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Effects of attention on a relative mislocalization with successively presented stimuli

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ABSTRACT

Previous studies yielded evidence that the precision, with which stimuli are localized in the visual periphery, is improved under conditions of focused attention. The present study examined whether focused attention is able to correct a mislocalization recently observed with successively presented stimuli: when observers are asked to localize the peripheral position of a briefly presented target with respect to a previously presented comparison stimulus, they tended to judge the target as being more towards the fovea than was its actual position. In three experiments the mislocalization was tested under conditions with focused and distributed attention. Results revealed that the mislocalization increased with distributed attention and disappeared when stimuli appeared consistently at predictable positions and thus under conditions of focused attention. However, when a procedure with a trial-by-trial cueing was applied the mislocalization was only reduced, but not wiped out completely. In a recently developed dynamic field model consisting of interacting excitatory and inhibitory neuronal cell populations the results were explained as an attentional modulation of spontaneous (baseline) levels of neural activity.

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1. Introduction

Spatial acuity of the visual system is known to be of high precision in the fovea, but decreases drastically when stimuli are presented in the retinal periphery (e.g. Badcock & Westheimer, 1985; Skavensky, 1990). Especially with brief presentation times, the localization of stimuli is often impaired or even distorted (e.g. Mateef & Gourevich, 1983; O'Regan, 1984; van der Heijden, Müsseler, & Bridgeman, 1999). The present paper is concerned with the question whether and how a mislocalization with successively presented stimuli is improved when spatial attention is directed to the stimuli beforehand.

Valid cueing is known to improve response speed, but also visual detection and discrimination of peripherally presented stimuli (e.g. Downing, 1988; Pilz, Braun, Altpeter, MacKeben, & Trauzettel-Klosinski, 2006; Posner, Snyder, & Davidson, 1980). Most importantly in the present context, localization precision was reported to benefit from focused visual attention (e.g. Egly & Homa, 1984; Newby & Rock, 2001; Tsal & Bareket, 1999, 2005; Tsal, Meiran, & Lamy, 1995; Yeshurun & Carrasco, 1998). For instance, in a study of Prinzmetal, Amiri, Allen, and Edwards (1998) a dual task was used to investigate the effect of attention on localizing peripherally presented targets. Observers had to run two tasks either simultaneously or successively. First they identified a foveally presented letter and secondly they localized the perceived position of a briefly presented dot in the periphery. The accuracy of identification and the precision of localization were improved with successively presented stimuli, that is, when attention was focused on one location at a time instead of being distributed over two locations (but see also Newby & Rock, 2001).

Using a cueing paradigm, Tsal and Bareket (2005) tested the effect of attention on localization performance in two conditions. In their first experiment, attention was either directed to one of five target positions by a valid pre-cue (focused attention condition) or to all five positions (distributed attention condition). The results showed that identification accuracy as well as localization precision was enhanced under focused attention. The second experiment compared performance in a single task with a dual task in order to examine whether limited attentional resources lead to decreased localization precision in the distributed attention condition. The single task just required localizing a peripheral target at one of four randomized positions whereas in the dual task observers first had to localize the target and subsequently to identify a letter within a central three-letter array. With undivided attention, localization precision was improved reflecting a reduced dispersion of localization judgments in single-task conditions. In dual-task conditions attentional resources were engaged in the concurrent identification task revealing decreased localization precision accordingly.

In another study of Tsal and Bareket (1999, see also Tsal & Lavie, 1993), observers localized a briefly presented letter that could

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appear within a leftward, foveal and rightward circle. Cueing consisted in a briefly color change of one circle. On 75% of the trials, the target letter appeared in the cued circle (valid cueing) and on 25% of the trials in one of the two remaining circles (invalid cueing). Position judgments were gathered by touching on the perceived position. Findings yielded increased localization precision in conditions of valid cueing. The authors interpreted their findings in accordance with the assumption that preattentive processing establishes coarse localization of stimuli, while focal processing provides for fine localization (Cohen & Ivry, 1989, 1991; Tsal, 1999; Tsal & Shalev, 1996; Tsal et al., 1995).

One result of the previous studies was that focused spatial attention improves localization precision in that it reduces the dispersions in localization judgments. The present experiments examine whether focused attention is also able to correct a mislocalization observed with successively presented stimuli (Bocianski, Müsseler, & Erlhagen, 2008; Müsseler, van der Heijden, Mahmud, Deubel, & Ertsey, 1999, Experiment 5): when observers are asked to localize the peripheral position of a briefly presented target with respect to a previously presented comparison stimulus, they tended to judge the target as being more towards the fovea than was its actual position (Fig. 1). Two findings indicate that the observed mislocalization is related to or based on locally working attentional mechanisms: firstly, varying the temporal interval between stimuli yielded that the mislocalization increased at first (up to a stimulus-onset asynchrony [SOA] of 250 ms) and then turned into a reversed effect of more outer judgments (with 500- and 700-ms SOAs; cf. Bocianski et al., 2008, Experiment 2). Thus, the point of inflection from more-foveal to less-foveal and even to more peripheral localization errors corresponded roughly with the point in time at which priming mechanisms in reaction times are known to turn into inhibition mechanism (cf. the inhibition of return, e.g. Klein, 2000; Posner & Cohen, 1984). The correspondence in the temporal point of inflection may indicate one common underlying mechanism. Secondly, varying the spatial distance between stimuli revealed a decrease of the mislocalization with larger inter-stimulus distances (Bocianski et al., 2008, Experiment 3). Thus, the mislocalization is observed only with nearby presentations of comparison stimulus and target indicating that the peripheral presentation of the first stimulus (the comparison stimulus) attracts attention to its location, which affects the spatial processing of the incoming nearby-presented second stimulus (the target).

Further, the dynamic neural field model, which we applied to account for the localization error also contained attentional components (cf. Bocianski et al., 2008). In this model, stimulus location is encoded by a localized activity pattern of large populations of excitatory and inhibitory neurons that are ordered according to

their spatial tuning. The population response to a brief stimulus presentation is transient in nature. The activity first increases due to strong recurrent excitation within the population, and then decays back to a resting state when the recurrent inhibition starts to dominate the population dynamics. Further, the neural activity elicited by a stimulus shows an asymmetric profile that is slightly shifted in the direction of the fovea. This bias copes with a systematic mislocalization of peripherally flashed stimuli observed in absolute localization tasks (e.g. Müsseler et al., 1999, Experiment 4; van der Heijden, Van der Geest, De Leeuw, Krikke, & Müsseler, 1999; Stork, Müsseler, & van der Heijden, 2010). The critical point is that when comparison stimulus and target establish two distinct, but coupled neural pools, the baseline activity of the previously presented comparison stimulus pre-activates neurons of the target population before the target is presented. Thereby the bias of the first population as a response to the comparison stimulus enforced the more foveal shift of the targets' population activity and thus models successfully the observed mislocalization (for further details see Bocianski et al. (2008)).

