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"Spatial Distribution of the Inhibitory Effect of Peripheral Non-Informative Cues on Simple Reaction Time to Non-Fixated Visual Targets"

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SPATIAL DISTRIBUTION OF THE INHIBITORY EFFECT OF PERIPHERAL NON-INFORMATIVE CUES ON SIMPLE REACTION TIME TO NON-FIXATED VISUAL TARGETS

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Abstract—It is known that reaction time (RT) for the detection of a light target at extrafoveal locations is lengthened by a previous non-informative light cue at the same location. We describe an additional inhibitory effect from cues remote from the target but occurring within the same lateral or altitudinal visual hemified. Subjects made a speeded key-press response to the second of two successive light flashes in a pair while maintaining fixation. Each of the two flashes could appear at random in one of four positions, two in the right and two in the left visual fields, or two in the upper and two in the lower visual fields. We found an RT prolongation not only for cued over uncued positions, but also for within-field non-coincident cue-target pairs over between-fields cue target pairs. The within-field inhibitory effect, though smaller than the same-location effect, was fully apparent even when the target occurred at 1° of visual angle from the midline and at 2° from the cue. Both effects were seen with cue-target asynchronies ranging from 0.2 to 1.5 sec. The results are relevant to the understanding of the neural mechanisms for covert shifts of attention across the main meridians of the visual field.

INTRODUCTION

ATTENTIONAL changes in the ability to detect or recognize visual stimuli can be analysed by measuring simple or choice reaction time (RT) as a function of whether attention is selectively allocated to the targets or to distractors, or divided among targets and distractors. As a simple example, RT for the detection of unstructured photic targets in different extrafoveal locations is shorter at expected positions, and longer at unexpected positions, compared with a baseline condition in which target expectancy is the same for all possible positions [22, 24]. Since such expectancy-based changes in RT can be observed while eye position is held constant by fixation, they cannot be accounted for by ocular responses leading to foveation of the stimuli. As a consequence these and other related findings have prompted the hypothesis of an attentional focus that can be shifted like a spotlight over visual space independent of eye movements [2, 11, 20].

In these RT studies positional expectancies for extrafoveal target positions are usually engendered by cues that are remote from the cued positions and, hence, are apt to signal them solely by reference to a predetermined system of symbolic relations connecting each cue to a specific position. Subjects are typically presented with one such symbolic cue (e.g. an arrow or a digit) at the point of fixation, and are thus set by the positional information provided by the cue to respond to a target in a specific location away from fixation. In these conditions decreases in RT at the specified locations are clearly the result of cognitive and voluntary processes because they imply, first, the recognition of the positional information provided by the cue, and second, the deliberate alignment of the attentional spotlight with the cued position. The increase in RT at unexpected locations is viewed as a measure of the cost imposed by the initial misalignment of the attentional spotlight and the resulting necessity to redirect it before responding [22, 24].

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By comparison with the above symbolic or "central" cues, positional "peripheral" cues presented at or near the cued location should in theory be more effective in drawing attention to that location, because they should automatically elicit an orienting reaction toward the site common to both cue and target, even when eye movements are not allowed. Unlike the attentional shifts induced by central cues, but similar to overt orienting of the eyes toward peripheral cues, such covert orienting of the attentional spotlight is likely to take place in an almost reflexive fashion, that is without requiring cognitive and voluntary processes [12, 27]. Peripheral cueing of this kind has indeed proved highly effective as a means for providing advance positional information which facilitates the discrimination or detection of structured visual targets briefly presented at cued locations [6, 13]. In contrast, the detection of simple luminous targets at extrafoveal locations, though strongly enhanced by foreknowledge of target position afforded by central cues, may be interfered with by peripheral cues presented at or near the stimulus location. It is now widely acknowledged that simple RT to luminous targets in extrafoveal locations can be affected by prior stimulation of the same locations in ways that probably have to do with selective attention, but are unrelated to the responder's expectations. A peripheral visual cue unpredictive of the probable position of the upcoming visual target may induce a small and fleeting facilitation of RT to a target occurring at or near the cued location within 100 msec after the cue, but at longer cue–target temporal separations, lasting from 200 msec to more than a second, RT to targets in the cued location is markedly retarded compared to uncued locations [17, 18, 21, 26, 34]. There is solid evidence that this RT retardation is independent of retinal processes such as local adaptation or the periphery effect, as well as of response biases due to probability guessing [17, 18, 21]. Rather, it appears to be caused by a selective inhibition of the orienting reaction, either overt or covert, toward the target as a direct or indirect consequence of the occurrence of a cue at the same location. Various mechanisms have been proposed to underlie the inhibition of orienting to recently cued locations [17, 18, 21, 34], but at present there is no decisive evidence in favour of any specific hypothesis.

The understanding of the mechanisms of the inhibitory effect of peripheral cues may be helped by a more precise knowledge of its spatial characteristics. Is inhibition limited to locations in the immediate vicinity of the cue or does it affect larger areas of the visual field? Some evidence in favour of the latter alternative was provided in an experiment of MAYLOR and HOCKEY [18] and supported by TASSINARI *et al.* [34]. In this paper we report a replication of the inhibitory effect, describe an extensive quantitative evaluation of it, present new decisive evidence that it extends to wide portions of the visual field which are demarcated by the vertical and horizontal meridians, and discuss the possible neural substrates of this spatial pattern. As we indicated in a previous paper [34], since this spatial pattern is comparable to that recently described for RT costs induced by misdirecting attention with central visual cues [5, 9, 10, 30] or verbal instructions [34], the present findings may have implications for the understanding of the spatial organization of covert orienting in general.

EXPERIMENT 1

In most previous experiments the inhibitory effect was typically assessed by comparing RT for the second of two consecutive, but spatially coincident stimuli—the target following the cue at the same location—with RT for a target at a mirror image location in the opposite visual field [17, 18, 21]. Was the lengthening of RT in the former condition due to the occurrence of cue and target at the same location, or to the fact that they were on the same side of fixation?

Maylor and Hockey [18] reported that the inhibitory effect fell off quite sharply as the spatial separation between cue and target was increased. However, RT to targets which did not coincide spatially with the cue, but were on the same side of the vertical meridian, was consistently longer than RT to targets across the vertical meridian from the cue. Since in their experiments cues and targets appeared at a constant distance from the vertical meridian, the cue–target separation being varied along a line parallel to the meridian itself, their results do not reveal the spread of inhibition from the cued position along directions perpendicular to the vertical meridian.

