to 200 ms, resulting in a time-range from 130 to 150 ms after the onset of the probe. This time-range was adopted in Experiment 2, as it was designed as a direct control-experiment to Experiment 1. In all subsequent experiments the time-range was determined as the window within 100 and 200 ms post-probe, within which the difference between PD1 and PD2 was significant. In the Experiments 3, 4, and 5, this time-window was determined for the average of the different experimental conditions, whereas in Experiment 6 only the data from the 250 ms SOA was used. This resulted in analysis time-windows of 124 to 132 ms for Experiment 3, 116 to 132 for Experiment 4, 128 to 148 ms for Experiment 5, and 112 to 136 ms for Experiment 6. The meta-study detailed in section 9 was analyzed between 120 to 152 ms. Statistical testing was generally conducted using repeated measures analyses of variances (rANOVA), with a correction of degrees of freedom for non-sphericity (Greenhouse-Geisser algorithm) where necessary.

2.2.3 Analysis of the event-related magnetic field response

As detailed in the preceding section, the analyses in all experiments relied on the subtraction of individual efflux- and influx-components related to the processing of the probe (FP-minus-FO difference). Fig. 3a illustrates this measure at the example of the average magnetic field distribution over all subjects from Experiment 1, averaged in a window between 130 and 150 ms after the presentation of the probe and across all probe-distances conditions. The orange arrow depicts the approximate localization of the current origin underlying this simply structured distribution of magnetic efflux (red) and influx (blue). Green arrows symbolize the actual magnetic field surrounding the neuronal source, while the displayed color-scale distribution represents the part of the signal detected by the sensors. This illustrates, that magnetic efflux and influx represent the same underlying source. As the specific localization and orientation of a source with respect to the sensor array might favor the detection of one of the two components, the difference between the two was chosen as the basic measure (efflux-minus-influx), which can be understood as an average of the two components. Fig. 3b illustrates the high degree of inter-individual variability of this field distribution for four individual subjects. For this reason, the analysis was based on in the subjects' individual sensor configuration .

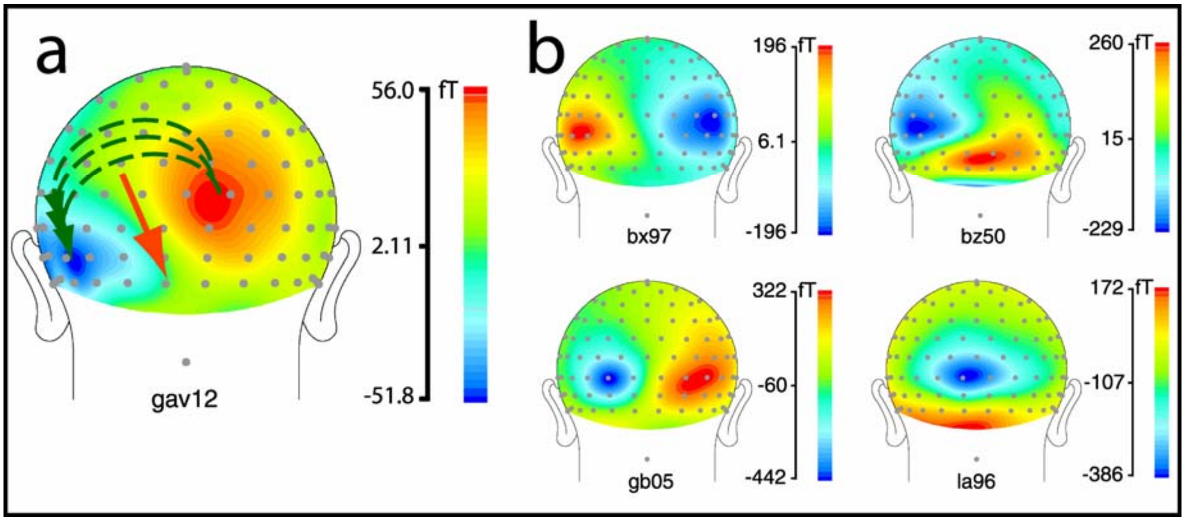

Fig. 3: *Average magnetic field distributions from Experiment 1.* Average field distribution from 130 to 150 ms post-probe of the probe-related response averaged over all probe- distances. **(a)** Across-subject average of all 12 subjects. The orange arrow symbolizes the approximate current source, while the green broken arrows depict the magnetic field. The blue-to-red scale represents the magnetic efflux (red) and influx (blue) that is detected by the sensors (gray dots). **(b)** Corresponding field distributions of 4 individual subjects.

2.2.4 Current source localization

For source localization, current source density estimates (SDEs) were computed using distributed current source estimates as implemented in the Curry 4.0 neuroimaging software. To maximize the signal-to-noise ratio, estimates were computed based on data that were averaged across all observers. This may blur the SDE distributions somewhat, but the goal of the localization was to assess the general location of the activity, and not to provide fine discriminations between nearby brain regions. Grand-average data were analyzed using the MNI brain

(Montreal Neurological Institute; average of 152 T1-weighted stereotaxic volumes from the ICBM project). To approach maximum precision in source analysis, a 3-D reconstruction of the head, cerebrospinal fluid space, and cortical surface was created using the boundary element method (Hämäläinen and Sarvas, 1989). A model of distributed sources was then estimated by means of the minimum norm least square method (Hamalainen and Ilmoniemi, 1994; Fuchs et al., 1999), yielding a model of the distribution of currents over the cortical surface.

The following sections will report the different experiments of this thesis separately. Specific introductions to the individual experiments will be given, followed by short sections dealing with methodological details specific for the particular experiment. The description of the results will be followed by a short discussion.

3 Experiment 1

3.1 Introduction

In order to investigate the spatial profile of attention, a passive probe-paradigm was used, that measures the response to a task-irrelevant probe stimulus as a function of its distance from the focus of attention. The experiment displays a number of design advantages and avoids several confounds in comparison to earlier studies: (1) The use of a task-irrelevant item solely probes cortical responsiveness without interfering greatly with the task. Thus, opposed to psychophysical investigations, no paradigmatical detours had to be taken to derive estimates of the attentional distribution. (2) Previous probe- or cuing-studies varied the location of the probe relative to a spatially fixed focus of attention – a situation that introduces unnecessary stimulation differences (Slotnick et al., 2002; Muller and Kleinschmidt, 2004; Muller et al., 2005). As sustained and transient attention are not equivalent (e.g., Ling and Carrasco, 2006), it is difficult to estimate the degree to which these findings bear on more natural conditions of a rapidly changing spatial focus. Here, the position of the target varied on a trial-by-trial basis, unpredictable for the subjects, whereas the position of the probe stimulus was fix, circumventing this shortcoming. (3) The present experiments avoid a confound of previous studies addressing the spatial distribution of attention. Specifically, several studies confound spatial distance with the presentation in different visual hemifields (see section 1.4.2; e.g., Caputo and Guerra, 1998; Slotnick et al., 2002; Muller and Kleinschmidt, 2004), which is problematic insofar, as the two cortical hemispheres appear to possess partly independent resources (Luck et al., 1989; Cavanagh and Alvarez, 2005). In this study, the search array was confined to a single quadrant, which avoids confounding distance with a presentation in different hemifields (both horizontal and vertical).

3.2 Methods

3.2.1 Paradigm and stimuli

Stimuli and task of Experiment 1 are illustrated in Fig. 4. While fixating the center of the screen, observers searched for a red target C (luminance: 38 cd/m^2) among eight blue distractor Cs (luminance: 18 cd/m^2) presented at an isoeccentric distance from fixation (8° of corresponding visual angle) in the lower right quadrant (Fig. 4a). The background was homogenously colored in gray (luminance: 12 cd/m^2). Each search frame was presented for 700 ms, followed by an interstimulus interval (ISI) of 650-850 ms (boxcar distribution). Spacing between Cs was constant (1.35°), and each C subtended 0.8° of visual angle (see also Fig. 14b). The gap of each C varied randomly between left and right, and observers indicated the position of the gap in the target C by pressing one of two buttons with the right hand (index finger for gap on the left, middle finger for gap on the right). The distractor Cs were randomly displayed in one of four possible gap-orientations (left, right, up, down). The target C appeared randomly at one of the nine possible stimulus locations (illustrated in Fig. 4c), thus, forcing subjects to change the spatial focus of attention from trial to trial.

On 50% of the trials, a white ring (the probe stimulus) was flashed around the central C for 50 ms, starting 250 ms after the onset of the search frame on frame-plus-probe trials (FP). In the other 50% of trials, no probe was presented (frame-only trials, FO, Fig. 4b). Because the probe position was constant and the target position varied, there were five target-to-probe distances, ranging from probe-distance 0 (PD0; target at probed location) through probe-distance 4 (PD4; target four items away from probe, see Fig. 4c). Each experimental session was separated into 10 runs lasting 6 minutes. During each run, 90 FP and 90 FO trials were presented, with 10 trials per probe-distance condition at each position, amounting to a total of 100 FP and FO trials for each position throughout the complete session.

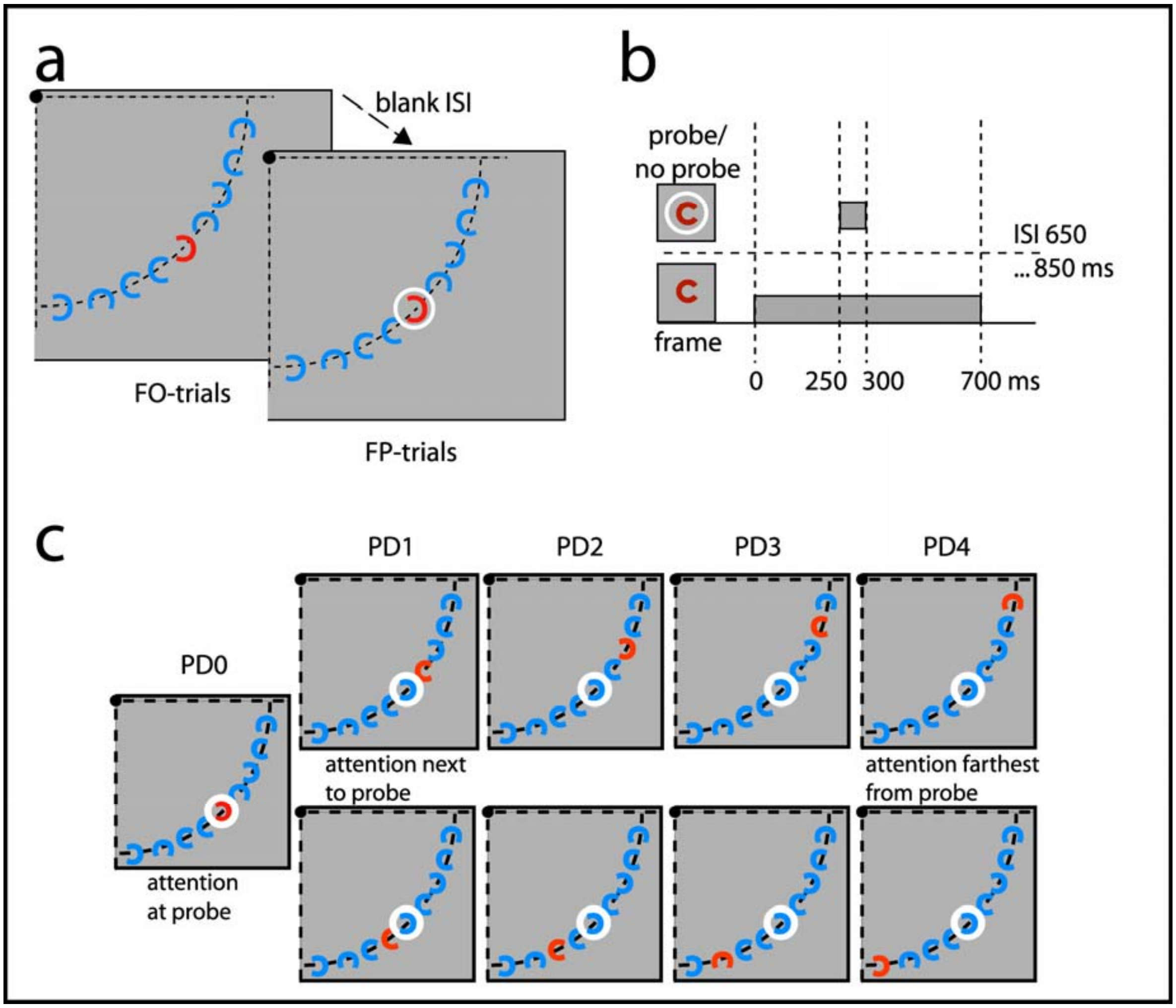

Fig. 4: *Illustration of the paradigm.* **(a)** 9 Cs were presented at an isoeccentric distance from fixation (black dashed line; this line only serves illustration and was not present in the display, which is also the case for all following illustrations). There was always one red C present, that subjects had to discriminate (gap left or right). Its position varied randomly between the trials. Trials were separated by a blank presentation varying in duration between 650 and 850 ms. **(b)** On half of the trials, a probe stimulus, that was irrelevant for the task, was flashed for 50 ms around the central C, starting 250 ms after the onset of the search array (FP trials). On the other half of the trials no probe was presented (FO trials). **(c)** The target C could appear in nine possible locations, at 5 different distances with respect to the fixed probe location (PD0 through PD4).

3.2.2 Subjects and analysis

12 observers (10 females, mean age: 23.4) took part in Experiment 1. All observers were neurologically normal students of the OvG-University Magdeburg,

gave informed consent, and were paid for participation. All experiments were approved by the ethics committee of the OvG-University Magdeburg.

To isolate the event-related magnetic field (ERMF) response elicited by the probe from ERMF activity reflecting target processing, the ERMF response triggered by FO trials was subtracted from the ERMF response triggered by FP trials. This was done for targets at all nine positions separately (positions 1 through 9). As already outlined above, this subtraction leaves (under ideal conditions) only the pure probe-elicited activity as a function of distance from the focus of attention. Such approach, thus, eliminates differences due to the mere change of sensory stimulation between trials (Luck et al., 1993; Luck and Hillyard, 1995; Vogel et al., 1998), as well as activity reflecting attentional focusing onto a particular target item. For most of the analysis the data was collapsed over the two directions away from the center stimulus, resulting in only 5 probe-distances (PD0 through PD4).

If not specifically mentioned, all parameters concerning stimulation, paradigm and procedure in the following experiments were the same as in Experiment 1.

3.3 Results

3.3.1 Behavioral Performance

To evaluate observers' behavioral performance, response times (RT, s. Fig. 5) and response accuracy were subjected to two-way rANOVAs with factors target location (position 1 through 9) and probe presence (present vs. absent). Generally, observers' responses to the targets were slightly faster for no-probe trials (mean: 539 ms) than for probe trials (mean: 543 ms), as reflected by a significant main effect of probe presence (F[1,11]=6.8, p=0.025). This presumably reflects backward masking of the target by the probe. There was also a significant main effect of target location on RT (F[3.9,43.2]=6.0, p<0.001) and a marginally significant interaction between target location and probe presence (F[4.4,48.2]=2.2, p=0.079). Inspecting Fig. 5, two causes are responsible for the main effect of target position. On the one hand, subjects responded slower to targets at the probe-position, which was confirmed by a separate one-way rANOVA comparing the RT at the probe-position with the average RT at the other positions (F[1,11]=20.4, p=0.001). On the other hand, responses to targets above this position (i.e., towards the horizontal meridian) were given faster than to those below it (i.e., towards the vertical meridian), which is supported by a two-way rANOVA with factors probe-distance (PD1 through PD4) and direction from the probe-position (towards the horizontal meridian vs. towards the vertical meridian). This analysis yielded a significant main-effect of direction from the probe-position (F[1,11]=60.5, p<0.001). The marginally significant interaction between the factors target location for all nine positions and probe presence in the first analysis is based upon the fact that the probe did not influence RTs at all probe distances to the same degree. Separate one-way rANOVAs with factor probe presence for the nine target locations revealed that the subjects’ response times were significantly enhanced only at position 3 (F[1,11]=23.6, p=0.001), position 5 (F[1,11]=8.9, p=0.012), and position 6 (F[1,11]=7.4, p=0.02). Positions 3, 8, and 9 were also influenced by the probe, but statistical analyses did not validate these effects. Subjects produced generally low error-rates (mean: 1.8%). Conducting the same analyses of variance for discrimination accuracy yielded no statistically significant effects.