It is important to stress that the stimulus-induced dynamic modulation of baseline activity can be seen as a neural instantiation of 'transient focal attention' models that have been proposed in the past to account for various visual illusions (Aschersleben & Müsseler, 2010; Erlhagen & Jancke, 2004; Jancke & Erlhagen, 2010; Kirschfeld & Kammer, 1999; Müsseler, Stork, & Kerzel, 2002; Steinman, Steinman, & Lehmkuhle, 1995). Recent studies of neural mechanism underlying attention have revealed that (tonic) shifts in baseline activity may occur at a time when the visual field still remained empty (for a review see Driver and Frith (2000)). The finding has been interpreted as neural substrate for a preparatory allocation of attention to stimulus positions that the observer may anticipate due to the blocked experimental design for instance. Typically the pre-activation is assumed to be of center-surround organization with facilitation at the attended location and attention suppression at larger distances (Slotnick, Schwarzbach, & Yantis, 2003; Smith, Singh, & Greenlee, 2000).

All these considerations point to attentional mechanisms involved in the mislocalization. Therefore, the present study aimed to investigate whether directing attention beforehand to the position where target and comparison stimulus will appear, is able to affect the localization judgments. As the studies mentioned above revealed an improvement of localization precision owing to attentional allocation, we expected on the one hand that focused attention could reduce or even eliminate the observed mislocalization. On the other hand, the mislocalization was expected to become worse with more distributed allocation of spatial attention. Consequently, in Experiment 1 stimuli were presented only in one hemifield allowing observers to focus the position in the visual field where the stimuli appeared. In contrast, stimuli were presented with less spatial certainty in Experiment 2 by introducing various presentation positions. Accordingly we assumed the mislocalization to be reduced in Experiment 1 while it should be increased in Experiment 2. Finally, Experiment 3 examined the effects when an auditory cue indicated the presentation position of the stimuli before each trial.

2. Experiment 1

Two presentation conditions were compared: firstly, target and comparison stimulus were presented unpredictable to the left or right of fixation on the horizontal meridian. This condition basically replicates previous experiments (Bocianski et al., 2008; Müsseler et al., 1999, Experiment 5), in which a mislocalization was observed when stimuli were presented successively. We assumed that prior to presentation attention is more or less divided
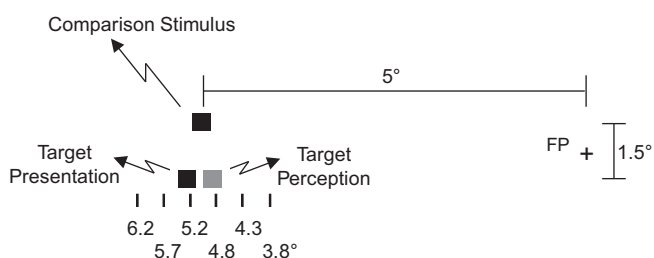

Fig. 1. The mislocalization under consideration. Observers fixated a cross in the middle of a screen. An upper square (comparison stimulus) and a lower square (target) are flashed successively (e.g., temporally separated by a stimulus-onset asynchrony of 100 ms) to the left or to the right of the fixation cross (here 5° to the left). When participants' task is to judge the position of the target relative to the comparison stimulus, they perceive the target as being more towards the fovea than the comparison stimulus.

to both visual hemifields in this condition. Secondly, target and comparison stimulus were presented predictable either to the left or right of fixation. This condition allowed observers to focus their attention to the positions where the stimulus appeared. If localization precision is improved by allocating attention spatially, the mislocalization was expected to be reduced or even to be eliminated.

Additionally, stimuli were also presented simultaneously in both conditions. Previous studies have shown that localization judgments were more or less error free with simultaneous presentation, as target and comparison stimulus were assumed to be processed as one stimulus with veridical relative position information between them (see also Müsseler & van der Heijden, 2004).

In sum, we expected localization errors only in the condition with successively presented stimuli, which appeared unpredictable in the left or right hemifield. The mislocalization was expected to be reduced or error free with simultaneously presented stimuli or with successively presented stimuli, which appeared predictably only in the left or right hemifield.

2.1. Method

2.1.1. Apparatus and stimuli

The experiment was controlled by a Macintosh computer with Matlab software using the Psychophysics Toolbox extension (Brainard, 1997; Pelli, 1997). The stimuli were presented on a 22″ color CRT monitor (Iiyama Vision Master Pro 513, 100 Hz refresh rate, 1024×768 pix). The observers sat at a table in a dimly lit room with their head placed on a chin rest 50 cm in front of the monitor.

Two single dark squares (1.9 cd/m^2) with a size of $0.33° \times 0.33°$ were peripherally presented on a light background (68 cd/m^2): an upper square (the comparison stimulus) and $1.4°$ below it a lower square (the target). The horizontal position of the comparison stimulus remained constant at $5°$ in the left or right hemifield. The position of the target varied horizontally relative to the mid-position of the comparison stimulus by $±0.2°$, $±0.7°$, and $±1.2°$. Hence, the target was presented at $3.8°$, $4.3°$, $4.8°$, $5.2°$, $5.7°$, or $6.2°$ eccentricity.

2.1.2. Design

Participants were randomly assigned to two different conditions: in the condition with unpredictable presentations, comparison stimulus and target were randomly presented in the left or right hemifield. Additionally, stimuli appeared either simultaneously (SOA 0 ms) or successively (SOA 100 ms). Consequently, for this group of participants the experiment contained the combinations of hemifield (left vs. right) × SOA (0, 100 ms) × probe positions (six positions between $3.8°$ and $6.2°$). All conditions were presented in a randomized sequence. Participants passed a training period of 1×48 trials and subsequently an experimental session of 4×48 trials.

