The attentional field has a Mexican hat distribution

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Abstract

We assessed the interference by distracter letters on target discrimination as a function of the distance between incompatible distracters and target. The slope of the response time—distance function supports a Mexican hat pattern of attentional modulation in the visual field. We relate the results to our recent finding of neural activity suppression in primary visual cortex coding locations in the vicinity of an attended region [Müller, N. G., & Kleinschmidt, A. (2004). The attentional 'spotlight's' penumbra: Center-surround modulation in striate cortex. *Neuroreport*, *15*(6), 977–980]. As behavioral performance parallels activity modulation of primary visual cortex but not other areas we propose that perceptual capacities are determined by attentional response properties of V1.
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1. Introduction

The existing models of spatial attention, e.g. spotlight (Posner, 1980; Posner, Snyder, & Davidson, 1980), zoom lens (Eriksen & St James, 1986; Eriksen & Yeh, 1985), gradient (LaBerge, 1983; LaBerge & Brown, 1986; LaBerge, Carlson, Williams, & Bunney, 1997) make different assumptions as to the size and boundary of attention-mediated perceptual facilitation (i.e., the 'attentional field'). Yet, most of them agree that this facilitation decreases monotonically with the distance from the focus of attention centered on the target. However, some studies have reported small regions of perceptual suppression surrounding the region of enhanced processing (Bahcall & Kowler, 1999; Caputo & Guerra, 1998; Carr & Dagenbach, 1990; Cutzu & Tsotsos, 2003; Eriksen, Pan, & Botella, 1993; Kim et al., 1999; Krose & Julesz, 1989; Mounts, 2000a,

2000b; Pan & Eriksen, 1993; Slotnick, Hopfinger, Klein, & Sutter, 2002; Steinman, Steinman, & Lehmkuhle, 1995). We have recently provided physiological evidence for surround inhibition in showing that neural activity in early visual areas coding locations in the vicinity of an attended location was suppressed (Müller & Kleinschmidt, 2004). Activity in early visual areas coding more distant locations was relatively enhanced compared to passive viewing but to a lesser extent than in those areas coding the relevant location. We suggested a Mexican hat-like distribution of attentional modulation within early visual cortex.

However, behavioral evidence for a true Mexican hat distribution of attentional modulation is still meager as even the studies which reported a surround inhibition lacked to confirm other predictions of the model. For example, most studies on surround inhibition describe a linear increase of perceptual facilitation with increasing distance from the attentional center (i.e., an inversely oriented gradient model), which would cover only part of a Mexican hat (i.e., the brim). In a Mexican hat model, processing of stimuli very close to the center of

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attention should still be enhanced. Further, the behavioral facilitation should level off at large distances. Instead, usually the most remote stimuli, i.e., directly opposite to the cued location in case of a circular array, yield the best performance.

The lack of evidence for a Mexican hat distribution may be related to some shortcomings of former studies with respect to the methods with which they mapped the attentional field (discussed in detail by Intriligator & Cavanagh, 2001). Generally, attentional distribution is addressed in tasks in which a cue or a salient pop-out stimulus first directs attention to a location. Subsequently, a target at this location either has to be compared to a second target at another location (Bahcall & Kowler, 1999; Cutzu & Tsotsos, 2003, Exp 1–3) or the target or a probe stimulus turns up at an uncued location (Cutzu & Tsotsos, 2003, Exp 4; Mounts, 2000a, 2000b). In either case, the distance between the uncued and the cued location is the critical variable. These studies find that stimuli which are presented closer to the cued location are less accurately reported than stimuli further away which is then taken as evidence for surround inhibition. This procedure has two main drawbacks: first, rather than addressing the distribution of attention while it is *focused* on the cued location, these paradigms test perception capabilities when attention has to cover the uncued location and thus depend on the speed and/or accuracy with which attention is either *shifted* to the uncued location or *split* between cued and uncued locations. Therefore, these studies are difficult to interpret with respect to the distribution of the attentional field during continuous focused attention. Their results could also be accounted for by models stating that attention is shifted to more remote instead of nearby locations as soon as the relevant information does not turn up at the primary focus or that splitting of attention in order to cover two targets is more easily accomplished at larger separations (see discussion).