The present experiment on RT for the detection of simple light stimuli was designed to test the spread of the inhibitory effect along the horizontal meridian of the visual field across fixation. The general plan was to present subjects with pairs of successive visual stimuli, each of which could appear in one of four fixed positions along the horizontal meridian of the visual field, two on the right and two on the left of fixation. The first stimulus in a pair, or cue, required no overt response, but the subject was to detect it in order to prepare for making a manual response to a second physically identical stimulus, or target. The dependent variable was the RT of such a response, while the primary independent variable was the relation between the position of the cue and that of the target in each pair of stimuli. For each target occurring in each of the four positions, the preceding cue in that pair might have occurred in one of four relative positions: at the same location, or at the other location on the same side of fixation, or in a mirror-symmetric or non-symmetric location on the other side of fixation. It was thus possible to compare effects on RT of prior stimulation of the same location not only with those of prior stimulation in two positions in the opposite hemifield, but also with those of prior stimulation at a different location within the same hemifield.

Method

Subjects. Six right-handed male subjects, ranging in age from 20 to 44 yr and with normal or corrected-to-normal vision, volunteered to take part in the experiment. They were all experienced with RT tasks and all but two were unaware of the purpose of the experiment.

Apparatus. Photic stimulation was performed with four solid-state miniature light-emitting diodes, LEDs, with round tips 5 mm in diameter (TIL 222) which could be driven individually by a 15 mA, 5 msec square pulse of current producing a gallium phosphide green light with a luminance of about 70 cd/m. The LEDs were attached to an horizontal arc perimeter, 57 cm in radius, mounted on a white tangent screen and facing a head- and chin-rest which was placed in its centre of curvature. Right in front of the head- and chin-rest the perimeter was marked with a white spot which provided the target for fixation. Two of the LEDs were placed on the right and two on the left of this mark, respectively at 10 and 30 cm from it. The response devices were two button-keys, mounted on brass cylinders which were rigidly positioned between the perimeter and the head- and chin-rest, 29 cm on the right and the left, 16 cm below and 22 cm in front of the fixation mark. Each key was connected with an electronic msec counter, and a key-press performed with a force equal to or higher than 60 g stopped the counter. The arc perimeter and the white screen behind it were constantly lit from above by two neon tubes which provided a background luminance of 0.15 cd/m^2. Sound stimulation could be provided by delivering 1000 Hz tone pips 50 msec in duration through a set of earphones.

Procedure. Each subject performed in six experimental sessions which were run on separate days. He sat in a soundproof room with the head positioned in the head- and chin-rest so that the midpoint between his eyes was at 57 cm from the fixation mark on the perimeter. At this viewing distance the visual angle between each of the four LEDs and its neighbour was 20°. Each session consisted of 64 trials and each trial involved the following sequence. First, an auditory warning signal indicated that the subject was to look binocularly at the fixation mark and to remain fixated until the end of the trial. Second, after an interval varying randomly from 1 to 3 sec, the cue was presented at one of the four positions by illuminating one of the LEDs. Subjects were instructed to make no overt reactions to the cue, and knew that the trial would be invalidated if they pressed the key or moved their eyes in response to the cue. (The term cue is indeed justified by the fact that it heralded the target.) Third, the target was presented at one of the four positions by illuminating the same LED as the cue or a different LED. The stimulus-onset asynchrony (SOA) between cue and target could take one of four values: 0.3, 0.6, 1.5 or 4 sec. The subject was to press one of the two button-keys with his thumb as fast as possible after seeing the target, thus stopping the electronic clock that had been started simultaneously with target onset. The right hand was used on three sessions and the left hand was used in the other three sessions; on the first session three subjects used the right hand and the other three used the left hand, and the two hands were alternated from session to session. The 64 trials in each session exhausted all possible combinations between the position of the cue, the position of the target and the duration of the SOA, and were randomly intermixed. Thus within each session the cue and the target in each pair appeared 16 times in each of the four positions, and there was no way to predict the position of the target from that of the cue. The maintenance of fixation throughout the trial was monitored by television. RTs shorter than 0.15 sec were considered anticipations and RTs longer than 1 sec were considered misses. Cue–target–SOA combinations on which a key-press to the cue, an anticipation, a miss or an intratrial eye movement had occurred were repeated at the end of the session until acceptable RTs were available for all 64 combinations. Anticipations and misses were recorded separately from acceptable RTs.

Data analysis. The means of acceptable RTs were computed across sessions for each subject for each of the 64 combinations separately for each hand. Thus each subject yielded 128 basic data points. Statistical analyses used analysis of variance with a multifactor repeated-measurement design and subjects as a random-effect variable [19], and two-tailed one-sample and paired t-tests for selected comparisons.

Results

In this and the following experiments the number of anticipations, misses and fixation errors was too low to allow analysis, hence the description will be restricted in every case to RT data. Further, in all experiments there were no systematic differences between the right and left hands, and therefore statistical analyses were performed on means across hands for each subject.

Preliminary analyses of the data revealed that RTs for lateral targets were consistently longer (by about 10%) than RTs for medial targets, regardless of the position of the cue. In order to simplify the presentation of the effects of the independent variables of interest, namely the positional cue–target relation and the SOA, this well known effect of stimulus eccentricity on visual RT [7] will not be further mentioned. However, as indicated below, when selected and restricted groups of RTs were compared, the eccentricity factor was controlled by contrasting targets at equal eccentricities, e.g. both medial or both lateral. An additional simplification for the description of the results comes from the fact that the position of the cue by itself proved to have no effect on RT.

In the main analysis of the data, RTs were subdivided at each SOA into four types of cue–target combinations: same-position (SP), same-field (SF), symmetric opposite-field (OFs), and non-symmetric opposite-field (OFns) combinations. In SP combinations target and cue were at the same location; in SF combinations target and cue occurred at adjacent locations on the same side of fixation; in OFs and OFns combinations target and cue were on opposite sides of fixation, respectively in a symmetric (both cue and target in the lateral or medial positions) and non-symmetric (cue lateral and target medial or vice versa) position. At each SOA, the data for each of these combinations were the means across the four stimulus positions of the RTs to targets preceded by cues in the appropriate positional relation. These means were entered into an analysis of variance with positional cue–target relation (SP, SF, OFs, OFns) and SOA (0.3, 0.9, 1.5 and 4 sec) as main factors. The analysis revealed highly significant effects from the first factor ($P < 0.001$), the second factor ($P < 0.005$) as well as their interaction ($P < 0.001$). Figure 1 shows the directions and the magnitudes of these effects. At the first three SOAs RT was longest for SP combinations, intermediate for SF combinations, and shortest for OF combinations, with no apparent difference between OFs and OFns combinations. At the longest SOA the values for the four groups were not noticeably different. As shown by paired *t*-tests, overall RT decreased considerably with increasing SOAs, with significant drops from the second to the third SOA ($P < 0.005$) and from the third to the fourth SOA ($P = 0.01$). However this gradual decrease was limited to the SP and, partly, the SF combinations, since the RT curves for both OF combinations remained relatively flat throughout the four SOAs (see Fig. 1).