In the condition with predictable presentations, stimulus presentation and design were the same except that comparison stimulus and target were presented blockwise either in the left or right hemifield. The sequence of blocks was counterbalanced between participants. Each block contained 1×24 training trials followed by the experimental session of 4×24 trials. Thus, the overall amount of trials was equal in both presentation conditions. For each participant the experiment lasted about 30 min including the training trials and the short breaks between blocks.

2.1.3. Procedure

The participants were instructed to retain their gaze on a central fixation cross which was visible throughout the experiment. Pressing a mouse button activated stimulus presentation. Each trial began with an auditory beep that was followed by stimulus presentation after 300 ms. Observers' task was to judge whether the upper square (comparison stimulus) or the lower square (target) was perceived more toward the periphery. For the upper square they pressed the upper button of a horizontally oriented mouse, accordingly for the lower square the lower button. After an interval of 1 s the next trial was initiated.

2.1.4. Control of eye fixation

The horizontal position of the right eye was monitored with a head mounted and infrared light reflecting eye-tracking device (Skalar Medical B.V., IRIS Model 6500). To adjust the gaze at the center of the screen (fixation point), observers passed a horizontal three-point calibration at the beginning of each block. Fixation had to be maintained within an area about $±1.5°$ of the centrally presented fixation cross. Trials in which the experimenter detected a saccade during stimulus presentation were excluded from data analysis. The mean exclusion rate was 0.71%, overall 15 out of 2.112 trials.

2.1.5. Participants

Eleven observers between 19 and 30 years of age ($M = 22$) took part in conditions with unpredictable left/right presentations, whereas another eleven fresh individuals, aged between 19 and 49 years ($M = 27$), ran through the blocks of predictable left/right presentations. All participants in the present and in the following experiments served for pay or course credit and reported having normal or corrected-to-normal vision.

2.2. Results

For every participant and condition the frequency of trials were counted in which the target was perceived more outer than the comparison stimulus. Probabilities of the judgments at the six target positions were entered in a Probit analysis of the Psignifit Software Package, which determined the 50%-threshold points of subjective equality (PSE) and the just-noticeable differences (JNDs, i.e. the 25% and 75% thresholds) for every participant and condition (bootstrap-software.org, cf. Wichmann & Hill, 2001a, 2001b). More eccentric deviations of the functions from the objective mid-position ($5°$) means that the point of subjective equality is more peripheral thus the target is perceived more towards the fovea (Fig. 2).

The PSE values were dependent variables in a 2 (unpredictable vs. predictable left/right presentations) × 2 (0 vs. 100 ms SOA) design with presentation condition as between-subjects factor and SOA as within-subjects factor.[1] The analysis of variance (ANOVA) with the PSE values showed a significant SOA effect [$F(1, 20) = 6.86$, $MSe = 0.082$, $p = .016$] and an interaction between SOA and presentation condition [$F(1, 20) = 7.25$, $MSe = 0.082$, $p = .014$]. Both effects originated essentially from a mislocalization (mean PSE value of $0.42°$) only observed with successively presented stimuli in the condition with unpredictable presentations at left/right positions. Accordingly, a paired t-test yielded a significant difference of this PSE value to the corresponding value of the 0-ms SOA (mean PSE value of 0.09, $t(10) = -3.12$, $p = .006$, one-tailed).

Separate for each SOA, the JNDs were dependent variables in 2 (unpredictable vs. predictable left/right presentations) × 2 (25%- and 75%-JNDs) ANOVAs in order to examine whether the slopes of the ogives were differentially affected by the attentional conditions. Different slopes would be indicated by an interaction of both factors, which was neither observed in the ANOVA of the 0-ms SOA nor in the ANOVA of the 100-ms SOA (both $F < 1$, ns). Instead, a

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[1] We abstained from analyzing the left/right hemifield separately. Our precursor study already showed that the mislocalization is not affected by the hemifield of presentation (Bocianski et al., 2008, Experiment 1). Therefore, in the present study results were averaged across this factor.
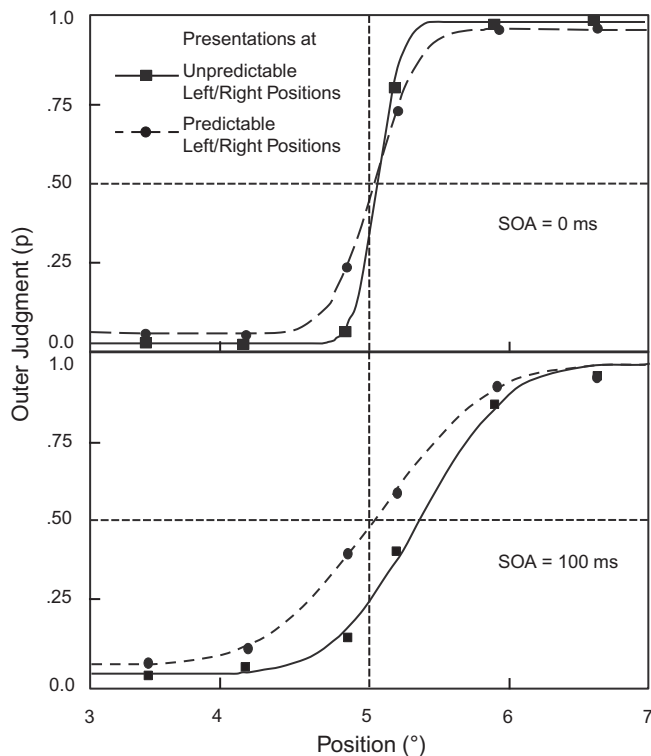
Fig. 2. Mean probabilities of outer judgments of the target and fitted functions for unpredictable and predictable presentation conditions. The upper panel depicts the probabilities with a stimulus-onset asynchrony (SOA) of 0 ms, the lower panel the probabilities with an SOA of 100 ms. A more eccentric deviation of the functions from the objective mid-position (5°) means that the point of subjective equality is more peripheral thus the target is perceived more towards the fovea (Experiment 1).

main effect of attentional conditions indicated a parallel shift of the ogives in the ANOVA of the 100-ms SOA [$F(1, 20) = 6.81$, $MSe = 0.207$, $p = 0.17$], but not in the ANOVA of the 0-ms SOA ($F < 1$, ns).[2]

2.3. Discussion

Two main results were observed. The first finding was that relative judgments were nearly error free when the two stimuli were presented simultaneously. We take that as evidence that in this case stimuli were processed as one stimulus with veridical relative position information between them (cf. Bocianski et al., 2008; Müsseler & van der Heijden, 2004). Additionally, judgments' certainty seems to be high with simultaneously presented stimuli as indicated by the steeper functions of the 0-ms SOA conditions than compared with the 100-ms SOA conditions.