The problem is often aggravated further by the fact that the stimulus at the uncued location has pop-out characteristics (i.e., a probe on a uniform background or a red letter among an array of black letters). Such pop-out stimuli can be detected without the need to focus attention (Treisman & Gelade, 1980), but once they are detected they are known to automatically attract attention thereby pulling away attention from the proposed center.

This raises another crucial point: the usual lack of control of stimulus alignment with respect to the vertical visual field meridian.[1] Several studies have shown a

bilateral field advantage for visual processing, i.e., superior processing when stimuli are presented in separate visual hemifields (Brown & Jeeves, 1993; Brown, Jeeves, Dietrich, & Burnison, 1999; Brown, Larson, & Jeeves, 1994; Kraft, Müller, Hagendorf, Villringer, & Brandt, 2002; Larson & Brown, 1997; Sereno & Kosslyn, 1991). Most studies so far have confounded distance with bilateral presentation: cue and target (or the two targets) were more likely to be located in the same hemifield at small separations and in different hemifields at large separations. Thus, the results of these studies cannot distinguish unequivocally distance from hemifield effects.

In order to circumvent these shortcomings of prior studies, we chose to use an adaptation of the classical flanker paradigm (Eriksen & Hoffman, 1973) instead. Subjects had to discriminate target letters that were shown at a fixed location on an imaginary hemicircle centered at fixation. Simultaneously to the target letter, distracter (or flanker) letters were presented at various positions on the hemicircle (see Fig. 1). These letters could either be neutral, compatible or incompatible with respect to the target, i.e., were linked with no, a congruent or a conflicting response with respect to the target letter. Compared to the studies criticized above, this paradigm avoids task relevant stimuli at uncued locations with the risk of unwanted shifts or splitting of attention.

Numerous studies have shown that nearby incompatible flanker stimuli, although irrelevant for the task, interfere with the responses to the target, making them
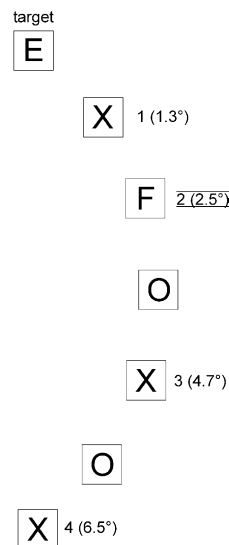

Fig. 1. Experimental stimuli. The figure presents an example for a trial in the difficult version of the task in which the letters E and F had to be discriminated at the uppermost position. An incompatible distracter letter is shown at position 2. Note that all other positions are occupied by neutral letters with respect to the target. The three other positions at which (in)compatible letters could be presented are marked and their distance to the target is provided (visual angle).

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[1] Note, that He, Cavanagh, and Intriligator (1996) and Intriligator and Cavanagh (2001) also reported differences of attentional resolution with respect to the horizontal meridian. This, however, is an issue different from the focus of our experiment where the amount of attention—not its resolution—which a stimulus at a given location receives is crucial.
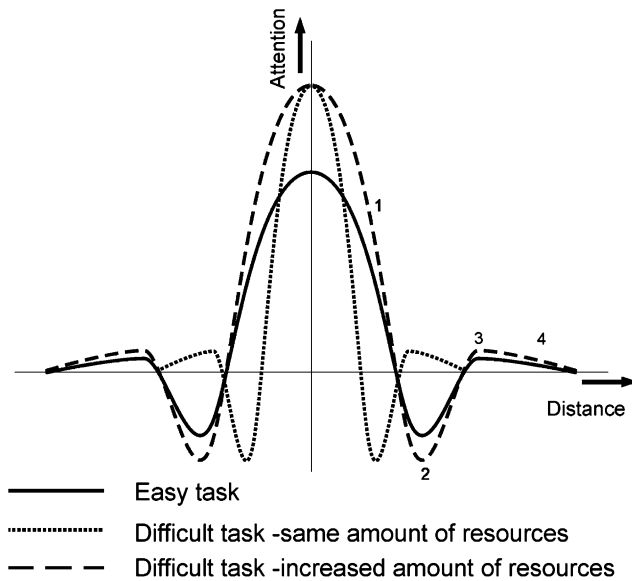
Fig. 2. The proposed Mexican hat like distribution of attentional modulation. The dashed lines represent the possible distributions of attention in the more difficult task depending on whether additional resources were made available or not. The numbers represent the different target-distracter distances and their related 'activation' within the attentional field.