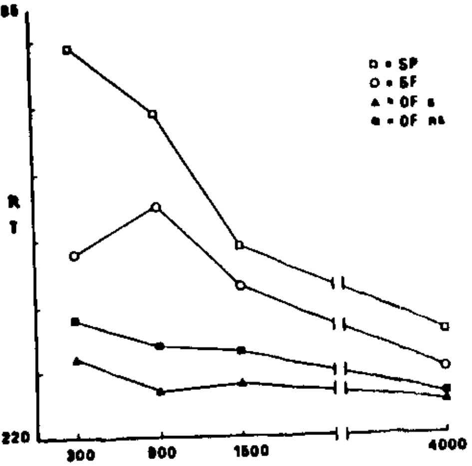

FIG. 1. Experiment 1. Reaction-time (RT) for same-position (SP), same-field (SF), opposite-fiel symmetric (OFs) and non-symmetric (OFns) combinations as a function of SOA.

The numerical differences between RTs for different combinations at each SOA, the statistical significance of their deviations from a null value, and the number of subjects complying with the overall pattern of results are presented in Table 1. Since a separate analysis showed that the two OF combinations did not differ from one another at any SOA, their RTs were pooled, so that the differences in Table 1 are between three sets of RTs: SP, SF and pooled OF. The difference between SP and OF combinations is the inhibitory effect described in previous work [17, 18, 21, 26]. The difference between SF and OF combinations, showing an inhibition for locations away from the cue, is the novel finding of this study. It is apparent from the table that at the two first SOAs the differences between the SP combination and the other two combinations, as well as the difference between the SF combination and the OF combination, were all significantly greater than zero. At the third SOA, the SP and SF combinations did not differ significantly from one another, but their RTs were still significantly longer than those of the OF combination. No significant difference was found at the fourth SOA.

Table 1. Experiment 1. Differences between RTs for different cue–target combinations at each SOA. In brackets: number of subjects (out of 6) showing the difference

	SOA (sec)			
	0.3	0.9	1.5	4.0
	Difference in msec			
SP RT minus SF RT	30.0†	13.6†	5.8	6.6
	(6)	(6)	(3)	(4)
SF RT minus OF RT‡	12.9†	24.7†	12.3†	4.0
	(6)	(6)	(6)	(4)
SP RT minus OF RT‡	43.5†	38.3†	18.1*	10.6
	(6)	(6)	(6)	(6)

SP = same position; SF = same field; OF = opposite field; SOA = stimulus onset asynchrony.

*Significantly different from 0 at $P < 0.05$ (one-sample *t*-test).

†Significantly different from 0 at $P < 0.01$ (one-sample *t*-test).

‡Mean of the two OF combinations.

Three more selective analyses were aimed at a deeper evaluation of the RT effects of the spatial relations between cue and target. The first analysis was performed on subsets of SF and OF combinations. RTs to medial targets preceded by lateral cues on the same side were compared with RTs to the same targets when preceded by opposite medial cues. On these cue–target combinations the position of the targets was always medial, thus removing any effect of target eccentricity, and the distance between cue and target was in all cases 20°. However the first combination is an instance of SF combinations (both cue and target on the same side of fixation), while the other combination is an instance of OF combinations (cue and target on opposite sides of fixation). This analysis indicated that at the first three SOAs RT for SF combinations was systematically longer than RT for OF combinations, see Table 2, upper part, thus proving the existence of an RT differential between SF and OF combinations with identical targets and equal cue–target distances.

Table 2. Experiment 1. RTs (in msec) for medial targets preceded by lateral cues within the same field (SF) or by medial cues in the opposite field (OF)

	SOA (sec)			
	0.3	0.9	1.5	4.0
SF, lateral cues, medial targets	234.7	251.7	238.9	224.2
OF, medial cues, medial targets	220.0	222.6	219.5	221.4
Significance of difference (paired *t*-tests)	$P = 0.05$	$P < 0.025$	$P < 0.01$	n.s.
Number of subjects showing the difference (out of six)	5	6	6	4

The second analysis assessed if the difference between SF combinations and OF combinations varied between the lateral and medial positions. With SF combinations having medial targets and lateral cues, the mean RT across the first three SOAs was 18.1 msec longer than the corresponding mean for OF combinations with medial targets and lateral cues. This value was not significantly different from the 15.3 msec difference between SF combinations and OF combinations with lateral targets and medial cues. Thus the slowing of SF over OF combinations did not vary with the lateral or medial position of either cues or targets.

A third analysis was performed on the possible effects of cue–target spatial separation on

OF combinations. For each OF combination there was a relatively short cue-target distance, namely 20°, when both cue and target were medial; an intermediate cue-target distance, namely 40°, when the cue was lateral and the target was medial, or the reverse; and a relatively long cue–target distance, namely 60°, when both cue and target were lateral. The results for assessing the effect of the cue–target distance on OF combinations were split into four groups, allowing two separate comparisons, in each of which the target eccentricity factor was controlled. At each SOA, RTs to medial targets preceded by short-distance cues were compared with RTs to medial targets preceded by intermediate-distance cues; and RTs to lateral targets preceded by intermediate-distance cues were compared with RTs to lateral targets preceded by long-distance cues. The results of these comparisons, summarized in Table 3, indicate a generally insignificant influence on RT from changes in cue-target distance, with a single exception which is best attributed to chance.

Table 3. Experiment 1. RTs (in msec) for medial and lateral targets on OF combinations as a function of cue-target spatial separation

	SOA (sec)			
	0.3	0.9	1.5	4.0
Medial cues and targets (20° cue–target separation)	220.0	222.6	219.5	221.4
Lateral cues, medial targets (40° cue–target separation)	226.7	226.5	226.9	215.0
Significance of difference (paired t-tests)	n.s.	n.s.	n.s.	n.s.
Medial cues, lateral targets (40° cue–target separation)	248.8	242.1	238.4	237.1
Lateral cues and targets (60° cue–target separation)	244.7	231.3	237.3	228.9
Significance of difference (paired t-tests)	n.s.	$P<0.05$	n.s.	n.s.

Discussion

The results confirm that RT for the detection of a lateralized light target is differentially affected by the previous presentation of an identical cue at the same or a different location. When both cue and target occur on the same side of the fixation point, either the left or the right, RT is longer than when the two stimuli occur on opposite sides of the fixation point, one on the right and the other on the left. RT lengthening is maximal (33.3 msec across the three first SOAs) when cue and target appear at the same location (SP combinations), i.e. the condition that was explored in the experiments of POSNER and COHEN [21], MAYLOR [17], MAYLOR and HOCKEY [18] and POSSAMAI [26]. However there is also a smaller, but highly significant 16.6 msec RT lengthening (mean across the first three SOAs) on SF combinations, i.e. with cues and targets occupying different locations on the same side of fixation. Both effects are present at the first three SOAs but not at the fourth, hence they must come to an end at some time between 1.5 and 4 sec from the cue.