The second and main finding was that the mislocalization emerged only when both stimuli are presented successively at unpredictable left/right positions, but not with predictable left/right positions in one hemifield. This disappearance of the mislocalization with predictable positions was hypothesized to originate from focusing attention to the positions where the stimuli were expected to appear. Thus, the present pattern of results can be interpreted as another demonstration of improved localization performance when attention is beforehand directed to the position of stimulation (e.g. Tsal & Bareket, 1999, 2005). The subsequent experiment examined the reversed effect, that is, whether more distributed spatial attention decreases localization performance.

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[2] Additionally, the differences between the 25%- and 75%-thresholds were always significant in the ANOVAs of the JNDs. As this finding is trivial, it is not reported here in detail.

3. Experiment 2

The previous experiment indicated an improvement in localization performance when stimuli appeared predictably at one position compared to when they appeared unpredictably at two positions. As an explanation we assumed that attention is allocated more effectively to one position than to two positions yielding to an improvement of localization performance. But instead of assuming that only a single position can be attended at once (Eriksen & Yeh, 1985; McCormick & Klein, 1990; Posner, 1980), more recent work has demonstrated that attention can be split over two up to four positions (Awh & Pashler, 2000; Franconeri, Alvarez, & Enns, 2007; Kramer & Hahn, 1995). Thus, it is likely that a certain amount of attention was allocated to both left and right positions even when stimuli were unpredictably presented in the left or right visual field in Experiment 1. Consequently, localization performance could be even more impaired when presentation positions are distributed to a larger visual field. With this condition the mislocalization was assumed to increase.

3.1. Method

3.1.1. Stimuli, design and procedure

Participants were again randomly assigned to two different conditions: as in Experiment 1, the first group of participants was confronted with unpredictable presentations of the stimuli on the horizontal meridian, that is, comparison stimulus and target were presented left or right from fixation with an eccentricity of 5°. Modifications regarded the second condition. Here observers also judged random presentations in the left or right visual field, but stimulus positions were not only on the horizontal meridian, but varied additionally in their vertical position. These positions were randomly chosen between 5° upwards and downwards at the left–right eccentricities of 5°. Thus, in this condition stimuli appeared unpredictably at multiple positions in the left or right visual field.

Again, participants were instructed to retain their gaze on the central fixation cross, but eye movements were not recorded in the present experiment, as stimuli appeared with equal probability in the left or right visual field. Additionally, retaining fixation was much more convenient for the participants than moving the eyes and the presentation of stimuli was much too short to execute target-directed eye movements successfully.

3.1.2. Participants

Eleven individuals between 19 and 30 years of age ($M = 24$ years) were paid to participate in the condition with unpredictable presentations at left or right positions and eleven participants between 19 and 30 of age ($M = 22$ years) run the experiment with the additional variations of stimulus positions on the vertical dimension.

3.2. Results and discussion

The observed mislocalization of Experiment 1 was successfully replicated in the present experiment: when stimuli appeared either to the left or right of fixation on the horizontal meridian, an essential mislocalization (mean PSE value of 0.29°) was observed with successively presented stimuli, but localization performance was nearly error free with simultaneous presentation (mean PSE value of 0.03; solid lines in Fig. 3). The amount of mislocalization increased when stimuli positions varied additionally on the vertical dimension (mean PSE values of 0.77° with successively presented stimuli and 0.01° with simultaneously presented stimuli, dashed lines of Fig. 3).
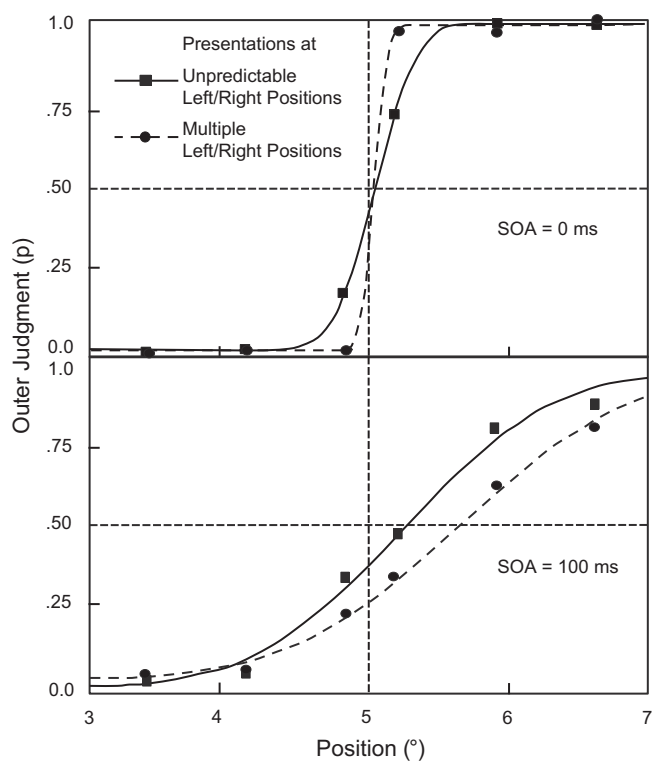
Fig. 3. Mean probabilities of outer judgments of the target and fitted functions for unpredictable left/right presentation conditions and multiple left/right presentation conditions. Note, that the condition with "unpredictable left/right positions" is now the more certain condition with regard to the attentional allocation. The upper panel depicts the probabilities with an SOA of 0 ms, the lower panel the probabilities with an SOA of 100 ms (Experiment 2).

A 2 (presentation condition) × 2 (SOA) ANOVA with the PSE values as dependent variable revealed a significant effect for the SOA factor [$F(1, 20) = 15.56$, $MSe = 0.183$, $p = .001$] and non-significant tendencies for the condition factor [$F(1, 20) = 3.34$, $MSe = 0.586$, $p = 0.083$] and the interaction [$F(1, 20) = 3.79$, $MSe = 0.183$, $p = .066$]. However, a t-test between the PSE values of the conditions with successive presentations (SOA 100 ms) was – as expected – significant with $t(10) = -2.48$, $p = .016$, one-tailed. This is evidence that an increased uncertainty of stimulus position and thereby a more distributed spatial attention led to an increase of the localization error.