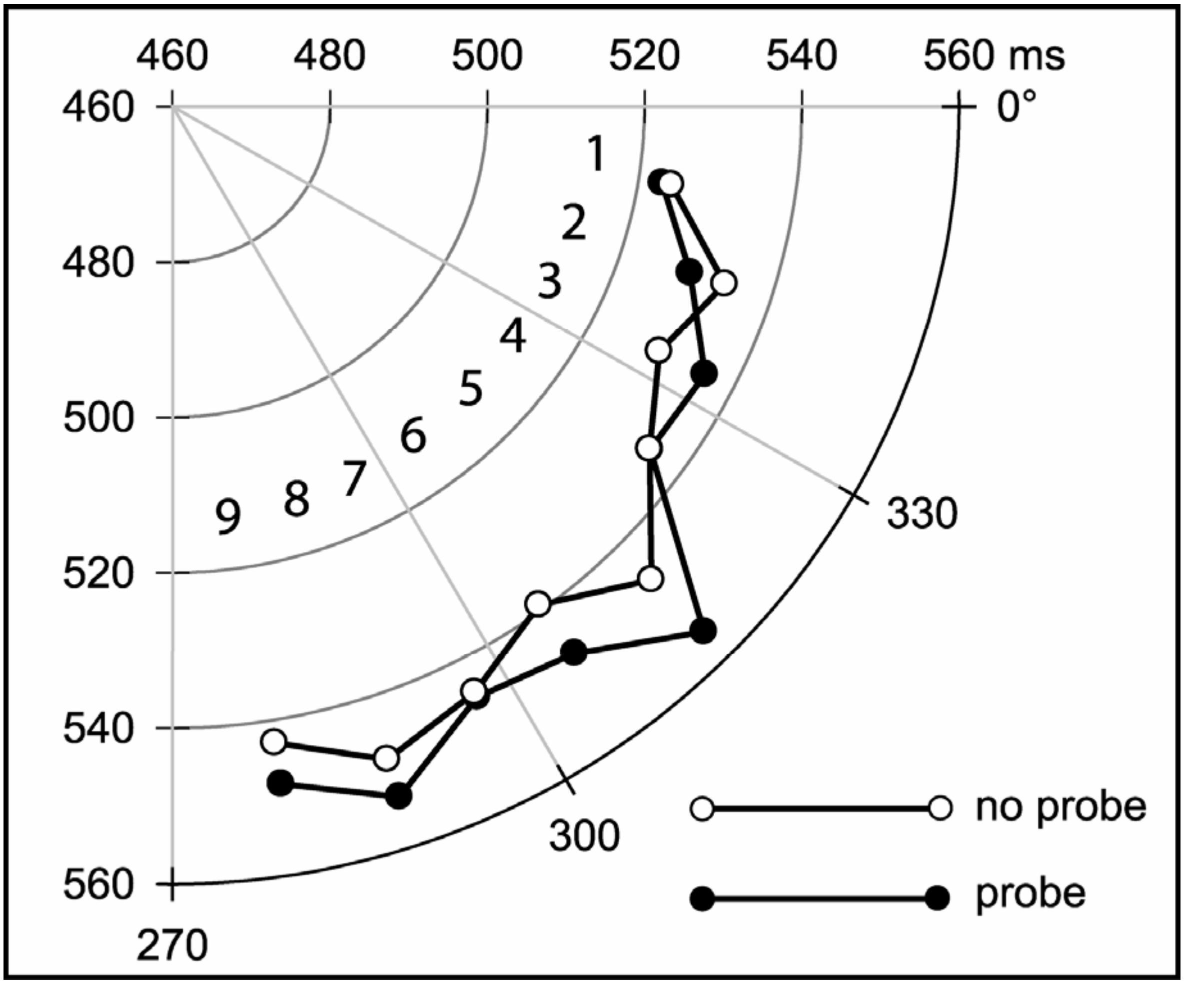

Fig. 5: *Response time pattern.* For each of the nine positions, two RT-values are depicted. FO trials (no probe) are represented by open circles, while FP trials (probe) are represented by filled ones. Numbers 1 through 9 denote the target position, depicted at their respective directional angle.

3.3.2 Magnetoencephalographic results

Fig. 6a displays the ERMF distributions of the FP-minus-FO difference between 130 and 150 ms for each of the nine target locations (averaged across observers). The corresponding difference waveforms taken from sensors showing maximum influx and efflux effects of each observer are illustrated in Fig. 6c. Measures for each target-to-probe distance were collapsed across mirror-symmetrical positions. As visible from the ERMF distributions and waveforms, the probe-related response was largest when attention was focused on the probe’s location (PD0, position 5), and smallest when attention was adjacent to the probe (PD1, positions 4 and 6).

Target-to-probe distances beyond PD1 produced intermediate responses (PD2 through PD4, positions 3 and 7, 2 and 8, 1 and 9). Taken together, the response in the displayed time-window was generally maximal around 140 ms, a time-range that corresponds to the N1 component elicited by the probe. During this time-range, the response differences were also largest between the different probe-distances. When inspecting the waveforms in Fig. 6c, it appears that there is also a small delay in latency for PD1 relative to PD0 and the other probe-distance conditions. However, a statistical comparison of the peak-latency for the PD0 and the PD1 condition indicated that this difference was not statistically significant (F[1,11]=2.5, p=0.14).

The bar graph in Fig. 6b provides a quantification of the average ERMF effect between 130 and 150 ms. Shown are average differences between each individual observers' efflux and influx maximum over the occipital cortex. Again, attending to the location adjacent to the probe's location (PD1) led to a smaller probe response than attending to the probe's location (PD0) or attending to locations farther away from the probe (PD2 through PD4). For a statistical validation of this profile, the magnitude of the magnetic field response between 130 and 150 ms was subjected to a one-way repeated measures analysis of variance (rANOVA) with a factor of target-to-probe distance (5 levels: PD0 through PD4). This analysis revealed a significant effect of target-to-probe distance (F[2.3,25.5]=4.08, p=0.021). Subsequent pair-wise rANOVAs revealed the following pattern of response amplitudes: PD0 larger PD1, and PD1 smaller PD2 (PD0 vs. PD1: F[1,11]=8.9, p<0.05; PD1 vs. PD2: F[1,11]=14.4, p<0.01), which indicates that the probe-related response was significantly smaller when the probe was at the location adjacent to the target location (100fT) than when it was at the target location (173fT) or two locations away (151fT) from the target. The fact that the cortical responsivity at PD1 is significantly smaller relative to farther away locations indicates that the inhibition surrounding the attended location is confined to a narrow region. This is particularly obvious from Fig. 6b which shows that the pattern of cortical responsivity adjacent to the target location is rather symmetrical, and thus, consistent with a narrow ring of suppression. This symmetry of surround attenuation was confirmed by a two-way rANOVA with factors probe-distance (PD1 vs. PD2) and direction from the probe position (towards the horizontal meridian vs. towards the vertical meridian), which yielded neither a significant main-effect of direction from the probe-position (F[1,11]=0.1, p=0.926) nor a significant interaction of this factor with probe-distance (F[1,11]=0.3, p=0.598).

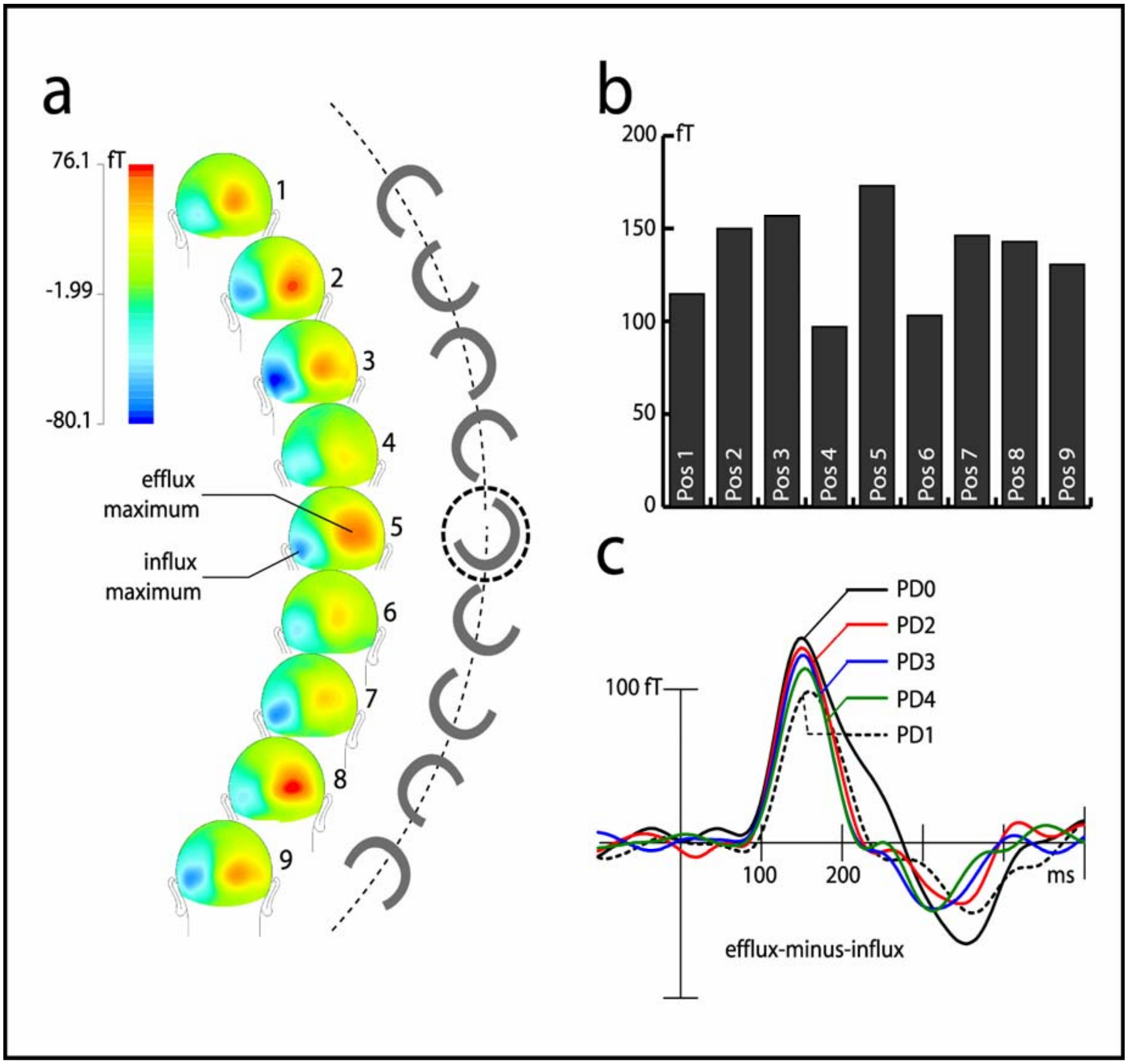

Fig. 6 (preceding page): *ERMF results of Experiment 1*. **(a)** Mean ERMF distribution of the probe-related response (FP-minus-FO difference from 130 to 150 ms, averaged across observers). Attending to the C next to the probe (positions 4 and 6) reveals a reduced response magnitude in comparison to both the probe-position (position 5) as well as the positions farther away from the probe (positions 1-3, 7-9). **(b)** Mean size of the probe-related response between 130 and 150 ms. The size of the effect represents the average of the ERMF difference between the observers' individual field maxima and minima. **(c)** Time course of the probe-related ERMF response (FP-minus-FO) for each probe-distance collapsed across corresponding conditions towards the horizontal and vertical meridian (positions 4 and 6, 3 and 7, etc.). Shown is the time-course of the ERMF-difference between corresponding efflux- and influx-field maxima (efflux-minus-influx, see panel (a)).

3.3.3 Source reconstruction

This section aims to identify the neuroanatomical current origin of the inhibitory activity surrounding the target as well as that of the activity enhancement at the target's location. It should be noted that it is difficult to separate suppressive and excitatory activity with confidence. This is because the attenuation surrounding the target can be measured only as a difference between the response at PD1 relative to other target-to-probe distances. Excitatory or inhibitory effects at these other distances may thus confound the activity estimate at PD1. Nevertheless, given the narrow extension of the suppressive zone, a sufficiently "neutral" measure of the inhibitory effect can be obtained by subtracting the probe-related response at PD4 from the probe-related response at PD1. Similarly, a reasonably representative measure of the excitatory effect can be obtained by comparing the PD0 versus PD4.

Fig. 7 shows the current source density estimates (SDE) for the excitatory effect (Fig. 7a) and the inhibitory effect (Fig. 7b) based on the average ERMF between 130 and 150 ms. The excitatory effect is larger in magnitude than the inhibitory effect. Both effects show a broad distribution over the occipital lobe with a somewhat greater magnitude over the left (contralateral) hemisphere. This broad distribution is consistent with previous studies showing attention effects across a wide swath of visual cortex (Moran and Desimone, 1985; Luck et al., 1997a; Tootell et al., 1998; Kastner et al., 1999). Although the presented SDEs do not have the resolution to permit a more detailed localization, it is clear that the attention-based surround suppression reaches its maximum in early visual cortex (see also section 9).

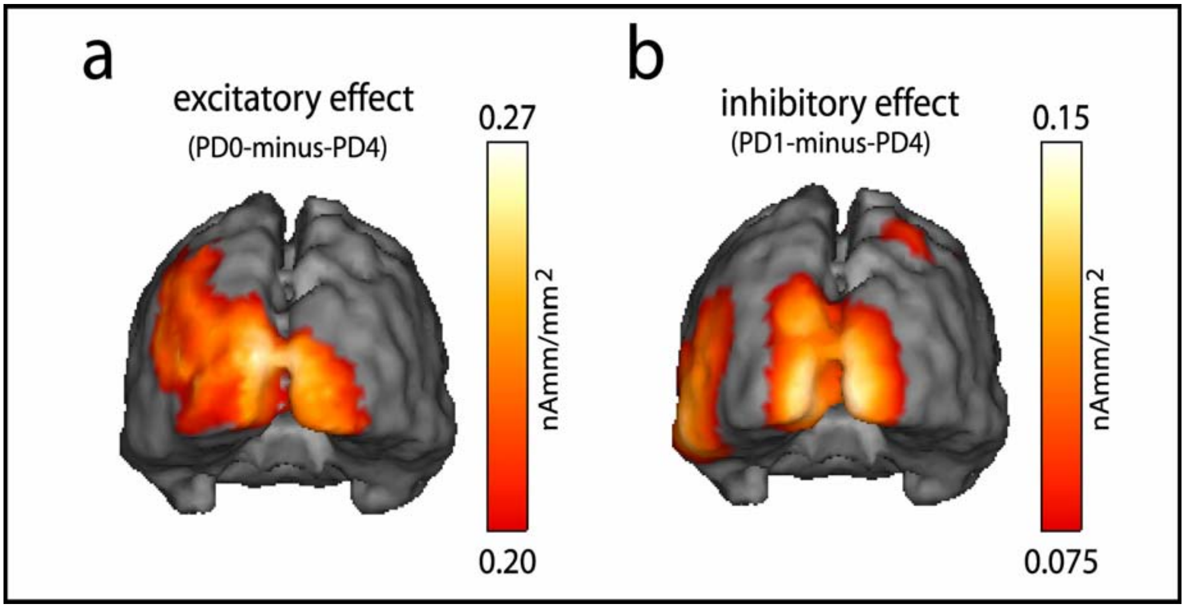

Fig. 7: *Distributed source analysis*. **(a)** Source density estimate (SDE) for the average attentional enhancement effect between 130 and 150 ms overlaid on a gray-matter surface segmentation of the MNI-brain (rear view). The SDE was computed from the difference between the probe-related effect (FP-minus-FO) of PD0 and PD4 trials. **(b)** SDE distribution reflecting the average surround attenuation between 130 and 150 ms. This SDE was computed from the difference between the probe-related effect of PD1 and PD4 trials.