In addition to being in general agreement with previous studies on the inhibitory action of prior stimulation on the speed of detection of luminous stimuli [17, 18, 21, 26], these findings prove that such inhibition is capable of spreading in space. In MAYLOR and HOCKEY's study [18] the inhibitory effect of the cue underwent a drastic reduction with an increase in distance between cue and target, the relation being clearly non-linear. We show here that inhibition is

by no means restricted to the cued location, but our results underline the importance of the relative positions of cue and target with respect to fixation for inhibition to occur. Regardless of cue–target distance, RT varies significantly according to whether cue and target are on the same side or on opposite sides of fixation. For example, medial targets preceded by opposite medial cues are responded to faster than medial targets preceded by lateral cues on the same side, even though the cue–target distance is identical in the two conditions. This finding cannot be ascribed to the cue being more inhibitory in the lateral than in the medial position, since the inhibitory effect on SF combinations is equal with medial and lateral cues. Further, RT of OF combinations is unaffected by the lateral or medial position of the cue, or by changes in the cue–target distance.

We are thus led to conclude that a cue presented on the right or left of fixation retards RT to subsequent targets appearing on the same side of fixation, whether at the same or a different location, ~~while leaving RT to targets contralateral to the cue virtually unaffected~~. To the extent that the inhibition of RT to a target preceded by an ipsilateral cue reflects a bias against reorienting toward recently stimulated locations [17, 18, 21], our data suggest that stimulation at a specific location on the right or left of fixation temporarily biases the visual system against reacting to targets appearing not only at that location, but also at other locations on the same side of fixation.

Because the right visual field projects to the left cerebral hemisphere, and the left visual field projects to the right hemisphere, lateral differences in the processing of visual input from either side of fixation are usually attributed to a functional division of labour between the hemispheres [1]. KINSBOURNE [14] among others has proposed that each hemisphere can generate an attentional bias, either overt or covert, toward the contralateral half space, and that a balanced activation between the two hemispheres is required for maintaining attention to the centre. In this connection, one may ask whether the inhibitory effect of a cue on ipsilateral targets can be linked to orientational biases arising from a differential hemispheric activation. It is not inconceivable, for example, that covert orienting toward one side of fixation is followed by some kind of refractoriness of the hemisphere responsible for the orienting response. If when detecting the cue our subjects covertly oriented to it, the hemisphere contralateral to the cue might have become temporarily refractory to targets presented in the same hemifield. Experiment 2 shows that such a hemispheric hypothesis does not suffice to explain the inhibitory effects of peripheral cues on visual RT.

EXPERIMENT 2

We repeated Experiment 1 using a different spatial arrangement of the four stimulus locations, based on the notion that while visual field points on each side of the vertical meridian are projected to the contralateral hemisphere, points along the vertical meridian are projected to both hemispheres [15]. Cues and targets were thus delivered above and below fixation along the vertical meridian, rather than on the right and left of fixation along the horizontal meridian. As in Experiment 1 the task involved responding to the second in a pair of light flashes, the target following the cue, and cue and target could occur on the same side or on opposite sides of fixation. However, SP and SF combinations had both cues and targets either above or below fixation, whereas with OF combinations the cue could be above and the target below fixation or vice versa. In Experiment 1 cues and targets of SP and SF combinations were projected to one hemisphere, and cues and targets of OF combinations were projected to different hemispheres. The crucial change in Experiment 2 was that all possible pairs of cues and targets were projected to both hemispheres because of the bilateral representation of the vertical meridian.

Method

The same six subjects of Experiment 1 were tested with exactly the same procedure. The only difference in the apparatus was a vertical bar which replaced the arc perimeter of Experiment 1 and served as a support for the four LEDs. There were two LEDs above the fixation point and two below it in a symmetrical disposition. The linear distance between each LED and its next was such that at the viewing distance of 57 cm it subtended a visual angle of 20° in analogy with Experiment 1. Thus there were two LEDs in the upper field and two LEDs in the lower visual field, one at 10° and the other at 30° from fixation. These two positions will be referred to respectively as inner and outer.

Results and discussion

In accord with several previous studies [7], RT was generally faster for inner than for outer positions, and for lower than for upper positions. However this variable did not interact with the two independent variables of the study, i.e. the positional cue–target relation and the SOA, and therefore it will be disregarded.

Data for SP, SF, OFs and OFns combinations were obtained as in Experiment 1. These data are presented in Fig. 2 and Tables 4–6 and can be directly compared with the corresponding data for Experiment 1 as they appear in Fig. 1 and Tables 1–3. The general outcomes of the two experiments were basically the same in that (a) the slowest RTs were those for SP combinations; (b) RTs of SF combinations were shorter than RTs of SP combinations, but longer than RTs of OF combinations; (c) OFs and OFns combinations had statistically indistinguishable RTs. The differences between SP, SF and OF combinations tended to decrease with SOA and to disappear altogether at the longest SOA. Analysis of variance showed significant effects for the positional cue–target relation ($P<0.001$), SOA ($P<0.005$) and the interaction between the two factors ($P<0.001$). A comparison between Figs 1 and 2 as well as between Tables 1 and 4 bears out the substantial qualitative and quantitative similarity between the general pattern of differences between SP, SF and OF combinations in Experiment 1 and that in Experiment 2.

Table 5 shows that at the first two SOAs, SF combinations with inner targets preceded by outer cues had significantly longer RTs than OF combinations with both inner targets and cues. This replicates Experiment 1, see Table 2, in demonstrating the occurrence of differences between SF and OF combinations with equal target eccentricities and spatial cue–target separations. The difference between SF and OF combinations at the third SOA was in the expected direction but did not reach significance.

Again in analogy with Experiment 1, the mean slowing of the SF over the OF combinations across the first three SOAs was approximately the same regardless of whether inner targets were preceded by outer cues (mean slowing 10.3 msec), or outer targets were preceded by inner cues (mean slowing 12.0 msec). The absence of a significant difference between the two slowings implies an equal inhibitory power of inner and outer cues on SF combinations.

A final point of concurrence with Experiment 1 was the independence of RT for OF combinations from changes in the cue–target distance across fixation, see Table 6 to be compared with Table 3, in keeping with the hypothesis of a general lack of effects from opposite cues.

differential

The major conclusion to be drawn from the combined evidence from Experiments 1 and 2 is that RTs to targets occurring at the same or a different location on the same side of fixation are systematically longer than RTs to targets preceded by cues on the opposite side of

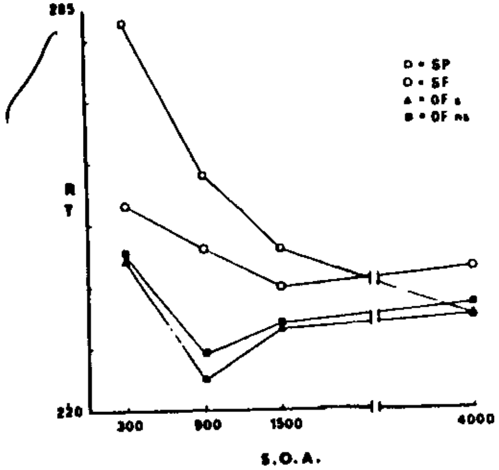

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Table 4. Experiment 2. Differences between RTs for different cue–target combinations at each SOA. In brackets: number of subjects (out of six) showing the difference

	SOA (sec)			
	0.3	0.9	1.5	4.0
	Difference in msec			
SP RT minus SF RT	30.2† (6)	11.9* (5)	5.8 (4)	−8.2 (2)
SF RT minus OF RT‡	8.0 (4)	18.9† (6)	6.6 (5)	7.0* (6)
SP RT minus of RT‡	38.2† (6)	30.8† (6)	12.4† (6)	−1.2 (3)

*Significantly different from 0 at $P<0.05$ (one-sample t-test).
†Significantly different from 0 at $P<0.01$ (one-sample t-test).
‡Mean of OFs and OFns combinations.