The ANOVAs of the JNDs revealed significant slope differences between the 0-ms SOA ogives [$F(1, 20) = 13.38$, $MSe = 0.01$, $p = .002$]. A steeper ogive in the multiple-left–right than in the unpredictable left–right condition is at odds with the assumed attentional mechanism. Instead, the opposite pattern of results was expected if attention decreases variance of position judgments and increases accuracy. It is beyond the scope of the present paper to speculate about the reason of this reversed finding with simultaneously presented stimuli. More importantly, the ANOVA indicated a tendency for a parallel shift between the 100-ms SOA ogives [$F(1, 20) = 3.56$, $MSe = 0.744$, $p = 0.74$], while slope differences were not observed between them ($F < 1$, ns). Hence, as expected, the mislocalization became worse with more distributed allocation of spatial attention (multiple-left–right condition).

4. Experiment 3

The previous experiments were based on the assumption that attentional allocations within an experimental block differed with spatial certitude (Experiment 1) or incertitude (Experiment 2) of stimulus presentations. In other words, spatial predictability was assumed to affect attentional allocation and thereby improved or impaired localization precision. The present experiment addressed this assumption with a cueing paradigm. The presentation of a left or right tone, for instance, is known to attract spatial attention to the left or right visual field (e.g. Mazza, Turatto, Rossi, & Umilta, 2007; Spence & Driver, 1994, 1997; Spence, Nicholls, Gillespie, & Driver, 1998). Consequently, the present experiment examined within a single trial whether valid spatial cueing to the left or right visual field improved localization performance compared to a condition in which attention is more or less divided between both visual fields.

4.1. Method

4.1.1. Stimuli, design and procedure

These were the same as in Experiment 1, except for the following changes. A trial started with two tones (square waves of 880 Hz for 50 ms presented by headphones t.bone HD-860) with an interstimulus interval of 630 ms. After another 630 ms comparison stimulus and target were displayed with an SOA of 0 or 100 ms. This equidistant sequence of three events (two tones and visual stimuli) made visual stimulation temporarily predictable (cf. Rodway, 2005; Sanders, 1975). Spatial predictability was varied in two conditions: in the first condition the tones were presented binaurally indicating that the visual stimuli appeared either in the left or right visual field (neutral cueing). In the second condition the tones were presented monaurally to the left or right ear only. A left tone announced the visual stimulation in the left visual field, a right tone the visual stimulation in the right visual field (valid cueing). Conditions were presented blockwise with the sequence of blocks counterbalanced between participants.

As in Experiment 1 eye fixations were controlled with the eye tracker. Trials in which saccades were detected during stimuli presentations were excluded from data analysis. The mean exclusion rate was 7.13%, overall 92 out of 1290 trials.

4.1.2. Participants

Ten individuals between 21 and 32 years of age ($M = 26$) passed both experimental conditions.

4.2. Results and discussion

Again, when stimuli appeared unpredictably either to the left or right of fixation, a mislocalization (mean PSE value of 0.43°) was observed with successively presented stimuli, but not with simultaneously presented stimuli (mean PSE value of 0.06; solid lines in Fig. 4). More importantly, the amount of mislocalization decreased when the visual field of presentation was announced by the monaural cue (mean PSE values of 0.30° with successively presented stimuli vs. 0.06° with simultaneously presented stimuli, dashed lines Fig. 4).

A corresponding 2 (binaural vs. monaural cue) × 2 (SOA) ANOVA with the PSE values as dependent variable revealed a significant main effect of the SOA factor [$F(1, 9) = 13.06$, $MSe = 0.71$, $p = .006$]. Independently of the cueing condition, this finding indicated a reliable mislocalization with successively presented stimuli compared to simultaneously presented stimuli.

A t-test between the PSE values with successively presented stimuli (SOA 100 ms) indicated the expected improvement in localization performance at validly cued positions [$t(9) = 2.25$, $p = .025$, one-tailed; lower panel of Fig. 4]. However, the mislocalization in this condition was not wiped out and was still different from zero [$t(9) = 4.68$, $p < .001$].

The ANOVAs of the JNDs revealed a tendency for slope differences between 100-ms SOA conditions [$F(1, 9) = 3.93$, $MSe = 0.044$, $p = .079$], but not between 0-ms SOA conditions
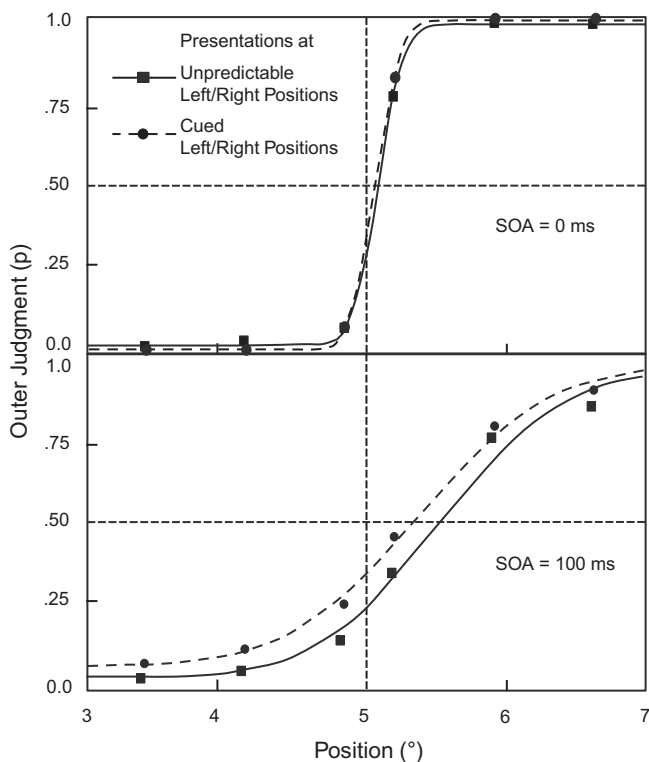
Fig. 4. Mean probabilities of outer judgments of the target and fitted functions for unpredictable presentation conditions and cued presentation conditions. The upper panel depicts the probabilities with an SOA of 0 ms, the lower panel the probabilities with an SOA of 100 ms (Experiment 3).

($F < 1$, ns). Again, a tendency for a main effect of attentional conditions indicated a parallel shift of the ogives in the ANOVA of the 100-ms SOA [$F(1, 9) = 5.07$, $MSe = 0.032$, $p = 0.51$], but not in the ANOVA of the 0-ms SOA ($F < 1$, ns).