less accurate and slower. [2] The crucial question in our study was how the distance between target and incompatible distracter letter would modulate behavior. This question has been addressed with the flanker task before (Eriksen et al., 1993; Eriksen & St James, 1986; Eriksen & Yeh, 1985). However, our study varied in several ways: (1) we controlled for hemispheric distribution of stimuli and (2) sensory input and (3) we assessed target-distracter distances over a much larger range. Doing so, we sought evidence for a Mexican hat distribution, which previous flanker tasks had failed to find. We computed the response time differences of trials with incompatible and neutral distracters and plotted them as a function of distance. In case of a Mexican hat distribution, the response time differences should be largest for nearby distracters, should then drop to zero in the hypothesized inhibition zone, then increase and finally taper off.

The distribution of attention is likely to vary across tasks. Lavie (1995) suggested that tasks which impose a high load on processing resources lead to stronger focusing of attention. Thus, if the amount of resources that is devoted to a task remained the same (reflected by the area under the function), then a more difficult task should yield a steeper and more narrow distance-response time function (LaBerge, 1983). Alternatively, additional resources may be activated in the more diffi-

cult task (see Fig. 2). To test these hypotheses, we varied task difficulty by manipulating the similarity of the two letters subjects had to discriminate at the target location.

2. Methods

2.1. Subjects

Ten healthy right-handed students (4 females, age 21–30 years) with reported normal color vision and normal or corrected-to-normal visual acuity were paid for their participation as subjects in the study conducted in conformity with the declaration of Helsinki.

2.2. Paradigm

The experimental paradigm is illustrated in Fig. 1. Stimuli were the dark-blue letters E, F, X and O (1° height, 0.6° width), presented on a light-gray background. The letters were presented within dark blue outlines of squares (side length 1.2°) that served as placeholders and were present permanently. Seven squares were placed in the right visual hemifield on an imaginary circle of 4° degrees radius centered in the middle of the 17″ computer screen (refreshing rate 75 Hz). Taking the top of the circle as 0°, the squares (and letters) were placed at 36° and at each 18° increment from that position (corresponding to 1.3° visual angle between two neighboring squares). Subjects were seated 1.5 m from the screen and fixated a marker in the middle of the screen throughout the whole experiment.

Letters were presented simultaneously within the seven squares for 150 ms with an interstimulus interval of 1.5 s. This procedure eliminated confound from non-attentional effects like differences in sensory masking which might have occurred in case only two letters with varying distance had been presented. The subjects' task was to indicate within 1 s after letter onset by button presses (keys 'v' and 'b' on a standard German computer keyboard, counterbalanced across subjects, pressed with index and middle finger of the right hand) whether the letter presented in the square at the top was an X or O in the easy version of the task, or an E or F in the difficult version of the task. At the target location, the letters X, O, E and F were presented in a randomized order. In neutral trials, all other locations contained neutral letters with respect to the target letters: in the easy version letters E and F, in the difficult version letters X and O. In incompatible and compatible trials, one location contained a distracter letter that interfered with the target response, whereas all other locations contained neutral letters. The crucial factor was distance of the (in)compatible distracter from the target. Four distances were chosen: (in)compatible distracter at the position next to the target (visual angle 1.3°), at the

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[2] Note that the effects from compatible distracters are much less clear and will not be discussed in this paper.

second next position (visual angle 2.5°), at the fourth position (visual angle 4.7°) and at the furthest position (visual angle 6.5°). [3]

Easy and difficult versions of the task were tested in different sessions at least 48 h apart in order to minimize interference from the preceding task due to the change in target-distracter assignment. Half of the subjects performed the easy version first, the other half performed the difficult version first. In each version, every distance was tested 1024 times. After a block of 16 trials subjects were allowed to rest until they started the next block by pressing the space key. At the beginning of a block, fixation mark and placeholder squares were presented for 3 s before the first letters were shown.