Table 5. Experiment 2. RTs (in msec) for inner targets preceded by outer cues within the same field (SF) or by inner cues in the opposite field (OF)

	SOA (sec)			
	0.3	0.9	1.5	4.0
SF, outer cues, inner targets	240.0	230.1	226.7	228.2
OF, inner cues, inner targets	224.3	214.8	226.8	220.2
Significance of difference (paired t-tests)	$P<0.025$	$P<0.05$	n.s.	n.s.
Number of subjects showing the difference (out of six)	6	6	5	5

Table 6. Experiment 2. RTs (in msec) for inner and outer targets on OF combinations as a function of cue-targets spatial separation

	SOA (sec)			
	0.3	0.9	1.5	4.0
Inner cues and targets (20° cue–target separation)	224.3	214.8	226.8	220.2
Outer cues, inner targets (40° cue-target separation)	230.5	211.3	224.0	227.5
Significance of difference (paired *t*-tests)	n.s.	n.s.	n.s.	n.s.
Inner cues, outer targets (40° cue–target separation)	260.0	245.8	244.4	245.7
Outer cues and targets	263.9	236.2	239.9	250.5
Significance of difference (paired *t*-tests)	n.s.	n.s.	n.s.	n.s.

60° cue-target separation

fixation, irrespective of whether cue and target are presented on the horizontal meridian, to the right and/or left of fixation (Experiment 1), or on the vertical meridian, above and/or below fixation (Experiment 2). In both cases the critical factor of the inhibitory effect is not simply the spatial coincidence of cue and target, but rather their ipsilaterality relative to fixation. In Experiment 2 the mean slowing across the first three SOAs over OF combinations is 27.1 msec for SP combinations and 11.2 msec for SF combinations. These values are comparable with the 33.3 and 16.7 msec values of Experiment 1.

The inhibition on the horizontal meridian seen in Experiment 1 might in principle be accounted for by a channelling of signals from both cue and target into a single cerebral hemisphere on SP and SF combinations, as opposed to the projection of cue and target to different hemispheres on OF combinations. Yet this interpretation cannot accommodate the results of Experiment 2, insofar as in this experiment visual signals were provided to both hemispheres on all cue–target combinations. The assumption seems justified that in the neural substrate for local light detection there exists a mechanism whereby detecting a light on one side of fixation, whether on the horizontal or vertical meridian, causes a temporary depression of the reactivity to subsequent light stimuli appearing on the same side of fixation along the same meridian. To the extent that inhibition is similar for stimuli along the vertical as well as the horizontal meridian, hemispheric refractoriness cannot be regarded as an indispensable element of the mechanisms. An important question that can be asked is: does the mechanism operate solely across fixation, or across any point along the two main meridians of the visual field? In order to answer this question, in Experiment 3 we dissociated the point of fixation from the centre of the stimulus array, so that cues and targets could be presented on one or both sides of the horizontal or vertical meridian off-line from fixation.

EXPERIMENT 3

In Experiment 3, condition A, we studied the inhibitory effect of ipsilateral cues by using a horizontal stimulus display to that of Experiment 1, but which was positioned above or below the fixation point. Thus ipsilateral or contralateral cues and targets were defined on the basis of their relative positions with respect to the vertical meridian rather than the fixation point. Similarly, in Experiment 3, condition B, we used a vertical stimulus array similar to that of Experiment 2, which however was positioned to the right or left of fixation, so that cues and targets could appear above or below the horizontal meridian along a vertical line away from fixation.

simila

Method

Subjects and apparatus. Six right-handed males aged 21–28, endowed with normal or fully corrected vision and unaware of the purpose of the study, served as subjects. The apparatus was the same as in Experiment 2; however, the bar supporting the four LEDs was horizontal in condition A and vertical in condition B; further, the fixation point was placed 10° directly above or below the centre of the horizontal bar in condition A, and 10° directly right or left of the centre of the vertical bar in condition B. In all cases there were two LEDs on each side of the vertical meridian (condition A) or the horizontal meridian (condition B), one at 10° and the other at 30° from the meridian.

Procedure. The sequence of stimuli on each trial was the same as in Experiments 1 and 2 but the four SOAs were 0.2, 0.6, 1.5 and 5 sec. The instructions for responding were the same as in Experiments 1 and 2. There were eight sessions, each comprising 64 trials, run on separate days. For three subjects the stimulus array was set horizontally (condition A) during the first four sessions, and vertically (condition B) during the other four sessions. For the other three subjects this order was reversed. In condition A a clearly visible fixation mark was provided 10° above the centre of the horizontal stimulus array in two sessions and 10° below it in the other two sessions. In condition B the same fixation mark was positioned 10° to the right of the centre of the vertical stimulus array in two sessions, and 10° to the left of it in the other two sessions. The order of positions of fixation within each condition was completely counterbalanced across subjects. Other procedural details were identical with those of Experiments 1 and 2.

RESULTS AND DISCUSSION

Since it was seen on a preliminary analysis that the effects of the main independent variables were unaffected by the two fixation requirements in both condition A (fixation above and below the stimulus display) and condition B (fixation to the right or left of the stimulus display), the data for the two fixation requirements were pooled in each condition. The data were then subdivided in SP, SF, OFs and OFns combinations separately for each condition, and are illustrated in Figs 3 and 4. A comparison of these figures with Figs 1 and 2 suggests that the effects described in Experiment 1 and 2 were completely replicated in Experiment 3, conditions A and B.