3.3.4 Electrooculographic results

Finally, an analysis of the EOG signal was conducted to rule out the (admittedly improbable) possibility, that differences in eye-movement contributed to the pattern of results. This possibility seems very improbable, in view of the rather strict artifact-rejection the raw data were subjected to before analysis. Even trials containing comparably small eye-movements would have been rejected. Nevertheless, to assess the influence of small eye movements remaining after artifact rejection the EOG was quantified separately for the horizontal and the vertical EOG in a time-window between 100 and 200 ms after the onset of the probe (Fig. 8). An inspection of Fig. 8 shows that EOG activity remaining after artifact rejection in this time-window was very weak (vertical EOG: -0.27 µV; horizontal EOG: 0.36 µV). In comparison to previous demonstrations, that eye-movements of 1° roughly elicit a 16 µV EOG response (Hillyard and Galambos, 1970; Lins et al., 1993), the fixation accuracy until at least 200 ms after the presentation of the probe (well beyond the time-window relevant for the ERMF effects) was very high. Furthermore, a one-way rANOVA comparing the magnitude of the EOG effects across different probe distances (factor probe-distance (PD0 through PD4)) yielded no significant effect, neither for the vertical (F[2.1,23.4]=0.4, p=0.689) nor for the horizontal EOG (F[2,21.7]=0.3, p=0.775). Altogether, it is safe to rule out eye-movements as a source contributing to the reported results.

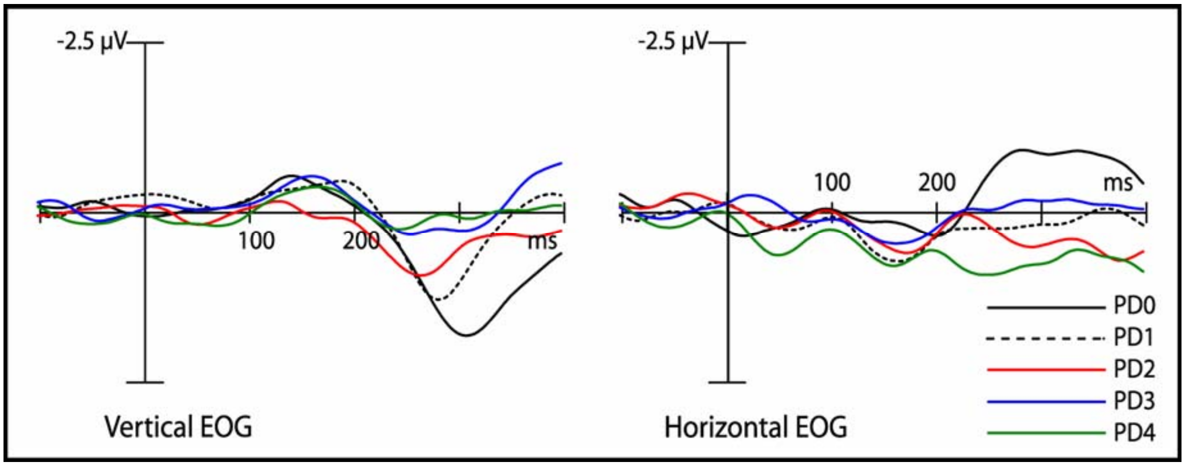

Fig. 8: *EOG results*. The results are displayed relative to the onset of the probe. During the first 200 ms there is generally little activity. Starting around 250 ms after the onset of the probe, there is some activity in both measures, especially for PD0.

3.4 Discussion

This experiment was conducted to probe into the spatial distribution of the focus of attention during visual search. Specifically, it was sought to provide neurophysiological evidence in favor of a complex center-surround structure (Mexican-hat profile) as opposed to the prevailing view that the focus of visual spatial attention represents a simple monotonic gradient. To this end, the cortical responsivity was passively probed while subjects performed a visual search task.

The results provide strong evidence in favor of a complex center-surround structure with a center enhancement surrounded by a narrow zone of inhibition. That is, a maximal probe response was found when the position of probe-presentation was the one being attended (PD0). The probe response next to the attended location was significantly reduced not only relative to PD0, but also to locations farther away, suggesting a narrow zone of true inhibition encircling the focus of attention, that levels off at more distant positions. As already detailed in the introduction, the observed change of the probe response reflects attentional processes, because confounding effects due to stimulus differences at different target locations can be ruled out (the FP-minus-FO difference eliminates such remaining after artifact rejection). Nevertheless, it is possible that a more subtle sensory confound may have caused the observed center-surround profile. Experiment 2 addresses this possibility.

Our observation that the “spotlight of attention” has a Mexican-hat profile adds new evidence to psychophysical findings, that already provided indications of this pattern (e.g., Bahcall and Kowler, 1999; Mounts, 2000a; Cutzu and Tsotsos, 2003; see section 1.4.2.1). It is important to acknowledge that the present experimental approach permits a more direct assessment of the spatial distribution of attention because it avoids a number of problems that psychophysical studies are typically faced with. Specifically, the present experimental approach investigates the distribution of attention during its regular functioning, and the measure (ERMF response) that probes the spatial profile is independent of performance. Most approaches in previous psychophysical studies have relied on probing the attentional distribution either by cuing (be it one position or more; e.g., Bahcall and Kowler, 1999; Cutzu and Tsotsos, 2003), or by the concurrent presentation of an irrelevant but salient distractor capturing attention (e.g., Caputo and Guerra, 1998; Mounts, 2000a). Unfortunately, these approaches may have forced processing strategies more complex than simple spatial focusing, like splitting the focus of attention or shifting attention from a salient item to the target. Furthermore, cuing (be it by a classical cue or through attentional capture of an irrelevant but salient singleton) always focuses attention prior (or simultaneously) to the actual task onto a position not identical with the position of the actual target.

The present current source localization results reveal that the surround attenuation arises in early to intermediate levels of the visual cortex, with a maximum effect in early visual cortex, presumably in V1. This is consistent with numerous demonstrations of attention effects in early and intermediate visual cortex, both in monkeys (e.g., Motter, 1993; Luck et al., 1997a), and in human observers (e.g., Tootell et al., 1998; Pinsk et al., 2004). In general, it appears that this modulation reflects recurrent activations in these early areas (Lamme and Roelfsema, 2000; Mehta et al., 2000a).

The distributional pattern observed in Experiment 1 is consistent with computational accounts, and in particular with the STM. As outlined in the introduction, STM predicts a downward propagating suppressive zone that increases with progressively lower hierarchical levels. Consequently, the number of neurons contained in the inhibitory surround increases with every layer on this downward traversal, which gives rise to an increment of the corresponding ERMF response (Tsotsos et al., 1995; Tsotsos, 2005). In sum, STM directly predicts the present observation that the current source activity reflecting the suppressive surround is largest at the lowest hierarchical levels of the processing hierarchy.

Considering the behavioral data, the lack of an effect of the probe on the RT for targets at position 4 indicates that the probe interferes less with the response when it is presented directly above the target position, which might be taken to argue in favor of an inhibitory zone surrounding the target. This is less obvious below the probe position (position 6), where probe-presence robustly influences the reaction. This effect completely disappears one position further away (position 7). Although one can only speculate here, this pattern may relate to the fact, that attentional (and perceptual) resolution appears to be finer towards the horizontal meridian (Carrasco et al., 2004). A possible inhibitory surround as reflected by the behavioral data might be less clear-cut towards the vertical meridian, so that position 6 still lies in the zone of central enhancement and position 7 reflects the inhibitory surround below the middle position. Importantly, the probe appears to gain influence again at positions farther away, probably representing the leveling-off of the suppression of the immediate surround. Taken together, the RT-data might be taken to suggest a Mexican hat profile, although distorted when compared to the ERMF data. Of course, RTs may not mirror the profile found in the ERMF response. In fact, it still takes some 300 ms until the manual response is given, and thus a vast number of neural processes take place in between the two events.

In summary, both the psychophysical and the neurophysiological data speak in favor of an attentional Mexican hat distribution, albeit the ERMF data provide the more reliable results. The behavioral results also argue against possible alternative explanations of the obtained Mexican hat profile. Specifically, response times do not differ vigorously between FO and FP trials (4 ms discrepancy), and accuracy was not affected at all. While the influence of the probe on RT was slightly different for different distances from the target (s. above), this is still in line with the assumption, that the FP-minus-FO difference yields a signal virtually exclusively representing the probe-related response. Finally, eye-movements could be ruled out as a significant contributor to the pattern of results. Notwithstanding this convincing evidence, another possible confound appears feasible, addressed in the next experiment.

4 Experiment 2

4.1 Introduction

Experiment 2 was designed to rule out a potential sensory confound in the first experiment, that may not have been fully eliminated by computing the difference FP-minus-FO. Specifically, there may have been secondary interaction phenomena between the target and the probe, that mimic a Mexican hat profile independent of attention. The focus of attention was defined as the red pop-out item in an array of homogeneous blue items. Pop-out items such as these are known to elicit enhanced bottom-up sensory processing (Schein and Desimone, 1990; Knierim and Van Essen, 1992; Beck and Kastner, 2005), with the possible consequence of a stronger subsequent refractory state. If this refractoriness results in a spatially extended sink of sensory responsiveness, and attention produces a simple but narrower gradient of enhancement, a Mexican hat distribution of cortical responsivity may arise (s. Fig. 9). Also, the position of the pop-out location might still be enhanced or neutral when the probe is presented, but its immediate surround might have been inhibited through lateral interactions (not depicted; see e.g., Braun and Julesz, 1998). Although the difference logic of Experiment 1 (FP-minus-FO) makes it very unlikely that the observed center-surround pattern was entirely caused by sensory-sensory interactions, it is possible that the pattern was somewhat distorted by these interactions. Experiment 2 was conducted to estimate the sensory-sensory interactions independent of attention and subtract them away from the attention effect. To this end, a rapid serial visual presentation (RSVP) task was added above fixation, that had to be attended in half of the trials, while the original task was performed in the other half of trials. Thus, conditions of identical sensory stimulation could be compared under varying attentional deployment, allowing an estimation of sensory-sensory interactions in the absence of attention, and to directly compare it with the results obtained under attentive processing. Moreover, the RSVP task should provide a reasonable baseline condition to further evaluate enhancement or suppression effects when attention is focused onto the search array.

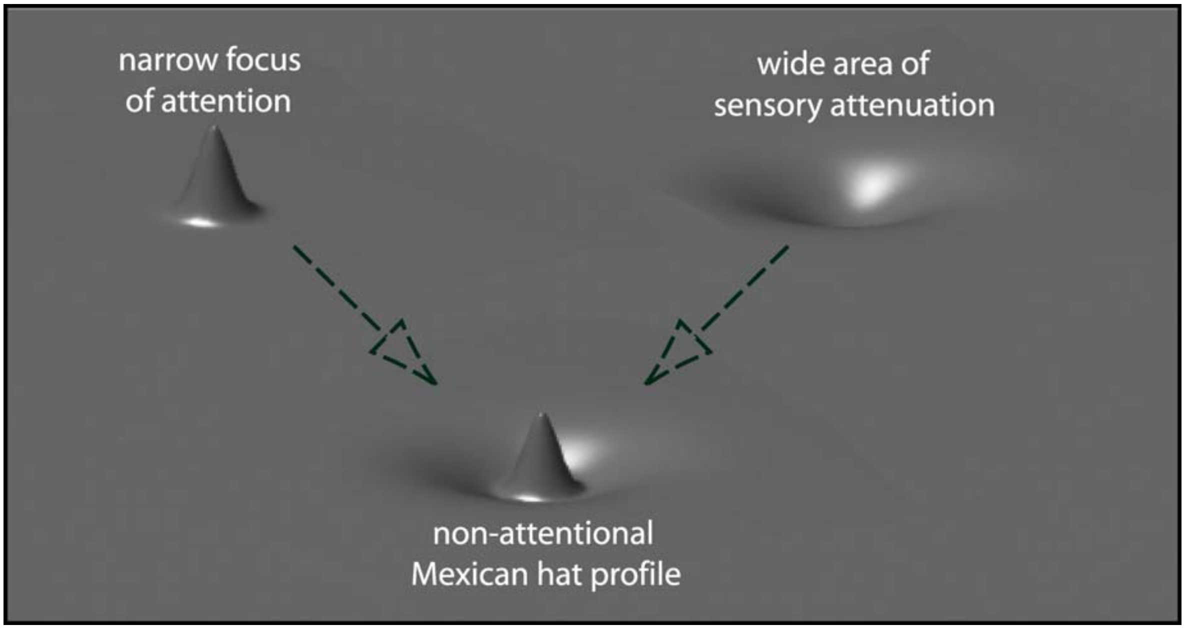

Fig. 9: *Illustration of a potential sensory confound.* A Mexican hat profile may arise, when a narrow focus of attentional enhancement combines with a wider area of sensory attenuation.

4.2 Methods

Experiment 2 contained two conditions (tested in separate trial blocks) that were variants of the procedure used in the first experiment. In both types of trial blocks, a rapid serial visual presentation (RSVP) stream of small characters at fixation was presented concurrently with the original search frames and probe stimuli (Fig. 10a). In the *attend-RSVP* blocks, observers had to perform a demanding target detection task while the search frames were irrelevant. This condition was designed to withdraw attention from the search frames, making it possible to evaluate the pure sensory effects of varying the target-to-probe distance. The letters were randomly chosen from a pool containing the uppercase letters A, E, I, K, L, N, T, V, Y, X (all subtending approximately 0.8°, presented 0.5° above the fixation spot). Beginning 100 ms before the onset of each search array, 10 letters were presented for 34 ms each, separated by an ISI of 50 ms (Fig. 10b). For each of the 10 letter presentations, all letters except of the X appeared with a probability of 10.6%, while the X appeared in 4.6% of the cases. The subjects' task was to indicate at the end of each stream, whether an X had been present (index finger) or not (middle finger), which was prompted by the presentation of a question mark after each RSVP stream. Thus, subjects had to monitor the RSVP stream during the whole duration of the search arrays.

In the *attend-search* trial blocks, observers ignored the RSVP stream and performed the search task as in Experiment 1. The *attend-search* block and the *attend-RSVP* block each consisted of 5 runs, and half of the subjects started with the *attend-search* condition while the other half began with the *attend-RSVP* condition to avoid potential effects of presentation order. The analysis was then conducted as in Experiment 1 for both conditions. If the results from Experiment 1 were caused by attention, the effects of probe-distance would be small or nonexistent in the attend-RSVP condition, whereas the attend-search condition should replicate the pattern observed in Experiment 1. Eight observers (mean age: 21.9) took part in Experiment 2. A total of 100 trials was collected for FO- and FP-trials at each target location, halved into the *attend-search* and the *attend-RSVP* condition.

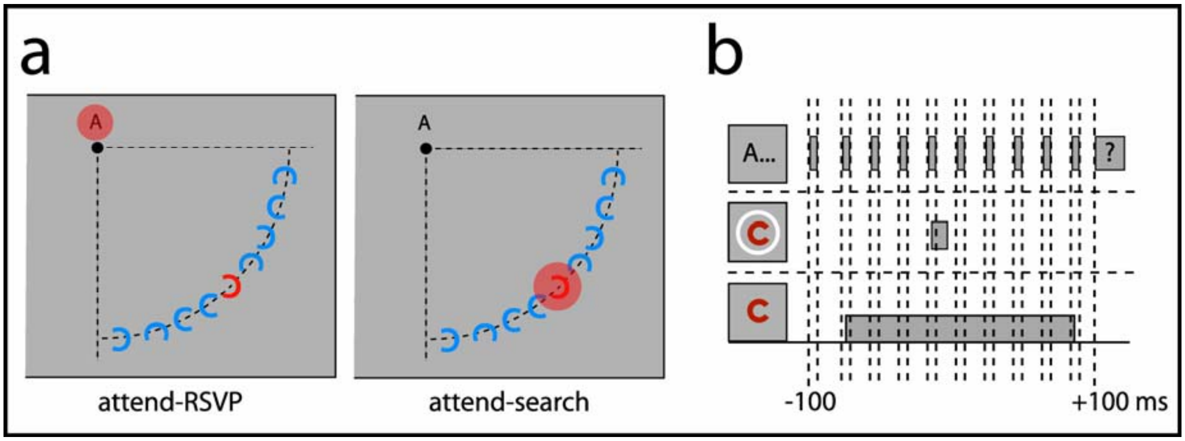

Fig. 10: *Paradigm of Experiment 2.* **(a)** In addition to the search array from Experiment 1, an RSVP stream was presented at fixation. While subjects attended to this stream in half of the trial blocks (as indicated by the red shading; attend-RSVP), they performed the original task in the other half of the blocks (attend-search). **(b)** illustrates the respective timing of the different stimuli. Each trial consisted of the search array (with or without a probe-stimulus after 250 ms) plus 10 letters. The letters were all presented for 34 ms, interleaved by 50 ms, starting 100 ms before the onset of the search array. After the last letter a question mark was presented, prompting the subjects to respond.

4.3 Results

The observers' overall behavioral performance during the demanding *attend-RSVP* blocks was rather good (94.2% correct) and did not vary between FO and FP trials (F[1,7]=0.3, p=0.601). This confirms that subjects focused attention on the RSVP stream and away from the peripheral items in a consistent manner.