Subjects were given written instructions before each session in which they were only informed about the task they had to perform but were left unaware of the experimental manipulations at the distracter locations. They completed four training blocks before each session and were instructed to respond as quickly as possible while keeping errors to a minimum.

2.3. Fixation control

In order to ensure central fixation and covert alignment of attention, eye movements during the experimental sessions were recorded with a digital infrared eyetracker (Ober 2, Permobil Meditech, Timra, Sweden) controlled by a personal computer that was linked via parallel port to another personal computer used for stimulus presentation (running the Experimental Run Time System software, Berisoft, Frankfurt, Germany). The stimulus computer also sent trigger signals to the eye recording system, so that the beginning of each trial could be identified. The setup included head stabilization with a chin and forehead rest and darkening of the experimental room. The number of saccades within 1 s after letter onset (corresponding to maximal response time) were counted. None of the subjects performed saccades on more than 1% of trials, so that we felt save to resign from excluding trials with eye movements.

2.4. Data analysis

Consistent with previous studies involving the flanker task, we focused on reaction time (RT) measures instead of accuracy as dependent variables. Eriksen and St James (1986) suggested RTs to be a more sensitive measure of the degree of concentration of attentional resources. Thus, we aimed at keeping accuracy levels

high to increase the number of correct trials where reaction times could be analyzed.

With median (to minimize the influence from outliers) RTs for correct answers a repeated measure ANOVA with the factors task (easy, difficult), compatibility (neutral, compatible, incompatible) and distance (very close (1), close (2), far (3), very far (4)) was calculated. Another ANOVA was calculated for RT differences between trials with incompatible distracters and those with neutral distracters. The latter was done in order to eliminate overall differences in response speed between difficult and easy trials, so that compatibility effects could be assessed more directly. In case of significant interactions, pairwise comparisons (Fisher's least significant difference) were calculated to follow the interaction.

Degrees of freedom and p-values were Greenhouse-Geisser corrected where appropriate.

3. Results

RTs were slower in the difficult task and in trials with incompatible distracters (see Fig. 3). Only the latter yielded significant variations with target-distracter distance. We found main effects for task difficulty ($F(1,9) = 15.2$, $p < 0.004$), compatibility ($F(1.8, 16.6) = 12.32$, $p < 0.001$) and distance ($F(2.5, 22.5) = 8.10$, $p < 0.001$). Order of the tasks (i.e., easy or difficulty session first) had no effect ($F(1,8) = 2.24$, $p = 0.173$), indicating that interference between easy and difficult sessions
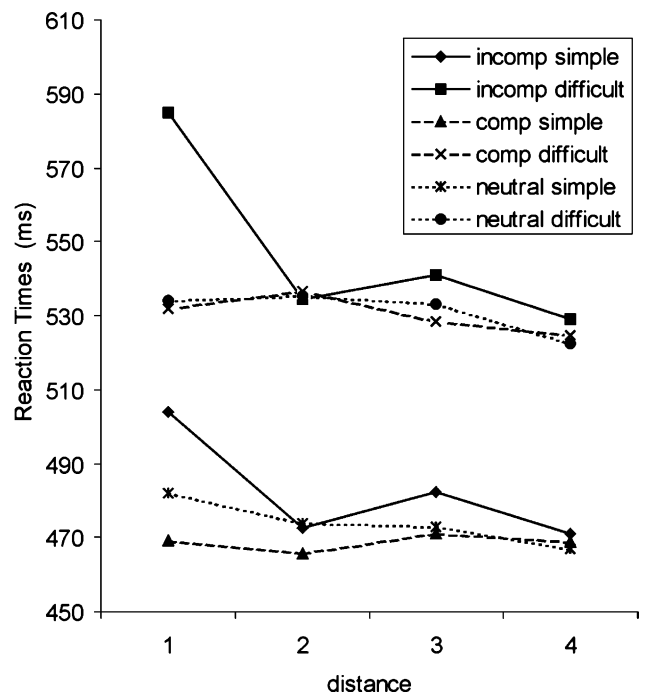
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[3] Selection of these values was driven by extensive pilot testing and previous studies {Sagi, 1986, #293} (Bahcall & Kowler, 1999; Mounts, 2000a; Sagi & Julesz, 1986) that showed the suppression zone at the given eccentricity to be located roughly at 2° from the attention center.