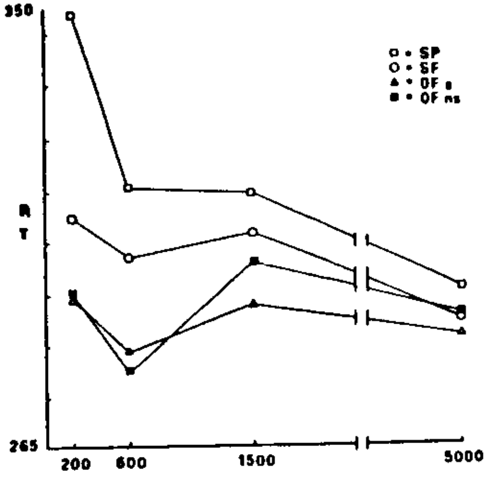


FIG. 3. Experiment 3, condition A. Reaction time (RT) for same-position (SP), same-field (SF), opposite-field symmetric (OFs) and non-symmetric (OFns) combinations as a function of SOA (msec

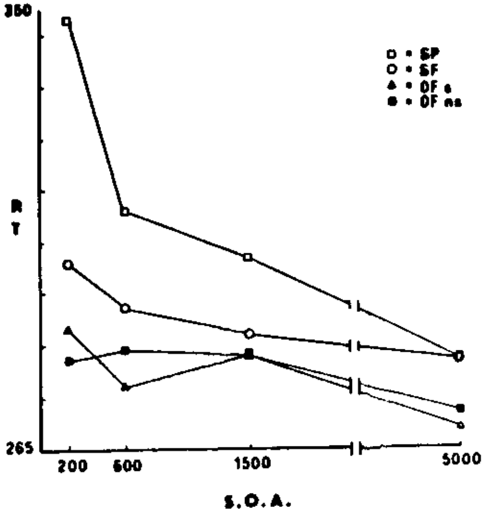


FIG. 4. Experiment 3, condition B. Reaction time (RT) for same-position (SP), same-field (SF), opposite-field symmetric (OFs) and non-symmetric (OFns) combinations as a function of SOA (msec).

An analysis of variance on the results of both conditions, having as factors axis of stimulus array (horizontal in condition A and vertical in condition B), positional cue–target relation and SOA, showed no significant effects from the first factor and its interactions. Therefore the effects of the two other factors and their interaction, which were all significant (respectively $P<0.001$, <0.05 and and <0.001), are summarized jointly for the two conditions in Tables 7–9. These can be compared with Tables 1–3 of Experiment 1 and Tables 4–6 of Experiment 2. The comparisons bear out the substantial similarity of the pattern of differences between SP, SF and OF combinations obtained in combined conditions A and B of Experiment 3 with that seen in each of the preceding experiments.

Table 7. Experiment 3. Differences between RTs for different cue–target combinations at each SOA. In brackets: number of subjects (out of six) showing the difference

	SOA (sec)			
	0.2	0.6	1.5	5.0
	Difference in msec			
SP RT minus SF RT	43.3† (6)	16.4† (6)	11.2† (5)	3.4 (4)
SF RT minus OF RT‡	15.7† (6)	15.7† (6)	7.1 (4)	6.2 (4)
SP RT minus OF RT‡	59.0† (6)	32.1† (6)	18.3* (6)	9.6 (3)

*Significantly different from 0 at $P<0.05$ (one-sample t-test).
†Significantly different from 0 at $P<0.01$ (one-sample t-test).
‡Mean of OFs and OFns combinations.

Table 8. Experiment 3. RTs (in msec) for medial and inner targets preceded by lateral and outer cues within the same field (SF) or by medial and inner cues in the opposite field (OF)

	SOA (sec)			
	0.2	0.6	1.5	5.0
SF, lateral or outer cues, medial or inner targets	289.7	289.2	287.9	273.7
OF, medial or inner cues, medial or inner targets	281.3	270.0	281.7	272.2
Significance of difference (paired t-tests)	n.s.	$P<0.05$	n.s.	n.s.
Number of subjects showing the difference (out of six)	5	5	5	3

In general accord with Experiments 1 and 2, in Experiment 3 the mean SP inhibitory effect (SP–OF) across the three first SOAs is 36.4 msec, and the corresponding value for the SF inhibitory effect (SF–OF) is 12.8 msec. Thus these inhibitory effects occur not only when cues and targets are aligned with the fixation point, but also when they occur on the same side of the vertical and horizontal meridians off-line from fixation. This implies that it is the ipsilaterality of cues and targets relative to the main meridians, and not solely to the fixation point, that causes the inhibitory effect. But does this mean that the inhibitory effect extends as far as the exact boundaries between opposite hemifields? The results of Experiments 1–3 do not allow a specific answer to this question since the shortest distance from cues and targets to the fixation point or the main meridians was 10°. Experiment 4 was designed to test the inhibitory ipsilateral effect with cues and targets very close to the fixation point.

Table 9. Experiment 3. RTs (in msec) for medial and inner, and for lateral and outer targets on OF combination as a function of cue–target spatial separation

	SOA (sec)			
	0.2	0.6	1.5	5.0
Medial and inner cues and targets (20° cue–target separation)	281.3	270.0	281.7	272.2
Lateral and outer cues, medial and inner targets (40° cue–target separation)	277.5	280.2	289.5	265.4
Significance of difference (paired t-tests)	n.s.	n.s.	n.s.	n.s.
Medial and inner cues, lateral and outer targets (40° cue–target separation)	299.1	284.4	294.4	297.3
Lateral and outer cues and targets (60° cue–target separation)	300.6	291.3	294.7	283.8
Significance of difference (paired t-tests)	n.s.	n.s.	n.s.	n.s.

EXPERIMENT 4

The basic plan of this experiment combined features of Experiments 1 and 2 in that there were four possible stimulus positions aligned symmetrically either on the horizontal or the vertical meridian across fixation. However the spacing of the four positions was partially different from that of Experiments 1 and 2. The two medial positions on the horizontal meridian, and the two inner positions on the vertical meridian were only 1° away from fixation. As in the previous experiments, the two lateral positions on the horizontal meridian and the two outer positions on the vertical meridian were about 30° away from fixation.

METHOD

Subjects and apparatus. Seven right-handed and one left-handed normally sighted or corrected-to-normal males, ranging in age from 25 to 44 yr, four of whom were unaware of the purpose of the study, served as subjects. The apparatus was the same as in Experiments 2 and 3, with the fixation point being always at the midpoint of the bar supporting the four LEDs.

Procedure. The task was the same as in the Experiments 1–3. There were four sessions, each consisting of 64 trials as detailed previously. Each subject performed on two sessions with horizontally aligned stimulus positions and two sessions with vertically aligned stimulus positions, and in each pair of sessions the responding hand was alternated between right and left with hand order counterbalanced across subjects. The four SOAs were 0.2, 0.6, 1.5 and 5 sec

Results and discussion

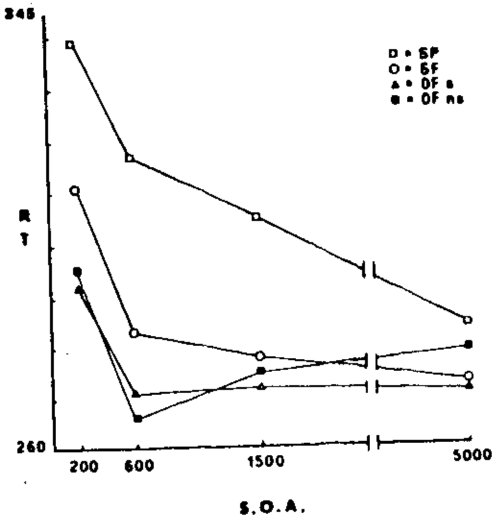
An analysis of variance with positional cue–target relation, SOA and axis of stimulus array as factors revealed significant effects from the two former factors ($P < 0.001$ in both cases) and their interaction ($P = 0.001$), but not from the latter factor or any of its interactions. This warrants a unified description of the results obtained with the two orientations of the stimulus array.