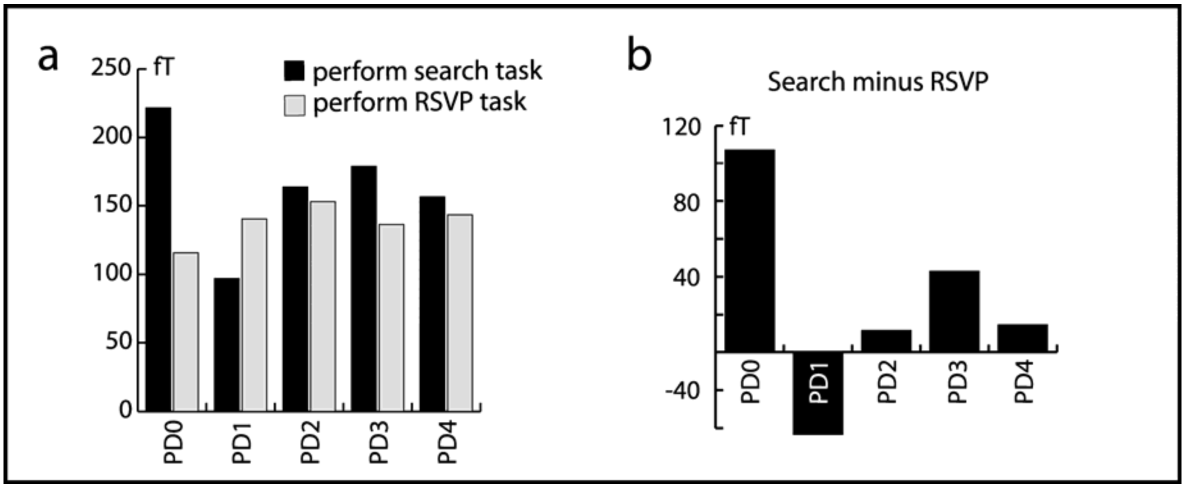

Fig. 11: *Results of Experiment 2.* **(a)** Mean size (average between 130 and 150 ms) of the probe-related response (FP-minus-FO, collapsed across corresponding probe distance conditions) when observers performed the search task (black), or when their attention was withdrawn from the search items by a demanding RSVP task at fixation (gray). The Mexican hat profile is observed for the attend-search but not for the attend-RSVP condition. **(b)** Differences between the probe-related response in the search and RSVP tasks at each target-probe distance. Note that a significant enhancement was present at PD0, neighbored by a significant suppression at PD1.

Fig. 11a shows the mean size of the probe-related ERMF response (FP-minus-FO trials) from 130 to 150 ms for the two conditions. Black bars illustrate the effect in the attend-search condition, while gray bars depict the attend-RSVP task. When search frames were ignored, the probe-related response exhibited a slight reduction when the target C appeared at or near the probe's location. However, pair-wise comparisons between PD0, PD1 and PD2 revealed no significant effect (all F-values < 1). In contrast, when observers performed the search task, the probe response profile resembled the pattern observed in Experiment 1, with suppression at PD1 compared to the adjacent probe-distances. This was statistically confirmed by significant differences in one-way rANOVAs with factor probe-distance between PD0 and PD1 (F[1,7]=18.6, p=0.004), and between PD2 and PD1 (F[1,7]=16.4, p=0.005).

Fig. 11b shows the difference in ERMF response between the attend-search and attend-RSVP conditions for each probe-distance. This difference eliminates the pure sensory response from the attention effect. These difference values were subjected to one-way rANOVAs with the factor task-type (attend-RSVP vs. attend-search), which revealed a significant enhancement at the probe-position (PD0, F[1,7]=18.8, p=0.003), and a significant suppression adjacent to it (PD1, F[1,7]=9.2, p=0.019). Although the difference scores at PD2 through PD4 were all positive, they were not statistically significant.

4.4 Discussion

Experiment 2 was conducted to rule out a potential sensory confound in the first experiment, namely, that the surround inhibition due to attention may partially result from sensory-sensory interactions between the search target and the probe. To this end, Experiment 2 contained an additional experimental condition (RSVP task) that permitted to evaluate the influence of such sensory-sensory interactions when attention is withdrawn from the search frame. Under this condition no differential profile was elicited by the probe that would explain the Mexican hat profile. Although there appeared to be a small reduction of the ERMF response at PD0 (which supports the notion of partial refractoriness at the target position), this effect was not statistically significant.

Taken together, the results of Experiment 2 provide clear evidence that the Mexican hat profile observed in Experiment 1 reflects a truly attention-driven effect. Attending the search array led to the Mexican hat profile as seen in Experiment 1. There was, however, little evidence compatible with such profile in the absence of attention. In addition, Experiment 2 provides a neutral baseline condition to estimate the relative amount of enhancement and suppression at the target and adjacent positions, respectively. That is, the enhancement found at the target location reflects true neural enhancement, and the negative deflection at neighboring position can be assertively related to active suppression.

5 Experiment 3

5.1 Introduction

Experiment 1 and 2 established that the Mexican hat profile represents a truly attention-related effect, that is not caused by the target defining feature-contrast (color pop-out). In Experiment 3 the generality of this notion is addressed by considering an additional type of feature contrast (luminance) that defines the target. Feature contrast effects are crucial bottom-up determinants of stimulus saliency (Nothdurft, 1992; Nothdurft, 2000), and have been shown to interact with top-down attentional modulations in early visual cortex (Hopf et al., 2004b). In particular luminance- and color-contrast discrimination have been reported to be influenced by attention in a modality specific way (Morrone et al., 2002, 2004), implying the action of different systems during attentional processing of the two dimensions, presumably because these feature-dimensions are - at least partially - processed by distinct neural systems (Ungerleider and Mishkin, 1982; DeYoe and Van Essen, 1988; Livingstone and Hubel, 1988). It is, thus, possible that the Mexican hat profile of attention varies in an attribute-dependent manner. STM, for example, predicts that the a spatial extent of surround inhibition depends on the hierarchical level of the top-most layer initiating the top-down WTA, which may be different for both feature dimensions.

5.2 Methods

Experiment 3 was identical to the previous experiments, except for the target-defining feature. As in the previous experiments, on half of the trial blocks, the target was defined by color-contrast (a red target item among blue distractors). On the other half of the trial blocks, the target was defined by luminance-contrast. The target C in the display was drawn in a brighter blue than the other eight Cs (Fig. 12). In order to completely eliminate luminance differences in the color-contrast condition, the color of the red C was adapted in luminance to be equal to the luminance of the distractors. For this experiment a black background (0.5 cd/m^2)

was chosen, while the distractors were dark blue (1.3 cd/m^2). The targets were either light blue (13 cd/m^2) or red.

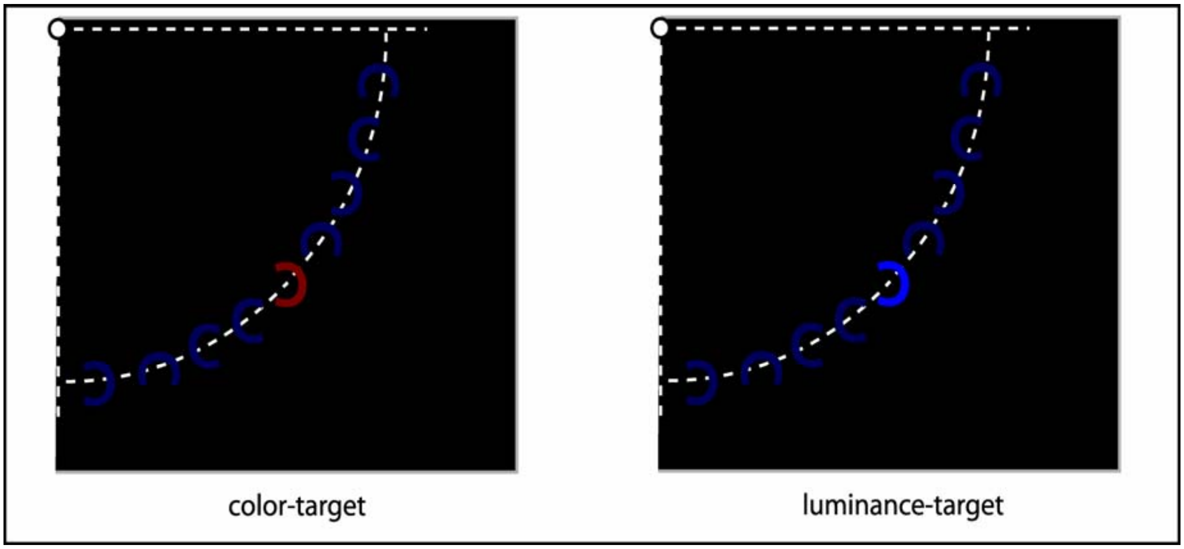

Fig. 12: *Paradigm of Experiment 3.* Two different features were used to define the target in different trial blocks. During half of the blocks, the target was a red C (color-target), while on the other half of the blocks, the target was defined by luminance, that is, it was of a lighter blue than the distractors (luminance-target).

Isoluminance between the target and distractors of the color-contrast condition was determined for each subject individually based on a flicker-fusion paradigm prior to the actual experiment (e.g., Shioiri and Cavanagh, 1992). This paradigm alternately started with two very light red squares (2.5 by 2.5°) presented peripheral to fixation (centered on target position 5 and the mirror-symmetrical position in the opposite lateral hemifield) or black squares. The squares flickered at a rate of 15 Hz on a background, that was colored in the dark blue of the distractors. The red-value of the squares could then be adapted both upwards and downwards to reach the point of minimal flicker sensation. As the chromatic pathway has a lower temporal frequency cutoff than the achromatic pathway (de Lange, 1958; Boynton and Kaiser, 1968; Kelly and van Norren, 1977), and does therefore not register the alternations, the flicker sensation at high frequencies is accomplished exclusively by the achromatic system. Thus, minimizing the sensation of flicker indicates the point of individual isoluminance.

10 subjects took part in Experiment 3 (6 females, mean age: 23.4). Color-contrast (*color-targets*) and luminance-contrast (*luminance-targets*) trials were presented in alternating trial-blocks.

5.3 Results

The subjects' overall behavioral performance was good under both conditions (both 96% correct). A one-way rANOVA with the factor target-type (color vs. luminance) indicated that there was no significant difference of response accuracy between the two conditions (F[1,9]=0.4, p=0.84). Subjects responded slightly slower to color-targets than to luminance-targets (514 vs. 507 ms), but this difference did not reach statistical significance (F[1,9]=3.01, p=0.12).

The ERMF response to the probe was quantified between 124 and 132 ms after probe onset, which revealed a Mexican hat profile (PD0 larger PD1 smaller PD2) for both conditions, with no obvious difference regarding their spatial profile (see Fig. 13). Planned two-way rANOVAs with factors target-type (color vs. luminance) and probe-distance (PD0 vs. PD1) confirm this impression, as there was a significant main-effect of probe-distance (F[1,9]=13.9, p=0.005), but no main-effect of target-type (F[1,9]=0.15, p=0.71). An interaction between the two factors (F[1,9]=0.17, p=0.69) was also not significant. The comparison PD1 versus PD2, also revealed a main-effect for probe-distance (F[1,9]=9.7, p=0.012), but neither a main-effect for target-type (F[1,9]=1.3, p=0.28) nor an interaction between the two factors (F[1,9]=0.6, p=0.82) reached significance. Direct comparisons of the different probe-distances with one-way rANOVAs comparing the two target-type conditions (color vs. luminance) yielded no significant results (all F-values < 1). Thus, the general pattern closely resembled that of Experiment 1, while no significant differences could be found for the two target-types.

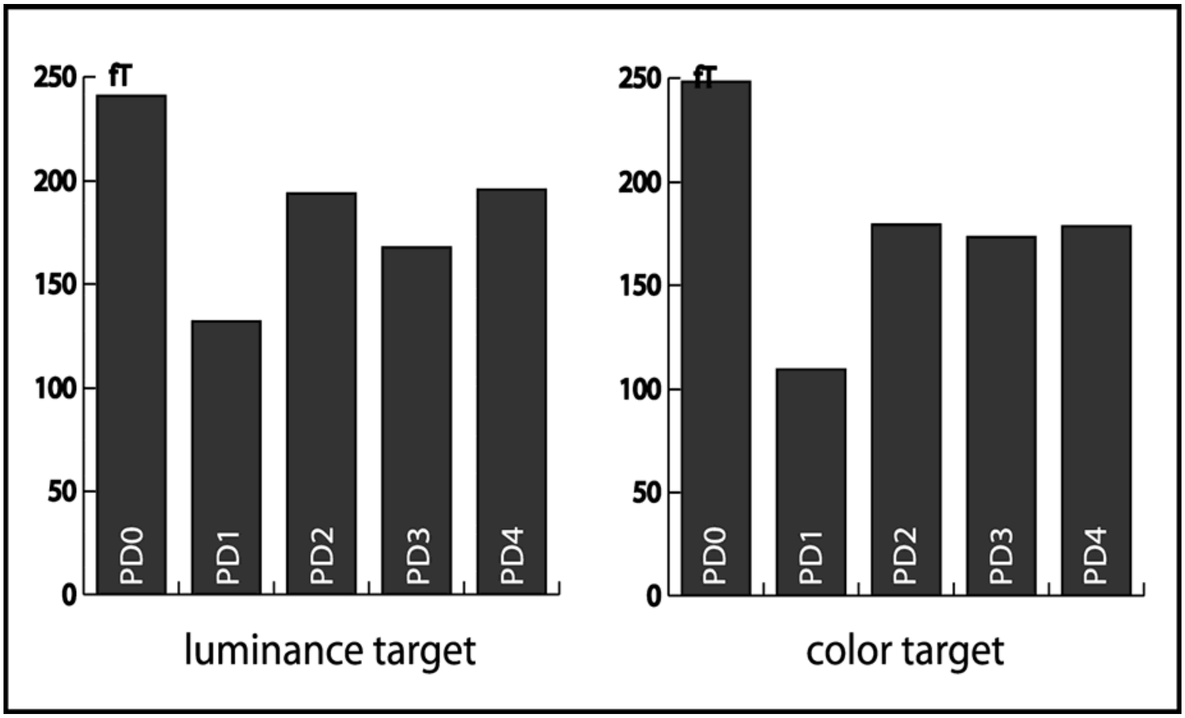

Fig. 13: *ERMF results of Experiment 3.* The ERMF amplitudes between 124 and 132 ms are displayed as a function of distance of the attentional focus to the probe (PD0 through PD4). Mexican hat profiles (PD0>PD1<PD2) are found under both conditions (color and luminance target), while no significant differences are present between them.

5.4 Discussion

Experiment 3 addressed the question whether the target defining feature contrast influences the Mexican hat profile differently when it appears in the luminance- in contrast to the color-domain. As mentioned above, there is psychophysical evidence that attention modulates luminance-contrast differently from color-contrast, possibly because these modulatory operations arise in different neural systems of the visual cortex. In terms of STM, this might lead to differential patterns of results, as the receptive field sizes of the neurons in the respective winning layer (and thus the extent of surround inhibition) might vary between the two conditions. The present results, however, show, that both luminance- and color-contrast defined targets led to very similar Mexican hat profiles, which seems to speak against feature specific mechanisms underlying the Mexican hat profile. The results of Experiment 3 suggest that no matter what form of bottom-up feature discontinuity signals the target location, this information is fed into a common top-down propagating selection pyramid. As a consequence the extent of the Mexican hat profile remains unchanged. This finding is not implausible in view of the fact that both spatial luminance- and color-contrast appear to be processed already in the primary visual cortex (Boynton et al., 1999; Engel and Furmanski, 2001; Conway et al., 2002). Of course, it is not possible to completely rule out differential effects on the size of the surround suppression, because spatial sampling was limited, so that subtle differences in the profile may have been overlooked.

6 Experiment 4

6.1 Introduction

Experiment 4 was conducted to investigate the influence of task-difficulty onto the pattern of attentional resource distribution. Numerous studies have demonstrated that the distribution of attentional resources depends on perceptual load, with high perceptual load being able to eliminate distractor interference. The Perceptual Load Model (PLM) by Lavie and co-workers (Lavie, 1995, 2005), proposes that the degree to which spatially separate, task-irrelevant distractors are processed, depends on the extent to which attentional resources have to be focused, mitigating or even abolishing their processing when attentional resources are completely exhausted. In contrast, under low load conditions, resources may be progressively released and “spill over” to distractor processing (Yantis and Johnston, 1990; LaBerge et al., 1991; Lavie and Cox, 1997; Rantanen and Goldberg, 1999; Lavie and Fox, 2000). Imaging studies have provided some evidence consistent with this notion. For example, Rees and colleagues observed with fMRI that a task-irrelevant moving dot pattern in the background of a word discrimination task activated MT when the load of this task was low, but not when it was high (Rees et al., 1997). Other fMRI studies established similar observations (e.g., Schwartz et al., 2005).