Fig. 3. Reaction times (RT) as a function of target-distracter distance.

which might have been caused by making the same letter a target in one version and a distracter in the other version of the task was negligible. The interaction distance × compatibility yielded a significant effect with $F_{(2.2, 19.7)} = 4.76$, $p < 0.02$. However, there was no task × compatibility interaction ($F_{(1.7, 15.7)} = 1.61$) and no task × distance interaction $F_{(2.9, 25.8)} = 0.47$.

In order to follow the distance × compatibility interaction, pairwise tests were performed. Only the comparisons between incompatible and neutral trials and incompatible and compatible trials yielded significant effects ($p < 0.001$, $p < 0.003$, respectively) but not between compatible and neutral trials ($p > 0.4$).

When incompatible, compatible and neutral trials were analyzed separately for distance effects, only incompatible trials yielded a significant effect ($F_{(2.5, 22.5)} = 16.2$, $p < 0.001$; $F_{(1.6, 14.4)} = 1.48$ for neutral trials, $F_{(2.2, 19.9)} = 2.18$ for incompatible trials).

Thus, target processing was modulated as a function of target-distracter distance only by incompatible distracters.

RT differences between incompatible and neutral trials are presented in Fig. 4. For RT differences between compatible and neutral trials there was a main effect of distance ($F_{(3, 27)} = 5.91$, $p < 0.01$) but not task difficulty ($F_{(1, 9)} = 1.24$). Pairwise comparisons revealed significant differences between distance 1 and all other distances ($p < 0.03$, $p < 0.05$, $p < 0.01$) and between distance 2 and 3 ($p < 0.05$) but not between distance 2 and 4 ($p > 0.3$) and 3 and 4 ($p > 0.5$). Fig. 3 confirms that at distance 2 incompatible and neutral trials did not yield different reaction times, whereas at the other distances incompatible distracters slowed the reaction times. This observation is further supported by a regression based curve estimation which showed that the RT-distance

relationship was best explained by a cubic function ($F_{(3, 76)} = 7.1$, $R^2 = 0.21$, $p < 0.001$; $F_{(1, 78)} = 7.9$, $R^2 = 0.09$ for the linear function, $F_{(2, 77)} = 7.8$, $R^2 = 0.17$ for the quadratic function).

Mean accuracy was 95.2% in the easy and 89.9% in the difficult task. The ANOVA revealed main effects for task difficulty ($F_{(1, 9)} = 19.54$, $p < 0.002$). Incompatible trials yielded more errors than neutral trials (main effect for compatibility $F_{(1, 9)} = 8.34$, $p < 0.02$) and more errors were committed at small distances (main effect distance $F_{(2.5, 22.5)} = 7.97$, $p < 0.001$). Further, there was a significant interaction compatibility × distance ($F_{(2.3, 21.2)} = 5.98$, $p < 0.007$) indicating that incompatible distracters interfered with target processing accuracy the most at small separations. Due to the small number of errors we resigned calculating further tests.