The results are summarized in Fig. 5 and Tables 10–12, which disclose the persistence of the ipsilateral inhibitory effect with the stimulus spacing used in this experiment. The mean SP inhibitory effect across the three first SOAs was 41.7; the corresponding mean SF inhibitory effect was 12.5 (see Table 10). Table 11 shows that over the three first SOAs RTs to medial and inner targets preceded by lateral or outer cues on the same side (cue–target distance 29°) were on the average 15.8 msec longer than RTs to the same targets when preceded by medial and inner cues on the opposite side (cue–target distance 2°). Taken together with the results of Experiments 1 and 2, these findings allow the conclusion that a cue at 30° from fixation inhibits a far ipsilateral target at 1° from fixation as much as a nearer ipsilateral target at 10° from fixation, since the effects in Experiment 4 were comparable to those of Experiments 1 and 2. Conversely, the combined results from Experiments 1, 2 and 4 suggest that the same inhibitory effect on a target at 30° from fixation is exerted by cues at 1 or 10° from fixation. Further, the proximity between medial and inner cues and targets on some OF combinations of Experiment 4 does not appear to result in inhibitory effects on these combinations. This is shown in Table 12 which makes it clear that on OF combinations both RT to medial and inner targets and RT to lateral and outer targets were unaffected by the cue being near of far from fixation.

In summary, the evidence indicates that targets appearing in the immediate vicinity of fixation are inhibited by non-coincident ipsilateral cues as effectively as targets remote from fixation, and cues close to fixation are fully inhibitory on ipsilateral far targets. Added to the results of Experiments 1–3, the results of Experiment 4 strengthen the point that the main meridians of the visual field are indeed boundaries to the spatial spread of the ipsilateral inhibitory effect.

GENERAL DISCUSSION

All the experiments described in this paper bear out an ipsilateral inhibitory effect of an extrafoveal visual cue on RT to a subsequent extrafoveal visual target. Inhibition is signalled by an elevation of RT to targets following cues on the same side of the main visual field meridians over RT to targets appearing on the side opposite the cue. The effect is long lasting (up to 1.5 sec or more) and is strongest when cue and target occupy the same position. The finding of a marked inhibitory effect at the cued position is in keeping with studies by Posner and Cohen [21], Maylor [17], Maylor and Hockey [18] and Possamai [26]. This study



PLEASE PLACE FIGS AND TABLE 10 ON PAGE 15

Fig. 5. Experiment 4. Reaction-time (RT) for same-position (SP), same-field (SF), opposite-field symmetric (OFs) and non-symmetric (OFns) combinations as a function of SOA (msec).

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Table 10. Experiment 4. Differences between RTs for different cue–target combinations at each SOA. In brackets: number of subjects (out of 8) showing the difference

	SOA (sec) 0.2	0.6	1.5	5.0
	Difference in msec			
SP RT minus SF RT	27.7†	33.2*	26.8†	10.4
	(5)	(6)	(5)	(3)
SF RT minus OF RT‡	18.2*	14.7†	4.5	−1.3
	(5)	(5)	(3)	(1)
SP RT minus OF RT‡	45.9†	47.9*	31.3*	9.1
	(6)	(6)	(6)	(3)

*Significantly different from 0 at $P < 0.05$ (one-sample t-test).
†Significantly different from 0 at $P < 0.01$ (one-sample t-test).
‡Mean of OFs and OFns combinations.

however extends the previous results by showing that inhibition affects not only targets presented at cued locations, but also targets occurring in the visual half field containing the cue. It occurs between right and left fields (Experiment 1) as well as between upper and lower fields (Experiment 2), both across fixation and across points of the main meridians away from fixation (Experiment 3), and seems independent of the eccentricity of target and cue positions over the explored range (from 1 to 30° from the main meridians, Experiment 4). According to the results of the last mentioned experiment, the effect is best depicted as an inhibition which irradiates in all directions from the cued location and arrives at the horizontal and vertical meridians without crossing them.

Table 11. Experiment 4. RTs (in msec) for medial and inner targets preceded by lateral and outer cues within the same field (SF) or by medial and inner cues in the opposite field (OF)

	SOA (sec)			
	0.2	0.6	1.5	5.0
SF, lateral or outer cues, medial or inner targets	297.7	275.7	269.1	263.0
OF, medial or inner cues, medial or inner targets	280.3	250.9	263.9	257.6
Significance of difference (paired *t*-tests)	$P = 0.08$	$P < 0.001$	n.s	n.s.
Number of subjects showing the difference (out of six)	5	5	4	3

Table 12. Experiment 4. RTs (in msec) for medial and inner, and for lateral and outer targets on OF combinations as a function of cue–target spatial separation

	SOA (sec)			
	0.2	0.6	1.5	5.0
Medial and inner cues and targets (2° cue–target separation)	280.3	250.9	263.9	257.6
Lateral and outer cues, medial and inner targets (31° cue–target separation)	275.6	260.5	261.2	264.3
Significance of difference (paired *t*-tests)	n.s.	n.s.	n.s.	n.s.
Medial and inner cues, lateral and outer targets (31° cue–target separation)	311.4	289.9	293.4	303.9
Lateral and outer cues and targets (60° cue–target separation)	316.9	284.1	281.2	296.6
Significance of difference (paired *t*-tests)	n.s.	n.s.	n.s.	n.s.

Current interpretations of inhibitory effects on RT from peripheral cues differ in the suggested mechanisms, but concur in viewing inhibition as the expression of some kind of spatially selective refractoriness of the attentional system. TASSINARI *et al.* [34] suggest that covert orienting to a peripheral cue implies a suppression of the natural overt orienting reaction toward it, thereby interfering with subsequent motor reactions to targets appearing shortly thereafter at the same place or in the same direction as the cue. Having found that inhibition follows a brief facilitation, POSNER and COHEN [21], MAYLOR [17] and MAYLOR and HOCKEY [18] believe that a peripheral cue first attracts the focus of attention to its location and then repels it to the advantage of other locations. Contrary to the prolonged subsequent inhibition, early RT facilitation from a peripheral cue is not an easily observable effect [26], and in our experience it is entirely absent with cue–target SOAs of 150 msec or more (Tassinari *et al.*, in preparation). Since no early facilitation from previous stimulation at the same location was seen in the present experiments, where inhibition was fully developed at the shortest cue–target SOA (200 msec), the issue of whether inhibition is always pursuant to facilitation [17] or sometimes independent of it [21] cannot be addressed on the basis of our results. The discussion will therefore be centred on the possible roles of the main meridians of the visual field in partitioning the spatial distribution of inhibitory effects on attention.