With respect to the present experiments, the predictions of the PLM are ambiguous. For example, it could be that high perceptual load causes surround suppression to increase (in strength and/or extent) with the consequence that distractors in the surround of the target become less interfering (stronger noise attenuation). Alternatively, it could be that with increasing load, surround suppression becomes reduced in favor of a pronounced center enhancement. This would decrease the influence of distractors due to a relative enhancement of the attended signal (stronger signal enhancement). Recent evidence from negative priming appears to support this possibility (Lavie and Fox, 2000). In contrast to the PLM, the STM predicts that the extent and depth of the inhibitory surround remains largely unaffected (as long as the layer where the global winner is calculated does not change due to task demands and stimulus characteristics; Tsotsos et al., 1995).

6.2 Methods

Experiment 4 differed from the first experiment in that in 50% of the trials (Fig. 14a) the items of the search array contained two gaps, one at the left and one at the right side. These gaps differed only slightly in size (Fig. 14b), and subjects had to indicate with an alternative button press (the same button-mapping as in Experiment 1) which gap was larger. The size of the gaps had a directional angle of 27° for the larger gap and 15° for the smaller gap (Fig. 14b specifies the corresponding visual angles in absolute distance). As reported below, the performance was nearly perfect for single-gap stimuli (96%), but dropped significantly for double-gap stimuli (68%), indicating that the task difficulty manipulation was effective. Double-gap stimuli (henceforth referred to as *hard trials)* were randomly mixed with single-gap stimuli (henceforth referred to as *easy* trials) within experimental blocks. Experiment 4 was performed by 18 subjects (13 females, mean age: 24.8).

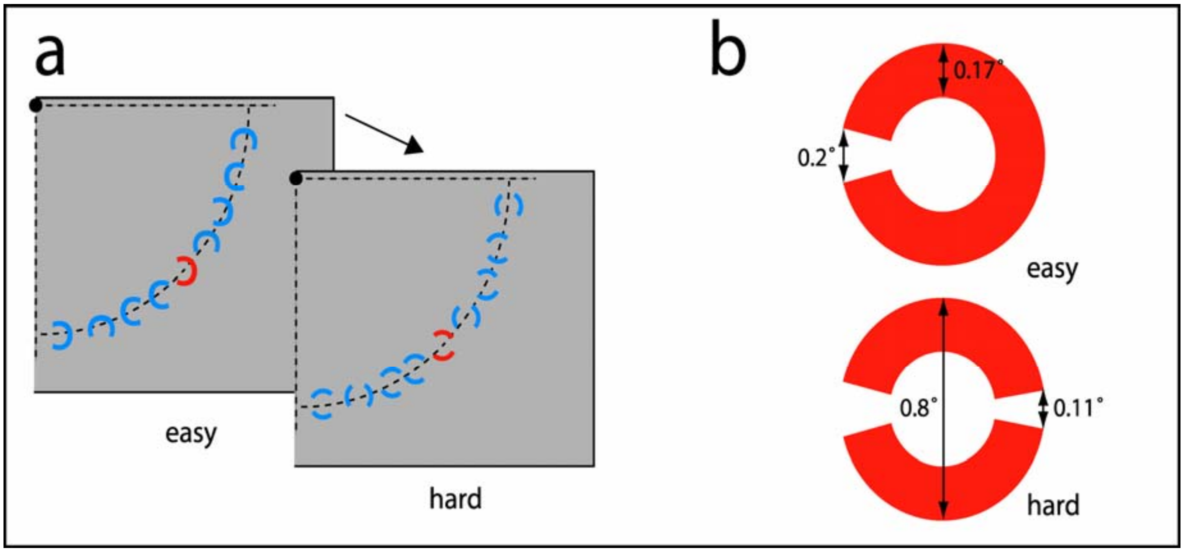

Fig. 14 (preceding page): *Paradigm and stimuli of Experiment 4.* **(a)** Two classes of stimuli were intermingled within the experimental blocks: the original stimuli from Experiment 1 (easy) and the same stimuli with an additional, slightly smaller gap (hard). **(b)** Both stimulus-classes subtended 0.8°, with a line-thickness of 0.17°. The large gap had an outer corner-to-corner distance of 0.2°, while the smaller gap was approximately half as wide (0.11°).

6.3 Results

As mentioned above, the task-difficulty manipulation proved to be very efficient. During easy trials, the level of performance was very high (mean: 96% correct responses), while the performance dropped markedly during hard trials (mean: 68% correct responses). Subjects responded much slower to hard trials (mean: 560 ms) than to easy ones (mean: 499 ms). Respective one-way rANOVAs with the factor task-difficulty (easy vs. hard), revealed significant differences for the RT-data (F[1,17]=86.5, p<0.001) as well as response accuracy (F[1,17]=707.7, p<0.001). Importantly, the portion of correct responses to hard trials was significantly different from the percentage predicted for chance performance (50%; one-sample ttest: T[17]=47.4, p<0.001).

The ERMF data was quantified between 116 and 132 ms after the onset of the probe. During this time-range the center-surround pattern found in Experiment 1 was replicated for both task-difficulty conditions (Fig. 15). To validate this pattern in both task-difficulty conditions, hierarchically dependent 2-way rANOVAs were computed. One overall rANOVA was set up to test the presence of the general pattern. This analysis included the factors probe-distance (PD0 through PD4) and task-difficulty (easy vs. hard), and revealed a significant main-effect of probe-distance (F[3,50.8]=19.8, p<0.001) but no main-effect of task-difficulty (F[1,17]=0.09, p=0.77), and no interaction between the two factors (F[2.7,46.6]=0.25, p=0.84). Subsequent pair-wise comparisons of the critical probe-distances yielded significant main effects for probe-distance when comparing PD0 with PD1 (F[1,17]=38.3, p<0.001), PD1 with PD2 (F[1,17]=9.8, p=0.006), and PD0 and PD2 (F[1,17]=4.6, p=0.047). Although the ERMF response at PD1 appears to be slightly smaller for hard than easy trials no main-effect of task-difficulty (p=0.63; p=0.27; p=0.8) and no interaction of task-difficulty times probe-distance (p=0.73; p=0.66; p=0.2) was found. To summarize, although task-difficulty significantly influenced discrimination performance, it did not influence the principal shape of the Mexican hat profile of cortical responsivity.

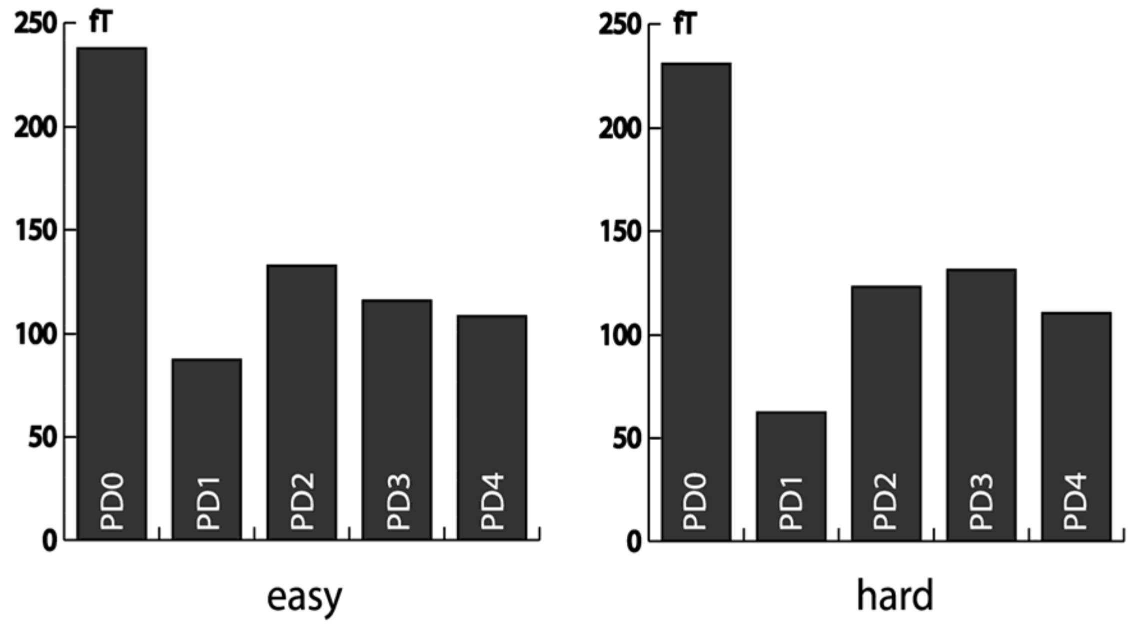

Fig. 15: *ERMF results of Experiment 4.* The ERMF amplitudes between 116 and 132 ms are displayed as a function of distance from the attentional focus to the probe. Both the easy and the hard condition lead to Mexican hat profiles, while no significant differences were found between them.

6.4 Discussion

This experiment was conducted to estimate the effect of task-difficulty onto the Mexican hat profile observed in the preceding experiments. The level of task-difficulty was varied in a trial-by-trial manner by mixing two classes of stimuli. During easy trials, subjects discriminated the orientation of the target C as in Experiment 1, whereas during hard trials the larger of two gaps in the target C had to be indicated. This modification led to pronounced differences in behavior, with slowed responses and enhanced error rates for hard trials. Nevertheless, the

ERMF response elicited by the probe was nearly identical under both task-difficulty conditions. Thus, the observed Mexican hat profile appears to reflect an attentional mechanism that is not directly influenced by load manipulations as conceptualized in the PLM – at least not at the time of probe presentation (250 ms after the onset of the search frame). So, conversely to the predictions of PLM, no enhanced response within the focus of attention was found for hard trials as compared with easy ones. The amount of surround inhibition was also not uninfluenced by task-difficulty. Though in contrast to the PLM, the result of Experiment 4 is in line with the prediction of the STM. Task-difficulty, according to the STM, is not directly predicted to cause pronounced changes of the Mexican hat profile.

One reason why task-demands may not have influenced the Mexican hat profile in the present experiment is the fact that subjects were not able to anticipate the trial-type (easy and hard trials were mixed randomly), with the consequence that eventual preparatory effects could not be differetially applied. Subjects may have simply prepared for a hard discrimination on each upcoming trial. Indeed, when compared with Experiment 1, it is noticeable that the response at PD0 (thus, within the focus of attention) is generally enhanced during both task-difficulty conditions (the PD0 vs. PD2 difference is significant here). Thus, it is possible that this enhancement reflects a preparatory effect that takes the potential difficulty of the upcoming trial into account. This would be in line with the results of Urbach and Spitzer, who found that subjects performed better in an identical task, when it was embedded in difficult trials as opposed to an environment of easy antecessors (Urbach and Spitzer, 1995). Further support for this notion stems from ERP experiments, that established a very early influence of attentional load on the processing of irrelevant distractors, presumably mediated by attentional selection prior to stimulus onset (Handy and Mangun, 2000; Handy et al., 2001).

In general, the results of Experiment 4 add to the notion that the Mexican hat profile reflects a more elementary attentional selection process, that might primarily relate to the process of localizing the target, rather than its discrimination. The targets were equally easy to find under both task-difficulty conditions (one red item among blue distractors), while only the discrimination process actually differed in difficulty. Of course, it is important to acknowledge, that the load manipulation may have influenced later stages of the attentional focusing process, not effectively probed with a frame-probe SOA of 250 ms. Also, it is possible that surround inhibition persists for an extended time range under high load conditions (but see Experiment 6). Further research will be necessary to clarify these issues. Experiment 6 will provide a more systematic investigation of different frame-probe SOAs.

7 Experiment 5

7.1 Introduction

Experiment 5 was set up to investigate whether the presence of distractor items in the search array would be critical for the Mexican hat profile to appear. There is abundant neurophysiological evidence suggesting that attentional suppression might be particularly important when distractors are concurrently present in the display (Chelazzi et al., 1993; Motter, 1993; Luck et al., 1997a; Pinsk et al., 2004; Schwartz et al., 2005). Furthermore, an ERP component reflecting distractor suppression (Luck et al., 1997b) has been demonstrated to increase in amplitude when distractor items are concurrently present in the display (Luck and Hillyard, 1994a). Psychophysical data have also supported this view. Locations formerly occupied by distractors produce slower probe reaction times than blank positions (e.g., Klein, 1988; Cepeda et al., 1998). Nonetheless, there is neurophysiological evidence indicating that attention may cause neural suppression also at spatial locations not occupied by distractors. Smith and colleagues have shown that an attended region is flanked by a wide-spread attentional inhibition zone coding for currently unattended and unstimulated locations (Smith et al., 2000; see also Tootell et al., 1998). Serences and colleagues reported suppression of blank positions already during the anticipation of upcoming distractors (Serences et al., 2004). Mounts observed with psychophysical measures that the amount of surround suppression did not depend on the number of distractors, but on the spatial distance of distractors to the target, implying that suppression acts on space per se, and not so much on the distractor items contained in that space (Mounts, 2000a).

Taken together, the available evidence points to alternative possibilities. The Mexican hat profile may be influenced by the presence and number of distractors as active neural suppression of items has been shown to be strongest in the presence of distracting items. Alternatively, in line with the observation that attentional suppression can act on blank space, the Mexican hat profile might not be affected by the presence of distractors. STM predicts a pattern of results, that only in part depends on the presence of distractors (Tsotsos et al., 1995; Tsotsos et al., 2001), with the central pass-zone and the surrounding zone of pronounced suppression being generally unaffected. Only the more distal surround may be influenced by distractor-presence or -absence.

7.2 Methods

Experiment 5 was designed to investigate whether the profile of activation found in the previous experiments depends on the presence of distractors or not. For this purpose the stimulus parameters of Experiment 3 were used (luminance-blocks), but distractors were present only in half of the trials (Fig. 16). Distractor-present and distractor-absent trials were presented in separate trial blocks. 13 subjects took part in Experiment 5 (10 females, mean age: 24.1). Subjects performed on 10 blocks containing 180 trials, amounting to a total of 50 trials per condition and target position.

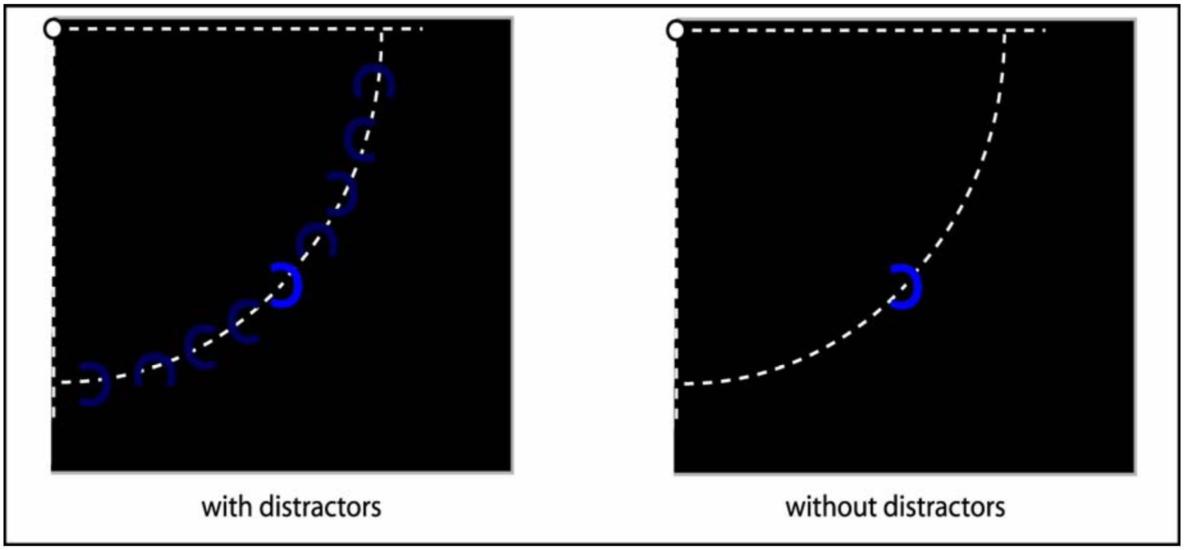

Fig. 16: *Illustration of the Paradigm of Experiment 5.* Half of the trial blocks of Experiment 5 were identical to the luminance-target trial blocks of Experiment 3 (with distractors), while the distractors were omitted in the other half of the trial blocks (without distractors).