4. Discussion

This study presents behavioral evidence for a Mexican hat-type distribution of attention-enhanced perceptual discrimination, i.e., of the attentional field. We found that distracter letters inducing a response incompatible to the one required by the target delayed response times the most when they were closest to the target letter (1.3°). Incompatible distracter letters placed 2.5° away from the target, on the other hand, did not delay responding compared to neutral letters whereas at 4.7° and 6.5° some interference was again measurable. As we controlled for sensory input by leaving the overall appearance of the stimulus array virtually the same throughout the whole experiment, variances in low-level, pre-attentive interference like sensory lateral masking across different target-distracter distances can be ruled out as cause for the observed effects. The same holds for confound from the bilateral field advantage (Brown et al., 1999; Larson & Brown, 1997; Sereno & Kosslyn, 1991). As all stimuli were presented at the right side of the vertical meridian, stronger interference from distracters at larger distances could not be attributed to their appearance in the hemifield opposite from the target. Instead, the observed distance effects are most likely related to the amount of attentional enhancement an incompatible distracter received at a specific distance. This interpretation is supported by previous demonstrations that only flankers that receive attention interfere with target processing (Freeman, Sagi, & Driver, 2001).

Our first finding, strongest interference from incompatible distracting stimuli when they are closest to the target, has been reported in numerous previous studies that addressed the so-called flanker effect (Eriksen & Hoffman, 1973; Eriksen et al., 1993; Eriksen & St James, 1986). Eriksen and colleagues proposed that the attentional window around a target cannot be focused
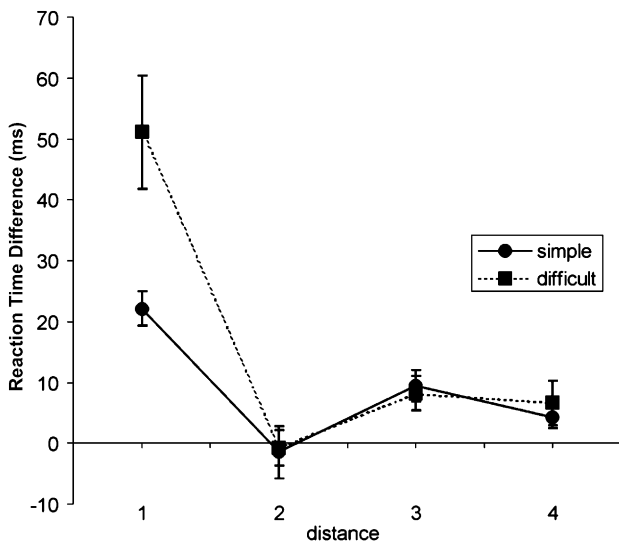

Fig. 4. RT differences between incompatible and neutral trials in the easy and difficult versions of the task. Bars represent standard errors.

infinitely and that stimuli which appear within the window would interfere with behavior. Consistent with William James's (James, 1890) conception of an attentional focus, margin and fringe, they further suggested a graded drop-off in processing resources, explaining the inverse relationship between performance and target-flanker distance in their studies.

Other than with flanker tasks, the studies cited above which found a suppression zone around an attended item reported in unison the worst performance when the relevant stimuli (i.e., either cue and target or two targets) were closest together. This obviously contradicts the finding of flanker studies including ours. The simplest explanation for this discrepancy is that most previous studies did not include stimulus separations that were in the range of Eriksen's and our smallest target-distracter distance. They thus simply may have picked values exclusively on the 'brim' of the supposed Mexican hat. Indeed the only study we are aware of (Bahcall & Kowler, 1999) which found a suppression zone and also tested small separations (~1° at 4° eccentricity) reported a trend in two of their three subjects for better discrimination performance at this small separation compared to the next largest at about 2°.

Apart from that, the most obvious difference between flanker studies and those reporting a suppression zone, is that while in the first, attention can be focused on a single location in the visual field whereas in the latter, two locations are relevant as either cue and target or two targets are spatially separate (see Section 1). The assumption of a single, stationary attentional window which enhances processing for nearby stimuli in the sense of Eriksen is a rather unlikely scenario for these paradigms. Instead, for their study, in which two target letters in an array of letters had to be reported, Bahcall and Kowler (1999) suggested that each of the targets is assigned to a separate attentional field. If the attentional fields were modeled by the difference of two Gaussians, then according to the authors the net processing strength would be reduced as soon as one attentional field would overlap with the negative region of the other attentional field, that is at close spatial separations. Alternatively, the limited resolution of attention fields might cause nearby stimuli to compete for the same resources as soon as they fall into the same field, whereas remote stimuli could make use of separate fields and resources.