All in all, the present pattern of results again demonstrated improved localization performance when attention is beforehand directed to the position of stimulation.

5. General discussion

The present study examined whether allocation of spatial attention exerted an influence on a recently observed mislocalization. Results of Experiments 1 and 2 showed that the mislocalization was absent with focused attention, medium with divided attention to two positions and large with distributed attention to a larger visual field. This result corroborates the finding of Franconeri et al. (2007), who found that response times increased with the set size of cued positions. The present experiments can be interpreted as an extension of this finding showing that the set size of cued positions does not only affect the speed of processing, but in a comparable manner also localization precision.

Comparing the results of Experiments 1 and 3 revealed that when stimuli were presented at predictable positions in blocked trials, the mislocalization disappeared, while it was only reduced with trial-by-trial cueing. The procedure with blocked trials allowed observers to constantly focus their attention to one position. In the interleaved procedure with trial-by-trial cueing, spatial attention was randomly attracted to the left or right visual field by a left or right tone (cf. Mazza et al., 2007; Spence & Driver, 1994, 1997; Spence et al., 1998). The difference in the findings of Experiments 1 and 3 can be taken as evidence that an allocation of attention succeeded better with blocked trials than with trial-by-trial cueing.

At least, two explanations of this finding are worth to be discussed here. First, the tones indicated only the visual field, but not the exact position of presentations, as – for instance – a peripherally presented visual cue would do.[3] Additionally, and contrary to blocked presentations, the alterations between presentations in the left and right visual field makes it necessary to continuously disengage from previously attended locations. As a consequence, the to-be-attended positions in trials with trial-by-trial cueing might be less spatially specified than the to-be-attended positions in blocked trials.

Second, in the procedure with trial-by-trial cueing the temporal tuning between tone and visual presentation could also be critical. It might not always be ensured that the disengagement from previously attended locations and the subsequent attentional shift to the new position in the contralateral visual field fits optimally in the interval between presentation of the cue and the visual stimuli. This may have also contributed to the fact that attentional allocations were less than optimal with trial-by-trial cueing. Both explanations refer to inter-trial processes responsible for the difference between Experiments 1 and 3.

It is also possible that the spatiotemporal course of attention shifts differed between blocked trials and trial-by-trial cueing. In blocked trials it is likely that attention is constantly focused at the area of stimuli presentations. In trials with trial-by-trial cueing, it can be assumed that attention 'moves back' to the fixation cross in between. Thus, there the sequence of attention shifts is always 'fixation cross → comparison stimulus → target'. Moreover, as targets' positions varied in accordance with the method of constant stimuli (cf. Fig. 1), conditions with less eccentric targets were always conditions with a change in direction of attention shifts, that is, attention shifted from the fixation cross to the comparison stimulus and back to the less eccentric target. Conditions with more eccentric targets were always conditions with a continuation in direction of attention shifts, that is, attention shifted from the fixation cross to the comparison stimulus and then onward to the target. It has been shown that a change vs. continuation in direction of an attention shift affects attentional processing (e.g. Rizzolatti, Riggio, Dascola, & Umiltà, 1987; Umiltà, Riggio, Dascola, & Rizzolatti, 1991; but see also Müsseler, 1994) and it seems likely that so does spatial processing.

Fortunately, we already conducted and published an experiment that is able to examine this idea (Bocianski et al., 2008, Experiment 1). In this experiment, the spatial arrangement of stimuli presentations was identical to the present experiments, but we introduced negative and positive SOAs. In half of the trials the comparison stimulus comes first and then the target (as in the present experiments), in the other half of trials the target was presented first and then the comparison stimulus. In the latter condition, the attention 'moves' from the less eccentric target towards the more eccentric comparison or vice versa. In other words, directions of attention shifts were completely opposite when contrasting the conditions of negative and positive SOAs. If the mislocalizations are affected by or even based on the change or continuation of attentional directions, the results should have been varied with conditions of negative and positive SOAs, but this was not the case. Thus, it is more likely, that the attentional conditions used in the present experiments induced variations in the baseline activity of input processing.

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[3] In a pilot study we examined the presentation of visual cues instead of the tones. The problem with visual cues was that they established a further reference point on the display and that presentations consisted now of a sequence of three successive events (cue → comparison stimulus → target). Therefore our choice was to use tones.

5.1. The dynamic neural field model

Converging lines of evidence from single-cell recordings in animals and imaging studies in humans suggest that a modulation of spontaneous baseline activity before stimulus onset may constitute a neural substrate for a top-down attentional mechanism (Driver & Frith, 2000; Slotnick et al., 2003; Smith et al., 2000). Typically it is assumed that these attentional modulations have a center-surround organization leading to an improved processing of visual stimuli appearing at the attended positions at the expense of the immediate surround. To directly test the hypothesis that a pre-shaping mechanism may account for the observed effect of focused attention on relative mislocalization we have adapted the dynamic neural field model of our previous study (Bocianski et al., 2008). To facilitate the understanding of results we first discuss basic mechanisms of cortical processing implemented in the model and highlight the main experimental findings that have constrained the modeling work. The interested reader may find mathematical details in Bocianski et al. (2008).

The model has been originally developed to investigate interaction effects observed in neural populations of cat primary visual cortex encoding horizontal stimulus position (Jancke et al., 1999). It has been later applied to the perceptual domain to discuss different localization errors associated with moving stimuli (Erlhagen, 2003; Erlhagen & Jancke, 2004; Jancke & Erlhagen, 2010). The model consists of a coupled network of excitatory and inhibitory neurons that are tuned to position in visual space. Due to the massive recurrent interactions within cortical areas, the processing of the location of even very small objects is associated with a widespread transient pattern of cortical activity (Fitzpatrick, 2000). The model explains the temporal evolution and spatial spread of the neural population activity in response to a briefly presented afferent input as the result of excitatory feedback from neurons with similar receptive field centers that is counterbalance by lateral inhibition (Jancke et al., 1999). The synaptic weight profile of the interactions, known as Mexican-hat organization, guarantees that the population activity remains localized in position space.