7.3 Results

Whether distractors were present or absent had a significant influence on performance. Subjects performed slightly more accurate (98% vs. 99%, F[1,12]=6.2, p=0.03) and faster (F[1,12]=85, p<0.001) without distractors (with distractors: mean 513 ms; without distractors: mean 465 ms).

The probe-related ERMF response was quantified in a time-window between 128 and 148 ms after probe-onset. As visible in Fig. 17, the Mexican hat profile could be replicated for the distractor-present condition (left side). Importantly, the distractor-absent condition also produced a Mexican hat profile, that was similar to the one found for distractor-present trials. Two-way rANOVAs with the factors probe-distance and distractor-presence (present vs. absent) confirmed this observation. Main-effects of probe-distance were observed for PD0 vs. PD1 (F[1,12]=14.3, p=0.003), and for PD1 vs. PD2 (F[1,12]=15.8, p=0.002), while distractor-presence did not reach significance (p=0.92; p=0.3). There was also no probe-distance times distractor-presence interaction (p=0.16; p=0.94). Notably, a comparison of PD0 and PD2 for distractor-present trials revealed a significantly larger response at PD0 than PD2 (F[1,12]=6.6, p=0.024). In contrast, no significant PD0 larger PD2 difference was found for distractor-absent trials (F[1,12]=0.5, p=0.51), indicating that the central enhancement was stronger for distractor-present than distractor-absent trials. Nevertheless, the overall Mexican hat profile did not differ significantly between the two conditions, as reflected by the absence of interactions between the factors distractor-presence (present vs. absent) and probe-distance for all probe-distances (PD0 through PD4; F[3.3,40.1]=0.9, p=0.483) and for the probe-distances of most interest (PD0 through PD2; F[2,23.4]=1.5, p=0.236). A direct comparison of each probe-distance between target-presence conditions revealed no significant effects (all F-values < 1).

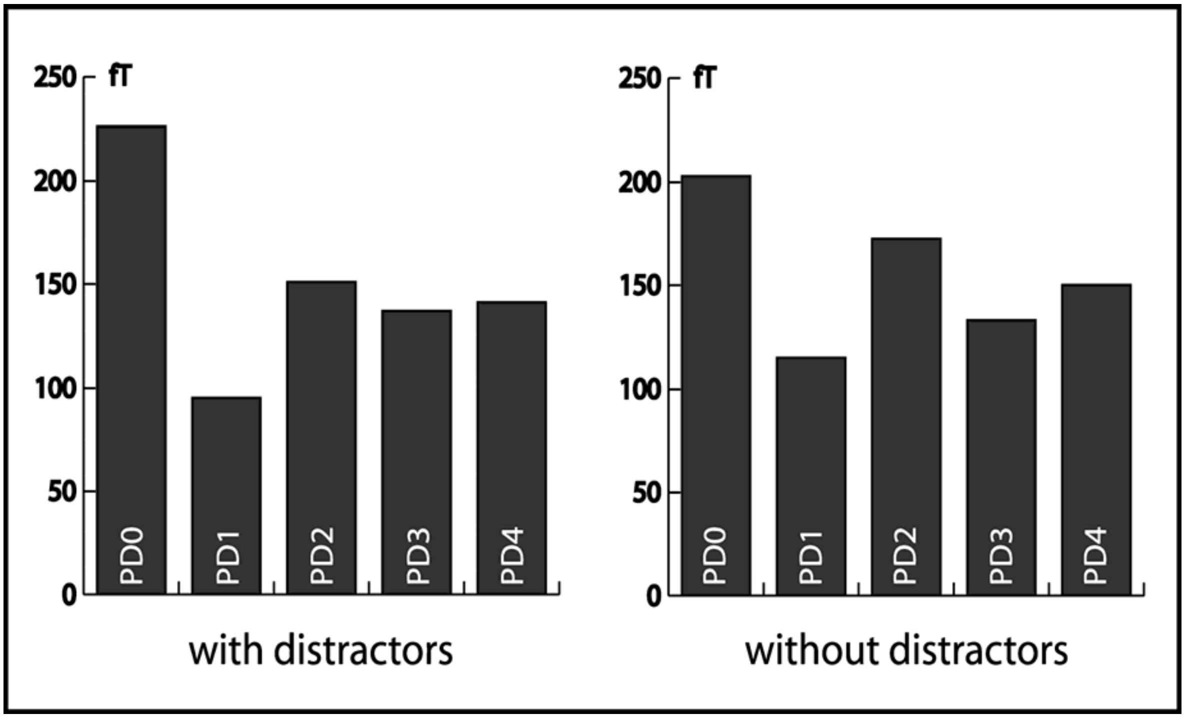

Fig. 17: *ERMF results of Experiment 5.* The ERMF amplitudes between 128 and 148 ms are displayed for the different probe-distances (PD0 through PD4). Mexican hat profiles (PD0>PD1<PD2) are found under both conditions (with and without distractors), while no significant differences were found between them.

7.4 Discussion

Experiment 5 was designed to investigate the importance of distractors for eliciting the Mexican hat distribution observed in the preceding experiments. To this end, trial blocks with distractors in the search array were compared with trial-blocks, where no distractors were present. Both conditions elicited robust Mexican hat distributions, indicating that the presence of distractors is not a critical determinant for the Mexican hat profile to appear. In general, little indications of a differential pattern between the two conditions were found. As both conditions were separated into different experimental blocks, anticipatory effects expecting the potential occurrence of distractors are not a feasible explanation for this lack of differential effects. Thus, the results argue for a mechanism that is mostly independent of the presence of distractors. This is in accord with the findings of Mounts, who related the Mexican hat profile in his psychophysical investigation to spatial distance per se, irrespective of the number of intervening distractors (Mounts, 2000a).

Additionally, the present results fit with fMRI observations, that have demonstrated a rather widespread distribution of attentional suppression in the absence of any distractors (Smith et al., 2000).

The Mexican hat profile may, thus, not directly relate to those class of modulatory effects of attention that become stronger with enhanced distractor presence or interference condition (e.g., Chelazzi et al., 1993; Luck and Hillyard, 1994a; Schwartz et al., 2005). Furthermore, the zone of surround suppression in the Mexican hat profile does not appear to correspond with the N2pc-effect (Luck and Hillyard, 1994a), even though, both modulatory effects arise in the same time range. The Mexican hat profile may also not underlie to psychophysical observations, that highlight suppressive effects only in the presence of distractors (Cepeda et al., 1998). Instead, the surround inhibition characterized in the present experiments appears to reflect an attentional selection process that operates in a more automatical and mandatory manner on parts of the visual space that are relevant for information selection. As some aspects of attention are clearly susceptible to the presence of distractors, it is important to consider that multiple attentional mechanisms are known to operate in parallel (Luck, 1995).

Beside the general similarity of the Mexican hat profile under both experimental conditions, there was one clear difference. The response to PD0-targets was enhanced relative to PD2 for the distractor-present condition, but not for the distractor-absent condition. Consistent with Experiment 4, this might reflect the reaction to an augmented attentional load (as the task was clearly more difficult in the presence of distractors, as indexed by decrements in the behavioral variables). This is in keeping with both psychophysical investigations (Urbach and Spitzer, 1995), and ERP findings (Handy and Mangun, 2000; Handy et al., 2001). Furthermore, it is worth emphasizing, the fact that the Mexican hat profile emerges in the absence of distractors rules out an explanation in terms of sensory-sensory interactions between the distractors and the target – a possibility that was raised in Experiment 2.

Finally, the outcome of Experiment 5 is in line with the prediction of the STM. According to the STM the suppressive surround arises as a “side effect” of a top-down propagating WTA that iteratively prunes away (suppresses) connections conveying information about locations adjacent to the attended object. This pruning process is triggered by a top-layer winner representing the attended item, but is as such not dependent on the presence of distractors. STM makes differential predictions concerning the concurrent presence of distractors in the display (Tsotsos et al., 1995; Tsotsos et al., 2001). The pass-zone in the center of the attentional focus and the surrounding inhibition are assumed not to be influenced by the presence or absence of distractors, which was confirmed by the present study. Concerning more distal locations, both increases (in higher-level areas) and decreases (in lower-level areas) in signal are predicted depending on the particular cortical level, while neither was evident in the present data.

8 Experiment 6

8.1 Introduction

Experiment 6 aims to analyze the temporal characteristics of the center-surround profile of attentional focusing. In order to obtain measures of the cortical activity profile evolving over time, the frame-probe SOA was systematically varied between 100 and 400 ms. There is considerable evidence suggesting that attention requires some time to dwell (Moore et al., 1996; Theeuwes et al., 2004; Duncan et al., 1994; Ward et al., 1996). Unfortunately different methodological approaches have led to very diverse estimates of how long it takes to focus attention onto a target (and to move on from item to item during search; for a more extensive review see Egeth and Yantis, 1997). Estimates suggesting short dwell times typically derive from studies using visual search tasks. For example, Wolfe reported search slopes that imply a serial focusing of attention every 40-50 ms (Wolfe, 1994; see also Treisman and Gelade, 1980). An extensive review of the literature by Wolfe revealed similar results, with an upper limit of about 150 ms per item (Wolfe, 1998). These estimates from visual search tasks are in stark contrast to the much longer dwell times typically observed by studies that addressed attentional dwell times more directly by means of measuring the temporal extent of interference between two targets presented in rapid succession. In these studies estimates varied between approximately 200 ms (Moore et al., 1996; Theeuwes et al., 2004) and 500 ms (Duncan et al., 1994; Ward et al., 1996).

Neurophysiological data in humans suggest attentional modulation to occur at an intermediate-to-late time-scale relative to behavioral measures from visual search. Specifically, the earliest modulatory effects of attentional location selection in extrastriate areas appear around 90 to 100 ms after stimulus presentation (P1; e.g., Heinze et al., 1994), whereas effects of feature selection start around 150 ms (Hopf et al., 2004a). The N2pc, which has been linked to distractor suppression (Luck et al., 1997b), is present in a time-window between 200 and 350 ms (Luck and Hillyard, 1994b, 1994a).

STM suggests that the Mexican hat profile results from a top-down propagating inhibitory modulation. Top-down modulatory effects have been characterized by neurophysiological studies showing that such modulations occur relatively late when arriving in early visual cortex areas (Lamme and Roelfsema, 2000; Mehta et al., 2000b, 2000a). If such process underlies the Mexican hat profile, the profile should not arise before approximately 200 ms after stimulus presentation. Experiment 6 investigates the time-course of the Mexican hat profile by analyzing different frame-probe SOAs that span a time-window between 100 and 400 ms.

8.2 Methods

In this experiment the stimulation conditions were identical to Experiment 3 (luminance-blocks) except for the frame-probe SOA, that was randomly varied within trial-blocks. between 100, 175, 250, 325 and 400 ms (see Fig.18). Sixteen subjects took part in Experiment 6 (12 females, mean age: 24.3).

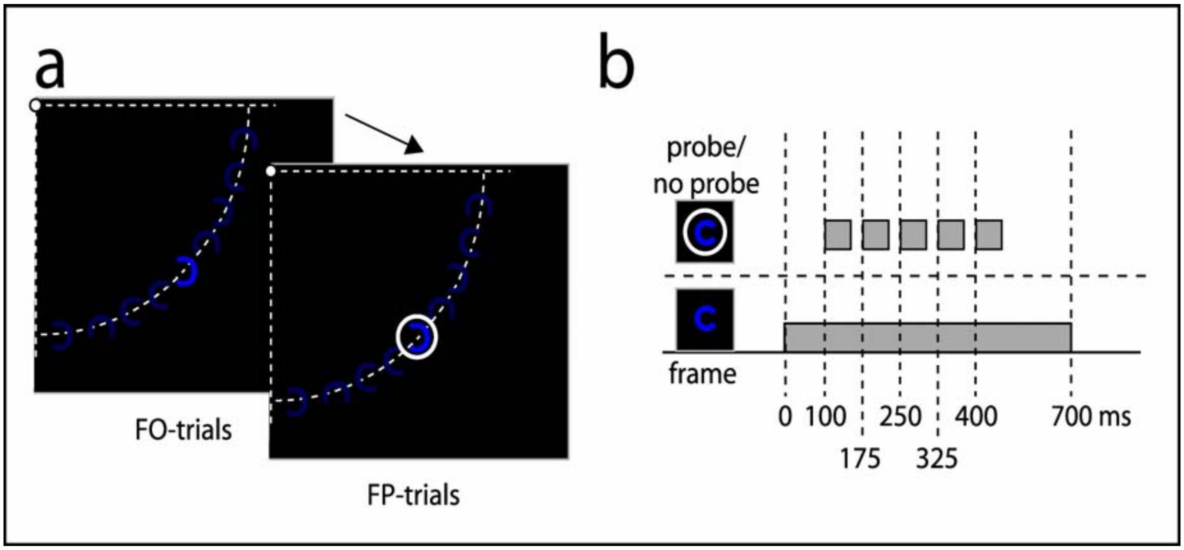

Fig. 18: *Illustration of the paradigm of Experiment 6.* **(a)** Experiment 6 used the same basic paradigm as the previous experiments, having FO-trials and FP-trials in half of the trials each. **(b)** In FP-trials, the SOA between the search-array and the probe-stimulus was varied randomly between 100, 175, 250, 325, and 400 ms.

8.3 Results

8.3.1 Behavioral Performance

As illustrated in Fig. 19b, subjects generally committed slightly more errors when a probe was present (96.7% vs. 97.5% correct). A two-way rANOVA with factors probe-presence (present vs. absent) and SOA (100, 175, 250, 325, 400 ms) yielded a significant main-effect for probe-presence (F[1,15]=38, p<0.001). In addition, the factor SOA (F[2.5,37.8]=10.1, p<0.001), as well as the probe-presence times SOA interaction was significant (F[2.7,40.7]=8.9, p<0.001), the latter reflecting the fact, that the performance decrement for FP trials was confined to only some SOAs. RANOVAs testing the different probe-SOAs individually revealed significant effects for the shortest SOA (100 ms: F[1,15]=51, p<0.001), and the longest SOA (400 ms: F[1,15]=7.8, p=0.013), while the difference at an SOA of 175 ms was only marginally significant (F[1,15]=4.3, p=0.055). No effects were found for the remaining two SOAs (250 ms: F[1,15]=0.3, p=0.6; 325 ms: F[1,15]=0.2, p=0.68).

The influence of the probe was also evident in the RT-data (probe-absent: mean 507 ms; probe-present: mean 518 ms). An overall two-way rANOVA with the factors probe-presence (present vs. absent) and SOA (100, 175, 250, 325, 400 ms) revealed a significant main-effect of SOA (F[2.1,31.5]=10.7, p<0.001) and probe-presence (F[1,15]=30.7, p<0.001). The respective interaction was also significant (F[2.8,42.8]=33.2, p<0.001). Separate rANOVAs for each SOA revealed that the most consistent effect of probe-presence was evident for the SOA of 100 ms (F[1,15]=69.1, p<0.001) and 175 ms (F[1,15]=17.2, p=0.001). SOAs beyond 175 ms revealed no significant effect (250 ms: F[1,15]=0.7, p=0.41; 325 ms: F[1,15]=0.1, p=0.74; 400 ms: F[1,15]=0.5, p=0.49). Taken together, it turns out, that probes presented soon after the onset of the search array deteriorated behavioral performance most, presumably because of backward masking. SOAs beyond 175 ms had little influence on performance, except for the SOA of 400 ms which interfered with the choice of the correct response.

8.3.2 Magnetoencephalographic results

The electromagnetic results are illustrated in Fig. 19a. The data was quantified in a time-window between 112 to 136 ms after probe onset. With an SOA of 100 ms, the probe did not elicit a profile that markedly differed between the different probe-distances. This was confirmed by a one-way rANOVA with factor probe-distance (PD0 through PD4), which yielded no significant effect (F[2.4,35.3]=0.8, p=0.483). Although the ERMF response for PD0 seems to be enhanced with respect to the other target locations, none of the pair-wise comparisons including PD0 yielded significant differences (all p-values above 0.1).