In this respect, Eriksen's notion of interference between flankers and targets could easily be extended to a model that assumes target-target interference at small spatial separations. Indeed, Intriligator and Cavanagh (2001) proposed that "selection appears to require that only a single item be present within the selection region in order to be individuated and scrutinized" (pp. 206). Finally, tasks using invalid cues or pop-outs require attention to be re-directed when the target (or probe) is presented at an unexpected location (Cutzu & Tsotsos, 2003, Exp 4; Mounts, 2000a). In this case, another explanation might account for better performance with far separation of cue and target. Bahcall and Kowler (1999) suggested that a good strategy to survey a visual scene would be to sample potential targets from remote, rather than closely-spaced regions. In other words, in case the relevant information does not turn up at the expected location, instead of shifting to the next element in a dense array, it might be advantageous to shift the center of attention (and/or the gaze) further away. This holds especially if one considers the rather large extent of attentional fields, because small shifts would cover largely overlapping regions, leading to an ineffective search strategy. In sum, differences in the experimental paradigms might explain why at the same distance, target-distracter interference might be strongest whereas discriminating two stimuli might be poorest.

Other than us, Eriksen and St James (1986) reported monotonically decreasing interference between target and distracter with increasing distance in line with an attentional gradient model (see also Castiello & Umilta, 1990; Downing & Pinker, 1985; LaBerge, 1983; LaBerge & Brown, 1986). That is, their data provided no evidence of a suppression zone. The most straightforward explanation for this discrepancy are again differences in experimental setup. Eriksen and St. James used a ring of letters that covered only 1.5° and assessed three target-distracter distances ranging from 0.5° to 1.5°. Thus, with all necessary caution when comparing displays with different eccentricities, they might just have measured at distances too small to fall within the suppression zone, i.e., the Mexican hat's 'brim'. This is strengthened by their reporting interference from the distracters at even the largest target-distracter separation.

Our results also extend prior findings with respect to performance at very large separations. Previous studies on this issue usually reported the best performance for the most remote separation of stimuli (i.e., 180°). Conversely, we found that interference from distracters at the two far separations was rather small with a tendency for the farthest separation to produce least interference. Correspondingly, a cubic function fitted the RT-distance relationship the best. The reason why others reported the best performance for opposite positions of two targets (or cue and target) might be that with this alignment the two stimuli came to be located in different hemifields. The latter is known to boost performance, presumably due to the fact that the two hemispheres can operate independently to some degree (Luck, Hillyard, Mangun, & Gazzaniga, 1989). However, Bahcall and Kowler (1999) still found the best performance for farthest separated stimuli when they controlled for hemispheric distribution. In line with our results and in support of a Mexican hat model, Cutzu and Tsotsos (2003) after they had increased their cue-target distance

by increasing the radius of the imaginary circle on which the letters were presented (their Fig. 4), observed some decline in performance at the largest distances between cue and target.

4.1. Task difficulty

Based on Lavie's studies (Lavie, 1995) we had expected that task difficulty—manipulated by similarity of the letters to be discriminated—should affect the slope of the assumed Mexican hat function. Lavie has shown that distracting flankers only interfere with target processing in easy, low-load tasks. If task load is increased, for example by embedding the target letter in a row of other letters, then flanker letters will cease to interfere with target processing. In other words, in demanding, high load tasks, attention seems to be more focused to the target location. In line with this assumption, flanker stimuli have been reported to affect target processing more under distributed than under focused attention (Ito, Westheimer, & Gilbert, 1998).

Contrary to that, although raw RTs indicated that the 'E/F' discrimination task was more difficult than the 'X/O' task, the ANOVA with the difference values between compatible and neutral trials showed no significant task effect, indicating that the slope of the RT-distance function was independent of task difficulty.