For a spatially symmetric weight profile, the model predicts the continuous evolution of a transient activity pattern centered over stimulus position. There are, however, experimental findings that are in line with the notion of a slightly asymmetric organization of recurrent interactions outside the foveal representation of visual space. Using a horizontal motion paradigm, Jancke and colleagues have recently shown (Jancke & Erlhagen, 2010; Jancke, Erlhagen, Schöner, & Dinse, 2004) that the peak latencies of neural trajectory representations showed a directional bias, as latencies were shorter for stimuli moving in the direction of the fovea compared to the opposite direction. This finding on the neuronal level fits quite well to evidence from behavioral studies that report a directional asymmetry for the latency of perception of small moving targets (Mateef & Hohnsbein, 1988). The dynamic field model may account for this emphasis on processing motion towards the fovea by assuming that each neuron in the population encoding horizontal stimulus position gets its highest input not from its nearest neighbor in position space but from a cell with a receptive field center slightly shifted towards the fovea (asymmetric weight profile, see Bocianski et al., 2008). Facilitating the processing of motion in one direction at the expense of the opposite direction may be in general beneficial for the visual system. However, spatially asymmetric interactions also constitute a possible neural substrate for the systematic mislocalization of briefly presented stimuli in the visual periphery (e.g., van der Heijden, Müsseler et al., 1999; van der Heijden, Van der Geest et al., 1999). Fig. 5 shows three snapshots of a model simulation with asymmetric recurrent interactions. A Gaussian input signal centered at 5° was applied for 10 ms to the model population encoding horizontal position. When
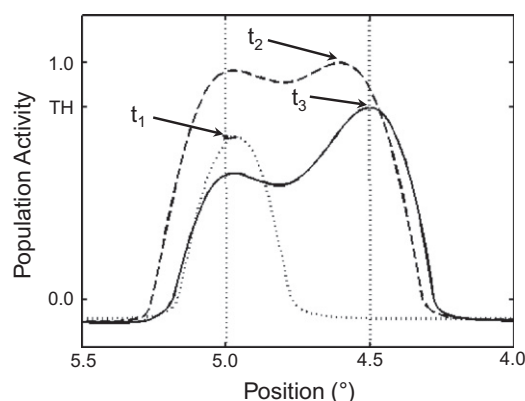

Fig. 5. Evolution of a self-stabilized, transient activity pattern encoding horizontal stimulus position. Three snapshots at successive times of the population response to a localized stimulus presented for 10 ms at position 5° are shown. Due to the recurrent excitation within the neural population the activity continues to grow in amplitude and width upon stimulus offset (time t_1). It reaches a peak value and then decays back to resting level (times t_2 and t_3) caused by the increasing feedback inhibition. The afferent input has to drive the activation beyond the threshold level 0 in order to trigger the self-stabilizing forces within the population. Weaker input leads to a subthreshold (<0) activation pattern. Due to the spatial asymmetry of the recurrent interactions the pattern does not evolve centered over stimulus position but expands in the direction of the fovea. At time t_3 the spatial expansion stops since an activation level *TH* has been reached below which the excitatory forces within the population are not strong enough anymore to sustain the process. The peak position of the activity pattern at the time of reaching *TH* is taken as a read-out measure for the localization error.

comparing the peak locations of the suprathreshold population response at different times of the evolution (t_1, t_2 and t_3), it becomes evident that the activity pattern does not evolve centered over stimulus position but expands and drifts in the direction of the fovea. The drifting stops when at time t_3 a certain activation level *TH* has been reached that reflects a dominance of recurrent inhibition over recurrent excitation within the network. The excitatory forces within the population are thus not strong enough anymore to further sustain the drift. For simplicity we take the peak position when reaching this activation level as a correlate for the absolute localization error, which is known to be about 10% of visual eccentricity (van der Heijden, Müsseler et al., 1999; van der Heijden, Van der Geest et al., 1999). It is important to stress that other read-out measures (e.g., center of gravity or averaging over a certain time interval) could have been chosen as well since the magnitude of the drift can be controlled by the model parameter defining the strength of the spatial asymmetry in the interactions (for a discussion see Bocianski et al. (2008)).

It is well known that the response of an individual neuron to a stimulus can be significantly affected by stimuli presented outside the classical receptive field. This surround effect, possibly mediated by long-range horizontal connections, shows that neurons may integrate information over a large area of visual cortex (Fitzpatrick, 2000). It has been suggested that spreading subthreshold excitation and inhibition may constitute a neural correlate of a cue-induced attention mechanism that alters the processing of spatial information (Kirschfeld & Kammer, 1999; Steinman et al., 1995). To test the impact of subthreshold interactions on the relative localization of successively presented stimuli we have introduced in our previous modeling study (weak) connections between two distinct neural pools representing the positions of the comparison stimulus and the target stimulus, respectively. Through the subthreshold interactions, the population response to the comparison stimulus causes time-dependent changes in the baseline activity level of the target population. We exploit here the fact that in the model only sufficiently strong input may trigger a suprathreshold activation pattern of a local population. The time-

dependent subthreshold interactions are first excitatory in nature leading to a partial depolarization of the target population. When the transient excitatory mechanism starts to decline, the target population becomes hyperpolarized due to the increasing subthreshold inhibition. Since a partial depolarization increase the drift of the population activity in foveal direction whereas a hyperpolarisation has the opposite effect, the dynamic field model with adequately adjusted parameters defining the subthreshold interactions is able to qualitatively and quantitatively explain the experimentally observed dependence of the relative mislocalization on the stimulus-onset asynchrony (for details see Bocianski et al. (2008)).

For a SOA of 100 ms used in the present study the model predicts that the target population at the time of stimulus presentation appears to be pre-activated due to the integrated subthreshold excitation from the comparison pool. The modeling results show that the relative position of the two suprathreshold activity patterns varies as a function of the spatial spread of the subthreshold excitation. If a larger portion of the neural population encoding the target stimulus becomes partially depolarized (for instance in Experiment 2) the distance between the population responses increases. For the current simulations we have increased the value of the model parameter defining the spatial spread (by a factor 2.5) to account for the larger magnitude of the relative mislocalization compared to the previous study. The rest of the model parameters were identical (for details see Bocianski et al. (2008)).