For the 175 ms SOA there was also no significant effect of probe-distance which was confirmed by a one-way rANOVA with factor probe-distance (PD0 through PD4) that did not find a significant effect (F[3.1,46.7]=1, p=0.42). For the SOA of 250 ms, the Mexican hat profile appeared, displaying the typical pattern of response amplitudes with PD0 larger PD1 smaller PD2. This is statistically confirmed by pair-wise comparisons between probe-distances (PD0 vs. PD1: F[1,15]=9.3, p=0.008; PD1 vs. PD2: F[1,15]=6.2, p=0.025).

Although the Mexican hat profile was still visible at the SOA of 325 ms, a statistical validation of the effect did not yield significant effects. That is, the significant difference between PD1 and PD2 was no longer present (F[1,15]=0.9, p=0.35). The most prominent difference is a stronger response at PD0 as compared to all other probe-distances. This was confirmed by single comparisons of PD0 with the different probe-distances (PD1 through PD4), that all yielded significant differences (PD1: p = 0.001; PD2: p = 0.031; PD3: p = 0.015; PD4: p = 0.037). After an SOA of 400 ms no Mexican hat profile was present, as evidenced by a lack of significance comparing PD1 responses with those elicited at PD2 (F[1,15]=0.5, p=0.5). But as for the 325 ms SOA the response at PD0 was still enhanced relative to more distant locations. This was reflected by a significant effect of target location (PD0 through PD4, rANOVA (F[2.8,41.5]=3.5, p=0.025), as well as by separate one-way rANOVAs comparing PD0 with the probe-distances

PD1, PD3, and PD4 (PD1: p=0.03; PD3: p=0.02; PD4: p=0.046), while no significant effect was found in the comparison with PD2 (p=0.18).

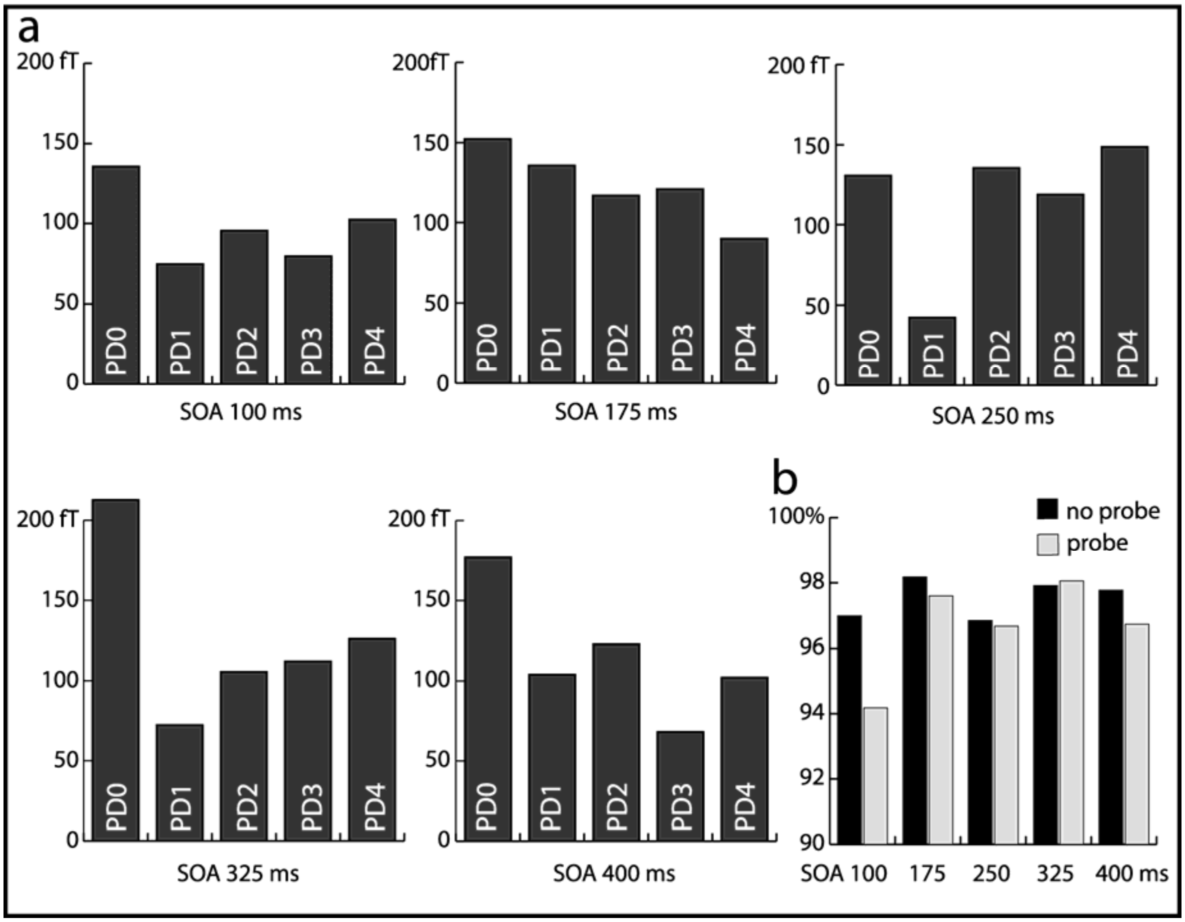

Fig. 19: *ERMF and behavioral results of Experiment 6.* **(a)** The ERMF amplitudes between 112 and 136 ms are displayed for the different probe-distances (PD0 through PD4) under the five different SOA conditions. A significant Mexican hat profile (PD0>PD1<PD2) is only evident after an SOA of 250 ms, while later SOAs primarily lead to a relative enhancement of the central position. **(b)** The performance accuracy data reveals the most detrimental effect of probe-presentation after the shortest SOA (100 ms), that is also evident (albeit weaker) after 175 and 400 ms.

8.4 Discussion

Experiment 6 systematically varied the SOA between the search frame and the probe onset (100, 175, 250, 325, and 400 ms). Comparing the behavioral data between FO and FP trials, it is evident that the probe has an interfering effect for short SOAs (100 and 175 ms) where it slows down reaction times and enhances errors rates. This presumably reflects backward masking. The reason for the detrimental effect of probe-presence on performance accuracy at 400 ms can only be speculated on.

Evaluating the ERMF data, the first significant Mexican hat profile was observed for an SOA of 250 ms. This yielded very similar activity profiles to those observed in the preceding experiments. In contrast, SOAs before 250 ms (100 and 175 ms) produced no differential activity profile. This timing is consistent with intermediate estimates of the attentional dwell time in psychophysical investigations (Moore et al., 1996; Theeuwes et al., 2004), and neurophysiological markers of attentional focusing in monkeys (e.g., Chelazzi et al., 1993) and humans (e.g., Luck et al., 1993; Luck and Hillyard, 1994b, 1994a, 1995; Luck et al., 1997b).

Interestingly, after 325 ms, surround inhibition is already tapering off, while a strong enhancement of the central position (PD0) can be observed, that appears to persist to some extent until 400 ms after the onset of the search array. Although one can only speculate here, this may reflect a refined coding of the attended object, once the influence of the surrounding items has been attenuated by surround inhibition.

The time-course of the Mexican hat profile observed in Experiment 6 parallels important stages of STM (Tsotsos et al., 1995). Specifically, STM predicts that an initial feedforward sweep is unaffected by attention. Indeed, no differential profile was observed within the first 175 ms after search frame onset. During the second phase STM proposes a downward propagating pruning operation, which results in a zone of spatially confined suppression. An activity pattern consistent with this second phase is present after 250 ms, as in the experiments reported in the preceding chapters. The third stage of STM is a second bottom-up traversal of the signal within the pass-zone, now purged from the influence of the neighboring distractors. This stage appears to be paralleled by a relatively enhanced responses at PD0 (i.e., within the focus of attention) during the 325 and 400 ms SOA condition. Taken together, this experiment shows that the Mexican hat profile arises as a temporary activity distribution that is present only during a short time-window (around 250 ms after stimulus onset), whereas pronounced relative enhancement of the information within the focus of attention appears later and persists longer.

9 Meta-analysis

9.1 Introduction

As the general stimulus configuration was identical in the different experiments, that only differed in some aspects without causing pronounced changes in the resulting profile (except for the attend-RSVP condition in Experiment 2 and the SOAs 100, 175, 325, and 400 ms in Experiment 6 – these conditions were excluded from the meta-analysis), the data from the different experiments were combined to form one data-set. The thereby elevated signal-to-noise ratio might help to uncover subtle asymmetries in the ERMF-data concerning the directions towards the horizontal and vertical meridian, and might allow for a more precise spatial localization of the underlying neural sources.

9.2 Results

For this analysis, ERMF data of all experiments with comparable stimulus configurations were averaged. This analysis revealed a Mexican hat profile very similar to the ones found in the respective experiments (see Fig. 20). It resembles a Mexican hat with a central “tip” (PD0) accompanied by two surrounding dips (PD1v (towards the vertical meridian) and PD1h (towards the horizontal meridian)), while the “brim” of the hat is formed by a rebound at positions PD2 through PD4 (both directions). The ERMF data was quantified in a time-window between 120 and 152 ms. During this window a prominent enhancement at the probe-position relative to PD2 was also evident. Both effects, surround inhibition and central enhancement, were statistically confirmed by significant effects of probe-distance in one-way rANOVAs comparing PD0 and PD1 with PD2 (PD0 vs. PD2: F[1,76]=98.4, $p<0.001$; PD1 vs. PD2: F[1,76]=22, $p<0.001$). An additional rANOVA comparing the responses at PD2 through PD4 found no indices of a differential response pattern beyond the zone of central enhancement and the encompassing suppression (F[1.98,151.1]=1.2, p=0.3). Thus, the Mexican hat is constituted of a prominent tip, encircled by two distinct dips, while the signal recovers again uniformly in the brim.

Considering the surround attenuation profile towards the horizontal and vertical meridian, the PD1 response is virtually identical for the two directions. From PD2 on, the response pattern is monotonically descending towards the horizontal meridian (with a maximum at PD2), while the maximum towards the vertical meridian is not reached until PD3. In contrast to this impression, comparing these two patterns with a two-way rANOVA with factors direction (towards the horizontal meridian vs. towards the vertical meridian) and probe-distance (PD2 vs. PD3) failed to yield a significant interaction (F[1,76]=2.6, p=0.11), indicating a mostly symmetrical pattern.

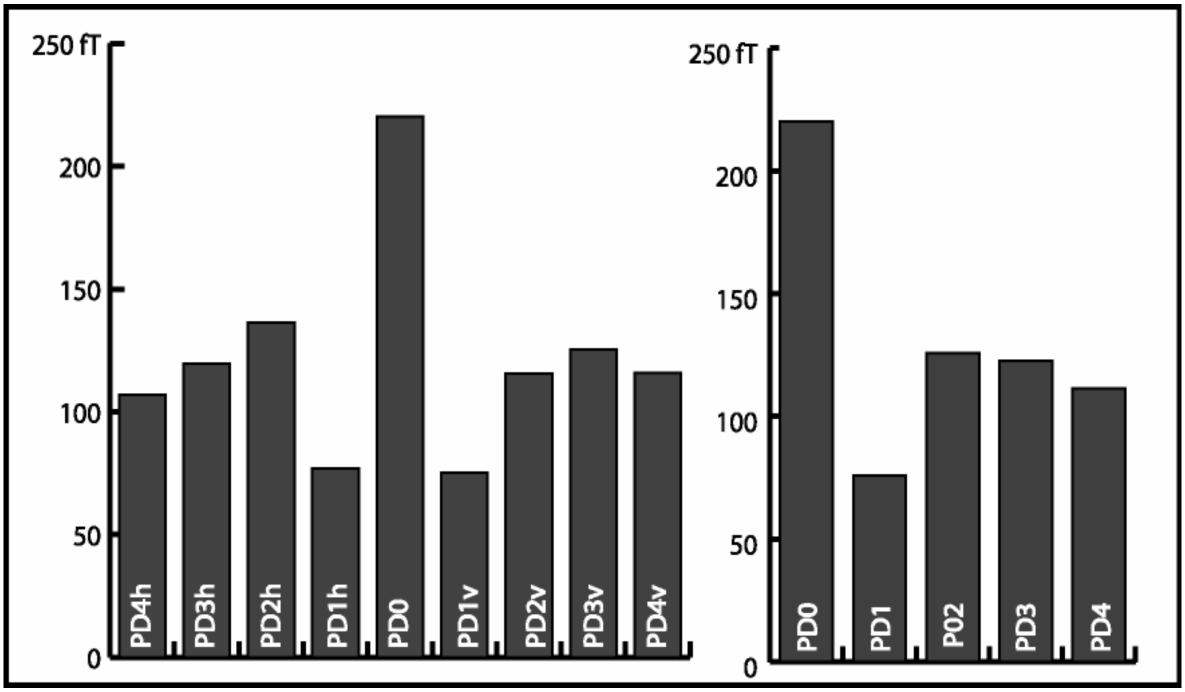

Fig. 20: *ERMF results of the meta-analysis.* The ERMF results were quantified in a time-window between 120 and 152 ms. The left part illustrates the unfolded pattern (indexing the direction towards the horizontal meridian (positions 1 through 4 in Fig. 6) with “h” and those towards the vertical one (positions 6 through 9) with “v”). The pattern resembles a Mexican hat, that is mostly symmetrical across the two directions. The right panel displays the same data collapsed across mirror-symmetrical locations with respect to the central position.

Current source localization was based on difference waves PD0-minus-PD4 (for estimating the excitatory effect) and PD1-minus-PD4 (for estimating the inhibitory effect), analogous to the approach pursued in Experiment 1. This resulted in very similar SDEs for both effects, originating in early-to-intermediate visual cortex areas along the ventral visual processing stream (Fig 21). Although the current strength is higher for the excitatory than the inhibitory effect, both SDEs are almost identical in their spatial distribution, indicating a neural sources at the same cortical level.

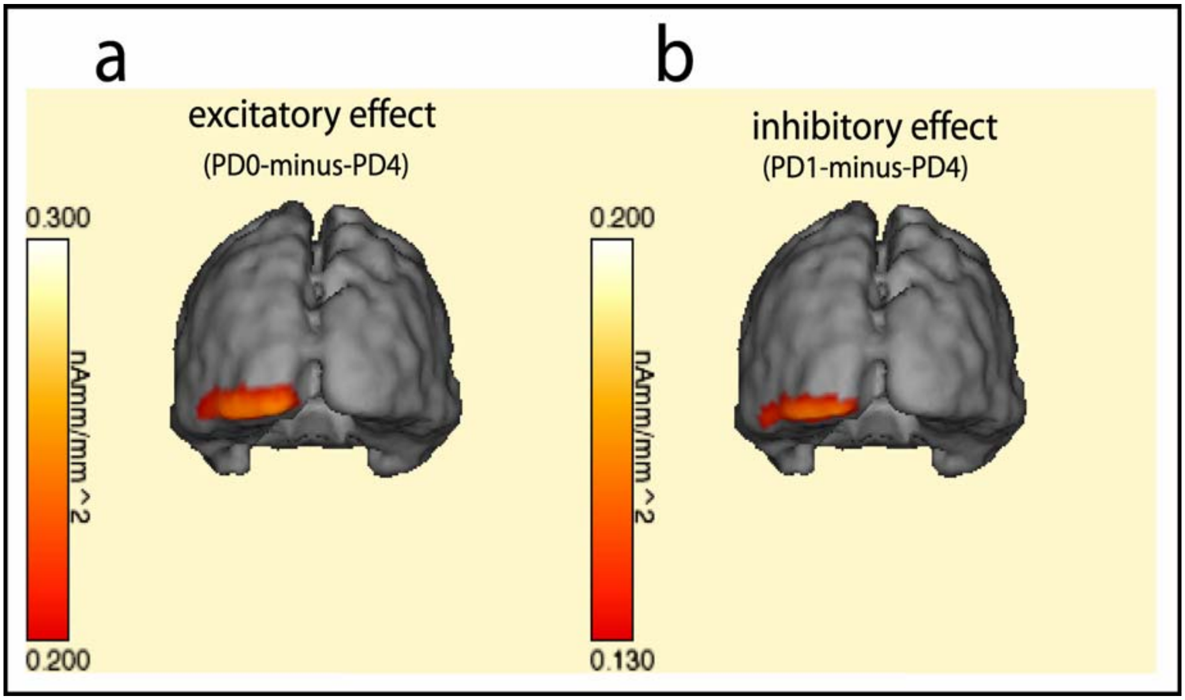

Fig. 21: *Distributed source analysis*. **(a)** SDE distribution for the average attentional enhancement effect between 120 and 152 ms. **(b)** SDE distribution reflecting the average surround attenuation between 120 and 152 ms. Both sources reside in early-to-intermediate visual cortex.