Theoretically, this could have been due to undersampling of the Mexcian hat and picking distances that matched the interceptions of two functions (see Fig. 2). However, Eriksen and St James (1986) made similar observations. They varied task difficulty by the number of letters that had to be searched for a target, i.e., manipulated the size of the attentional focus. Although increasing the attentional focus' size slowed overall response time, interference by incompatible flanking letters at a given distance remained the same. Thus, with a fixed slope, the area under the attentional gradient had to vary with the size of the focus, indicating that the amount of attentional resources employed by the subjects differed. If instead the amount of available resources had remained the same then broadening the attentional focus would have reduced the slope of the gradient. The authors, therefore, concluded that their "subjects were able to draw upon additional attentional resources to compensate for an increase in focus size" (p. 239). The same seems to apply for our experiment. As depicted in Fig. 2, the peak of the attentional gradient can be increased for the difficult task and still the slope may remain largely the same in case additional resources are provided. To summarize, the distribution (and resolution, see below) of spatial attention is highly task dependent, and this presumably also accounts for the differences in estimating attentional field sizes between tasks measuring detection abilities and reaction times (Handy, Kingstone, & Mangun, 1996). While the former operate at the limit of the processing system, the latter do not, so that attention does not need to be as strictly focused and the attentional fields appear larger (Cave & Bichot, 1999).

4.2. Physiology

We have recently provided evidence for suppression of neural activity in portions of striate cortex that code locations in the vicinity of an attended item (Müller & Kleinschmidt, 2004). We interpreted this finding as a putative physiological correlate for deteriorated perceptual processing near an attended location. Higher visual areas, on the other hand, showed a linear decrease of activity with increasing target-distracter distance consistent with an attentional gradient model. We related the different activity patterns across visual areas to their varying receptive field (RF) sizes, whereby only early visual areas have RFs small enough to allow subregions coding nearby locations to be modulated differently. However, RF sizes, even at the eccentricity of ∼7° which we used in our prior study, should allow a much finer spatial modulation even in higher areas (Smith, Singh, Williams, & Greenlee, 2001). That is, although RFs certainly determine the upper limit of resolution to be achieved by attention, there seem to be further factors involved. Indeed, Intriligator and Cavanagh (2001) determined the spatial resolution of attention near the fovea to be five times, in the periphery even to be twenty times lower than from what could be expected from the resolution capabilities of the visual system. They concluded that the locus of spatial selection does not lie within visual areas but within parietal cortex, a brain area with a rather coarse representation of external space. This notion is in line with recent fMRI studies addressing the neural network exerting top-down control of activity in visual cortex (Hopfinger, Buonocore, & Mangun, 2000; Müller, Donner, et al., 2003).

However, even though there is some agreement on the crucial role of the fronto-parietal network in attentional control, it remains an open question whether the surround inhibition is also top-down controlled or rather due to long range horizontal connections and lateral inhibition in early visual cortex itself (Angelucci et al., 2002), a well-established mechanism that in low-level vision subserves contrast enhancement. The latter seems tempting if one understands the mechanisms described here to be aimed at contrast enhancing as well—namely the contrast between attentional resources devoted to the target and to nearby possible distracters.

Recently, it has been shown that probes presented at locations formerly occupied by a distracter are less accurately reported than those at former blank locations, as if the first were selectively suppressed (Cepeda, Cave, Bichot, & Kim, 1998). Further, we have recently shown that activity for a given location also depends on

whether this location is part of a common object with the primarily attended one (Müller & Kleinschmidt, 2003) and whether this location falls within a small or a large attentional focus (Müller, Bartelt, Donner, Villringer, & Brandt, 2003). Together, these findings indicate a rather sophisticated and flexible modulation of visual cortex activity with the involvement of differentially specialized areas including object-related areas, eye fields etc. This suggests that even if lateral inhibition contributes to the center-surround modulation of the attentional field, there must be additional control from higher-order areas as to how this inhibition is exerted in a given specific task.

Acknowledgement

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