Any top-down or pre-cue input that effectively reduces the spatial spread of the stimulus-induced depolarization thus predicts a smaller relative localization error. To test the idea that an attentional modulation of the baseline activity before stimulus onset may account for the improved relative localization in the present experiments we have applied a tonic input of center-surround type to the two excitatory populations. It is modeled as a Gaussian minus a constant for simplicity. As shown in Fig. 6, this input results in a spatially structured resting level of the neural populations from which the processing of the afferent inputs starts. Relative to the homogeneous baseline activity without this additional input (solid line), the activity level appears to be suppressed
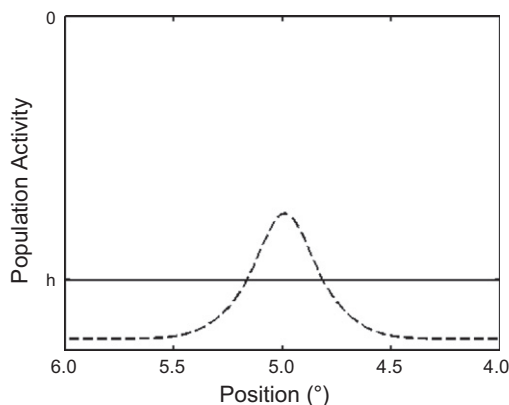
at all locations other than the attended location (dashed line). The comparison and the target stimulus were then successively presented with a stimulus duration of 10 ms and a SOA of 100 ms to the neurons encoding the stimulus position of 5° in the respective populations.

Fig. 7 compares snapshots of the suprathreshold activity pattern of the two excitatory populations for three cases that shall illustrate the modeling of the different attention conditions tested in the experiments. The same read-out procedure as in the previous modeling study has been applied to link the activity patterns to the answer in the position judgment task. The relative peak position of the two population responses at the time of reaching the fixed read-out activity level *TH* (compare Fig. 5) is taken as a correlate for the relative mislocalization (for a detailed discussion see Bocianski et al., 2008). Fig. 7a shows a model simulation of the case of a homogeneous baseline level representing the absence of focal visual attention. Both activity profiles are not centered over stimulus position suggesting a possible neural correlate for an
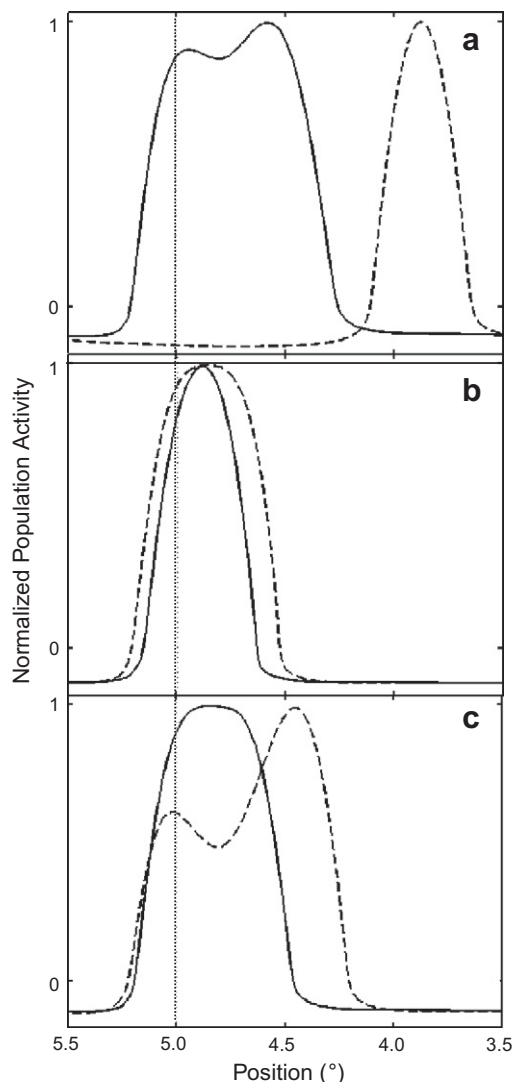

Fig. 6. Comparison of the baseline activity level of a population encoding position in the conditions with (dashed line) and without (solid line) attentional input. In the absence of any external stimulation of the population, the activity relaxes to a homogeneous resting state defined by the model parameter *h*. The application of a constant attentional input of center-surround type leads to a spatially structured resting state. Neurons encoding the attended location appear to be slightly depolarized and neurons in the surround slightly hyperpolarized relative to the *h*-level. The surround suppression extends beyond the limits shown in the figure. In line with experimental findings (e.g., compare Fig. 5e in Smith et al. (2000)) this means that directing attention to a particular location causes a decrease in activity at locations covering a large area of the visual field.

Fig. 7. In each of the three panels snapshots of the population activity associated with the target (dashed line) and the comparison stimulus (solid line) are plotted. The snapshots are taken when a fixed read-out activity level has been reached. The processing of position information starts from different baseline levels of activity: (a) homogeneous resting state (solid line in Fig. 6), (b) spatially structured resting state (dashed line in Fig. 6), (c) spatially structured baseline level with reduced amplitude of depolarization and hyperpolarisation compared to the case in panel (b).

absolute judgment error. However, the shift in the direction of the fovea is much more pronounced for the target stimulus (right profile) due the subthreshold excitation mechanism. The distance of 0.72° between the peak positions is in good agreement with the order of magnitude of the relative mislocalization reported in Experiment 2 (see Fig. 3). The situation is completely different when the processing of the afferent inputs starts from a spatially structured baseline level (see Fig. 6). A relatively small suppression of the unattended positions has a dramatic effect on the absolute and relative peak positions (Fig. 7b). The absolute shift is the direction of the fovea is small and the two activity profiles are overlapping. In this simulation the model predicts a tiny relative localization error of 0.02°. By assuming that the strength of the attentional input reflects the degree of spatial predictability it is also possible to account for the data in Experiment 1. Fig. 7c shows a simulation in which the attentional input used in Fig. 6 (dashed line) was multiplied by a factor 0.4. The model predicts a relative localization error in the order of 0.4° which represents an intermediate value between the extreme cases illustrated in Fig. 7a and b.

A final point worth mentioning is that the model makes no predictions with regard to the slope of the ogives, but predicts changes in positions. In accordance with the model, data of Experiments 1–3 indicated parallel shifts of the ogives in all experimental conditions, that is, with non-simultaneously presented stimuli.

It is important to stress that in line with the experimental findings the model predicts for a SOA of 0 ms a vanishing relative localization error independent of the attention condition. Since in the model the subthreshold connections between the two populations are bi-directional the excitatory spread from one population to the other is symmetric. The total input to the populations is thus at any time during the evolution of the suprathreshold activity profiles identical and consequently also their location in position space coincides.

Acknowledgments

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