9.3 Discussion

This overall analysis was based on an average across different experiments .This yielded a more precise estimate of whether the profile is fully symmetrical with respect to the two directions from the probe-position. There is experimental evidence compatible with surround inhibition to be a bit more sharp-edged towards the horizontal meridian, as in this direction a better attentional resolution has been demonstrated (Carrasco et al., 2004). The results of this meta-analysis here, however, do not reveal statistically significant effects.

An analysis of the neural sources underlying attentional enhancement and suppression, yielded an SDE distribution that was more tightly circumscribed as in Experiment 1 alone (see Fig. 7). The sources appear to be confined to early-to-intermediate visual cortex, and are strictly lateralized to the hemisphere contralateral to the side comprising the search arrays, which is consistent with numerous demonstrations of attentional modulations in these areas (e.g., Moran and Desimone, 1985; Luck et al., 1997a; Tootell et al., 1998). Furthermore, the spatial configuration did not differ between enhancement and suppression, while the central enhancement effect again appeared to be larger. This pattern is in direct accord with STM, as it predicts that the attentional modulation appears within neighboring units at the same hierarchical level (Tsotsos et al., 1995). Moreover, although attentional surround suppression is potentially also present in higher-level areas of the visual processing hierarchy, the detection of activity from lower-level areas is more robust because a larger number of neurons participates with each downward step in the hierarchy (Tsotsos et al., 1995).

10 General Discussion

The set of experiments reported in this thesis aimed at investigating the spatio-temporal profile of the focus of attention, that has been traditionally envisioned as a simple monotonic gradient. To this end, the cortical responsivity was probed by a task-irrelevant stimulus at varying distances from the focus of attention. Across the different experiments, evidence could be mounted suggesting that the focus of attention is not a simple gradient, but rather a Mexican hat shaped activity profile.

10.1 The spatio-temporal profile of the focus of attention

Traditional views have envisioned the focus of attention as a spotlight, a zoom-lens or a monotonic gradient. In a spotlight, resources are assumed to be evenly distributed throughout the attended area (Posner, 1980; Posner et al., 1980). Accounts in terms of the zoom-lens model do also propose a flat distribution of attentional resources, with the additional assumption that the spatial extent of the focus trades with the strength of the focus due to a fixed amount of attentional resources (Eriksen and James, 1986; Castiello and Umilta, 1990). Both notions, the fixed-sized spotlight and the zoom-lens, model have been challenged by experimental findings, that established a monotonic relationship between the distance from the focus of attention and the degree of attentional influence (e.g., Downing and Pinker, 1985; LaBerge and Brown, 1989).

A related question concerns the mechanism underlying these distributions. Whereas the classical conception of a spotlight implies that a region in space can be highlighted through enhancing the signal at this location, other investigators favor the notion of an aperture, that excludes the information from all other locations through suppression (Navon, 1990). Thus, either attentional enhancement or suppression of sensory processing is emphasized, and both notions have experienced experimental support both from studies investigating monkeys (e.g., Moran and Desimone, 1985; Treue and Maunsell, 1996; Vanduffel et al., 2000) and humans (e.g., Corbetta et al., 1990; Luck et al., 1993; Luck et al., 1997b), and it is commonly assumed that both mechanisms (relative enhancement of the relevant and relative suppression of the irrelevant information) coexist during attentional focusing. This notion has recently received more direct experimental support from studies that demonstrated a spatially structured cooperation of attentional enhancement and suppression (Smith et al., 2000; Slotnick et al., 2003; Pinsk et al., 2004; Schwartz et al., 2005).

The notion of coexistence has been incorporated in a number of computational models, which predict an inner structure of the focus of attention with a zone of relative enhancement encompassed by a region of pronounced suppression of sensory processing (e.g., Tsotsos et al., 1995; Raizada and Grossberg, 2003). The most prominent example of such a model is the Selective Tuning Model (STM) by Tsotsos and co-workers (Tsotsos et al., 1995; Tsotsos, 1999; Tsotsos et al., 2001). Importantly, in the STM the Mexican hat profile is not an ad hoc model assumption, but an emergent property of the computations involved (Tsotsos, 1990). STM proposes a three-stage process that ultimately prunes all inputs that contribute to the signal of the attended object but represent nearby items. After a first feedforward sweep of attention-independent processing through the visual hierarchy, the unit that best represents the attended object is determined. This is followed by a feedback traversal, that prunes away connections from units that do not directly signal the properties of the attended object but that of different objects concurrently present in the receptive field. As this pruning only affects the direct inputs to this unit, the resulting zone of inhibition is limited to the spatial extent of its receptive field size. This automatically prunes irrelevant input from within the receptive field of this unit, irrespective of the size of its receptive field (i.e., the inhibitory surround gets wider, the larger the receptive field is). In its center a zone of unaffected signaling, the pass-zone, refines the coding of the attended object in a second feedforward sweep of information flow through the hierarchy. The Mexican hat profile provides a very efficient solution of the problem of ambiguous coding in the massively convergent visual processing hierarchy. This coding ambiguity arises from the fact that the input of a cell representing the attended object is confounded by the signal of close-by stimuli, because receptive field size increases along the visual hierarchy. Thus, some mechanism is required that attenuates the confounding information from locations close to the attended one.

Albeit being very plausible from a computational viewpoint, little direct evidence in favor of a Mexican hat profile has been provided thus far. Relevant evidence has been mostly restricted to psychophysical experiments (e.g., Bahcall and Kowler, 1999; Mounts, 2000a; Cutzu and Tsotsos, 2003), whereas neurophysiological demonstrations have remained extremely sparse and of restricted scope (Slotnick et al., 2002; Muller and Kleinschmidt, 2004; Schall et al., 2004). The experiments of this thesis provide clear neurophysiological support in favor of a Mexican hat profile as suggested by the STM. Using a passive probe-paradigm while measuring the magnetoencephalographic response of human observers performing a visual search paradigm, Experiment 1 demonstrated that the focus of attention is surrounded by a narrow zone of suppression, that tapers off at more distant locations. Experiment 2 ruled out potential sensory explanations in terms of color pop-out or other bottom-up sensory effects, and revealed that the Mexican hat profile represents a truly attention-driven profile. The general pattern of results was relatively unaffected by several experimental variations. Specifically, rendering the target-discrimination more difficult, changing the target-defining feature (luminance versus color), and omitting the distractors from the search array all lead to similar results. Thus, the Mexican hat profile appears to be a rather general expression of attentional focusing, that only appears in the presence of attention (Experiment 2) but is uniformly elicited under various conditions that generally necessitate attentional focusing (see also section 10.2).

The present data provide support even more specific predictions of the STM. (1) While surround suppression is a rather common notion in many models of visual attention, STM predicts surround inhibition to appear as a very narrow zone with locations further away producing intermediate activity levels. The present data confirm this notion. Specifically, only the position directly adjacent to the focus of attention appears to be actively suppressed (Experiment 2), while positions further away are not consistently affected by attention at all.

(2) Because in the STM, surround suppression results from a delayed top-down propagating hierarchical WTA process, the time-course of the Mexican hat profile is predicted to appear with a certain delay relative to the ERMF correlates of the initial feedforward sweep of processing. STM predicts three traversals through the visual hierarchy (Tsotsos et al., 1995): (a) an initial feedforward sweep, that is mostly unaffected by attention, (b) a top-down process that prunes all connections contributing to the unit representing the attended object but reflecting other objects simultaneously present, producing a zone of suppressed responses surrounding the target object, and (c) a second feedforward traversal through the visual hierarchy that refines the coding of the attended object. Experiment 6 demonstrates that the Mexican hat profile appears around 250 ms, but disappears already after approximately 325 ms. This time range is relatively early but is definitively beyond the earliest feedforward sweep through the visual hierarchy. This timing is consistent with descriptions of a delayed attentional feedback reactivating areas early in the visual hierarchy after approximately 200 ms (Martinez et al., 1999; Lamme and Roelfsema, 2000; Mehta et al., 2000a; Noesselt et al., 2002). Furthermore, the timing is consistent with estimates of the attentional dwell time and neurophysiological findings on attentional focusing (Chelazzi et al., 1993; Luck and Hillyard, 1994a; Moore et al., 1996; Theeuwes et al., 2004).

(3) The top-down propagation account in STM does predict largest effects of surround suppression appear in lowest levels of the selection hierarchy. Consistently, current source analysis revealed maximal effects in early visual cortex areas, presumably V1. This is all the more notable, as numerous studies that compared the degree of attentional modulation across different visual areas have reported the largest effects in higher-level areas (Tootell et al., 1998; Cook and Maunsell, 2002).

(4) The Mexican hat profile characterized in the present experiments is independent of whether distractor items are present or not – an observation that confirms a principal prediction of the STM. STM makes differential predictions for the presence/absence of distractors at the different cortical hierarchical levels,

where it might lead to enhancement or suppression of responses in the periphery of the attentional focus. Importantly, these modulations appear outside the pass-zone in the center of the attentional focus and the surrounding inhibition. Thus, STM predicts a Mexican hat profile even in the absence of distractors, while there might be subtle changes in the response to stimuli presented at some distance to the attentional focus. As opposed to this prediction, little evidence for differential responsivity at the more distant positions (PD2 through PD4) was found, which might be due to the specific layer being probed.

The fact that the Mexican hat profile appears independent of distractors sets its underlying mechanism apart from a number of psychophysical demonstrations as well as neurophysiological correlates of distractor suppression. The majority of reserach into attention has emphasized that effects of attention are maximal (or even only present) in the presence of distractors (e.g., Moran and Desimone, 1985; Motter, 1993; Luck et al., 1997b; Cepeda et al., 1998). Thus, it would have been conceivable, that a less differentiated profile would result when the distractors are absent. However, the results turned out to be virtually identical with and without distractors in. This is in stark contrast to the N2pc, a component related to attentional focusing, that appears in a very similar time-range (approximately between 200 and 350 ms). For this component a strong relationship has been demonstrated between its amplitude and the presence of distractors (Luck and Hillyard, 1994a). Thus, while both, the Mexican hat profile and the N2pc component, appear within the same time-range, they seem to reflect differential processes (Luck, 1995). In contrast to the N2pc, the Mexican hat profile appears to represent a more elementary and automatic attentional selection process.

The generality of the Mexican hat profile is further emphasized by Experiment 3. Here, the target defining feature-contrast was varied between color and luminance. The fact that both feature-dimensions have been shown to be processed in an “attribute-specific” manner (Morrone et al., 2002, 2004) and in (at least partially) different structures of the visual system (DeYoe and Van Essen, 1988; Livingstone and Hubel, 1988) would suggest that a differential pattern of response might arise. However, the Mexican hat profile did not differ between the two feature-contrast conditions, suggesting that the neural operations that underlie the Mexican hat profile appear to be independent of this modification. Taken together, the Mexican hat profile appears to reflect an automatic attentional routine-like operation, that requires volitional initiation, but from then on takes place automatically.

10.2 Automaticity

The experiments reported in this thesis provide strong evidence for a complex inner structure of the focus of attention that resembles the shape of a Mexican hat. However, several results call into question, that this profile reflects a process that comprises all key-aspects related to visual attentional selection. For example, it is revealing not to find any difference with respect to the presence of distractors, because distractors typically give rise to strong attentional modulation effects on cell- firing (e.g., Moran and Desimone, 1985; Motter, 1993; Luck and Hillyard, 1994a; Cepeda et al., 1998). Also, the Mexican hat profile appears not to be altered by different levels of task-difficulty (Experiment 4), and across different target-defining feature-contrasts (Experiment 3). Nevertheless, it is not present in the absence of attention (Experiment 2). It thus appears that the process underlying surround inhibition does not so much reflect volitional aspects of attentional focusing, but a more automatic routine-like attentional process. In terms of the STM account, the downward cascade that eliminates the signal of nearby distractors, may be conceived of as a more mandatory routine that automatically refines the spatial coding of the attended object once it has been selected based on bottom-up calculations leading to a winner in the respective top-layer.

Routine-like attentional operations have been proposed by a number of authors (Ullman, 1984; Roelfsema et al., 2000; Cavanagh, 2004; Roelfsema, 2005). Cavanagh, for example, divides processing routines into three broad classes: vision routines, attention routines and cognition routines (Cavanagh, 2004). Vision routines are lowest in hierarchy, taking place fully automatically.

Attentional routines, are consciously initiated, but then proceed automatically. Finally, cognition routines represent combinations of attentional routines, that are under conscious control. It is conceivable, that surround inhibition is the result of an attentional routine. It clearly does not proceed with full automaticity, as Experiment 2 demonstrates that it is absent when attention is withdrawn from the search array, while it nevertheless appears to bear some automaticity as indicated by the similar results under various experimental conditions. Such a routine would semi-automatically segment the signal of the attended object from the overlapping representation of its surround, which appears a reasonable mechanism to counteract the blur introduced by neuronal convergence.

10.3 Center enhancement

Experiment 6 demonstrates, that an inhibitory surround has formed after approximately 250 ms, which is followed by a phase of markedly enhanced processing in the center of the focus, that peaks after 325 ms. The delay with which center enhancement builds up, argues in favor of separate processes underlying this enhancement and surround suppression, and is consistent with numerous demonstrations of attentional enhancement in ERP studies in humans (e.g., Hillyard and Münte, 1984; Mangun and Hillyard, 1991). This strong enhancement might coincide with a second bottom-up traversal through the visual hierarchy, once the interfering information from adjacent locations has been attenuated as predicted by STM (Tsotsos et al., 1995). Still, there is one aspect to this result that is not predicted by STM. Specifically, STM does not include a mechanism that actively enhances information in the very center of the attentional focus but solely relies on suppression of irrelevant information. Experiment 2, however, relates the augmented response at PD0 to active attentional enhancement, as the response during attentive processing exceeds that recorded in the absence of attention by far. Furthermore, Experiments 4 and 5 indicated that center enhancement, as opposed to surround suppression, might be susceptible to variations of task-difficulty and distractor-presence. It appears that additional attentional processes are active, consistent with reports of attention employing several separable mechanisms (Luck, 1995).

10.4 Relation to other phenomena

One objection to the interpretation of the experiments in this thesis concerns the recent demonstration of retinotopically specific suppression during the anticipation of distractors (Serences et al., 2004). As the probe-position was fully predictable throughout all experiments, it might be proposed that subjects developed a sustained “protective” inhibition of the probe-position (PD0). This is somewhat supported by a slight slowing of responses at PD0. However, such a sustained suppression strategy should influence the results in a comparable manner across the different probe-distances, and should nullify with the FP-minus-FO difference. Only in the unlikely case that subjects specifically set up extra suppression for the probe-position when focusing PD1-targets, a differential pattern including surround suppression might have resulted. This strategy, however, does not appear to be very probable, as the probe should not have interfered more with target discrimination than the surrounding distractors, that were present under all conditions. Indeed, the presentation of the probe only slowed responses by 4 ms in Experiment 1. Furthermore, this slowing was not symmetrical with respect to the probe-position, whereas the ERMF data were. Specifically, Position 4 (PD1 towards the horizontal meridian) showed no indications of an influence of the probe onto reaction times, which might be taken to argue in favor of a strategy suppressing the position of potential probe-presentation, whereas Position 6 displayed a robust probe-effect. Moreover, psychophysical investigations have demonstrated surround inhibition, despite the fact that distractor locations were unpredictable (Cutzu and Tsotsos, 2003). Additionally, the results of Serences and colleagues were gathered after very long SOAs, implying that it might take longer to establish this anticipatory effect, than the 250 ms between search frame onset and probe in the experiments detailed in this thesis. Finally, Experiment 6 demonstrated that the inhibitory surround is mostly restricted to a time-window around 250 ms after search frame onset. That a “protective” surround is only set up during this short time-window and turned off while a probe might still be presented, is not a reasonable possibility.

The results of the studies presented in this thesis might be relevant for the interpretation of studies that report indications of a split attentional focus. Specifically, many studies that report a split focus capitalize on the fact, that the measure of attentional modulation (be it a BOLD modulation, that of a behavioral variable, etc.) is reduced at a location intervening the two positions currently being attended (e.g., Awh and Pashler, 2000; Muller et al., 2003a; McMains and Somers, 2004). It is conceivable, however, that such reduction of activity reflecting the intervening space simply coincides with the inhibitory surround of the attended objects. Consistent with this notion, Awh and Pashler suggested that the lack of beneficial treatment through attention at the position intervening the split focus relies on suppression of the distractor processing (Awh and Pashler, 2000).

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