Several lines of evidence suggest that the vertical and horizontal meridians are not simply imaginary lines subdividing the visual field into quadrants, but rather constitute natural boundaries between psychophysically distinct regions of the visual space which are subserved by separate cerebral substrates. The most obvious functional separation is considered to occur at the vertical meridian, because it is known that there are many asymmetries in cognitive performances between the right and left visual hemifields. Since the organization of the optic pathways is such that the right visual field projects to the left hemisphere and the left visual field projects to the right hemisphere, lateral asymmetries in cognitive performances are best interpreted in terms of differential hemispheric specializations and interhemispheric transfer [1, 15]. The spatial pattern of the inhibitory effect described here cannot be linked specifically to hemispheric separation of function because the spread of inhibition appears to be limited by the horizontal as much as by the vertical meridian.

Perceptual differences between upper and lower visual fields have been much less investigated, but some have been discovered that perhaps can be attributed to functional differences between the cortical representations of these visual field regions [32]. Although the upper and lower quadrants of each side of the visual field project conjointly to the same (contralateral) hemisphere, this does not mean that they are mapped on the cortex in a physically continuous and functionally homogeneous manner. There is evidence that in non-human primates the extrastriate visual cortex contains distinct areas for the separate representation of the superior and inferior visual fields, and it has been suggested that this differential pattern of representation might provide a neural substrate for perceptual up-down asymmetries [3, 35]. However, spatially disjoint cortical representations of the right and left hemifields or the upper and lower quadrants are amply connected in an orderly fashion by inter- and intrahemispheric fibres, and it may be naive to think that their gross physical separation entails an even partial functional independence [34].

The relation of perceptual asymmetries between visual hemifields to the mechanisms of attention is an intriguing one. Many clinical and experimental findings suggest that the spatial distribution of visual attention along the left–right and up-down dimensions is not homogeneous, and that the horizontal and vertical meridians may be major sites of discontinuity in this spatial distribution. A neglect for the contralateral visual field can be easily produced in experimental animals by a number of cortical and subcortical lesions in one hemisphere [28], and left visual inattention is a well-known consequence of various forms of right parietal cortex damage in man [4]. Although the neglected field is by no means blind, it seems that patients with parietal lesions have difficulty in shifting attention away from the side ipsilateral to the damage, particularly across the vertical meridian [25]. Recently, cases of altitudinal neglect, i.e. selective inattention for the upper or lower visual fields, have been described in cats with midbrain lesions [16] and patients with progressive supranuclear palsy [23]. The disturbance here seems to involve a reduced capacity to shift attention in a vertical direction, particularly across the horizontal meridian.

Discontinuities in the spatial distribution of visual attention at the vertical and horizontal meridians have also been detected in experiments on normal man. HUGHES and ZIMBA [9] found that subjects cued to expect a visual stimulus in a particular location on one side of the fixation point along the horizontal meridian showed a modest facilitation of simple RT to stimuli presented not only at the expected location, but also in other locations within the same hemifield, whereas RT to stimuli presented in the opposite hemifield was uniformly retarded. By presenting stimuli along the vertical meridian according to the same paradigm these authors obtained comparable results and concluded that the principal transition between costs and benefits of positional expectancies for RT performance occurs at both main meridians [10]. Using stimuli distributed along the horizontal meridian, DOWNING and nker [5] were able to find costs at unexpected locations within the hemifield of the pected location, but costs were far greater and more uniform at unexpected locations thin the opposite hemifield. Further data and arguments in favour of the importance of the rizontal and vertical meridians in delimiting the spatial spread of the costs of the deliberate sallocation of attention have been provided by recent experiments of Rizzolatti *et al.*] and Tassinari *et al.* [34].

There is thus a suggestion that normal subjects exhibit two kinds of RT inhibition limited one side of the main visual field meridians. One kind of inhibition is caused by the liberate allocation of attention to the opposite side of the meridians, as demonstrated in the dies just described. The other kind of inhibition is induced by peripheral cues occurring ilaterally to the target, as demonstrated in the present paper. These two kinds of inhibition ay involve similar complex interactions between overt and covert response tendencies as ll as between processes of disengagement and redirection of attention, and may therefore pend on partially common neural mechanisms [34]. One possibility is that the activities of rebral areas representing the right or left visual fields or the upper or lower visual adrants are modulated in an at least partly independent fashion by separate attentional stems. If separate attentional systems exist for the control of the cortical representations of e right and left fields as well as of the upper and lower fields, and their organization follows e principle of reciprocal inhibition, a reduction in the activity in one attentional system and cortical target as a result of the arousal of an antagonistic system would be a matter of urse. The further assumption of a period of refractoriness of each attentional system llowing a selective activation from a peripheral cue may explain the ipsilateral inhibitory fect described here. Findings on evoked potentials during selective attention in man [8] are t incompatible with these possibilities but are still insufficient for reaching any definite nclusion.

More compelling correlates of the ipsilateral inhibitory effect may be found at the single euron level. An inhibitory effect of prior stimulation on visually elicited responses has been escribed for single neurons of the superior colliculus in both cat [29] and monkey [37] the asic finding is that the response of superior collicular neurons to optimal stimuli presented their receptive fields is attenuated by the previous presentation of another stimulus in a fferent part of the visual field. The following features of this electrophysiological henomenon are relevant to the behavioural inhibition described in the present study. First, e inhibitory effect occurs both when the two stimuli are superimposed and when they are parated by several degrees of visual angle, although at least in the monkey it is maximal in e first case. Second, the inhibitory effect is present for interstimulus intervals of up to etween 1 and 2 sec in the cat and above 100 msec in the monkey. Third and most important, e inhibitory effect is greatly reduced or abolished if the first stimulus is presented across the ertical meridian from the second. Unfortunately, changes in the inhibitory effect related to e presentation of the two stimuli across the horizontal meridian were not studied in either t or monkey. If the strength of the neural inhibitory effect could be shown to depend on the vo stimuli being on the same side of the horizontal (as well as vertical) meridian, then the nalogy between the electrophysiological findings and the RT effects described in this paper ould be nearly complete.

Since the superior colliculus is known to be generally important for overt orienting, and specially for visuomotor orienting [31, 36], the hypothesis that this same structure may be nvolved in visually guided covert orienting and its consequences as well is an appealing one. t any rate a firmer correlation between neural and behavioural phenomena in this area will be made possible only by expanding our knowledge of the conditions under which the ipsilateral inhibitory effect becomes manifest. Given the close conceptual relation between selective attention and premotor organization [33], further investigations must explore the role of directional constraints in the motor preparation of speeded manual reactions to extrafoveal light stimuli when the natural ocular orienting response to such stimuli is suppressed [34].

REFERENCES

1. Beaumont, J. G. *Divided Visual Field Studies of Cerebral Organisation.* Academic Press, London, 1982.
2. Berlucchi, G. and Rizzolatti, G. Selective visual attention. *Neuropsychologia* **25**, 1-3, 1987.
3. Burkhalter, A., Felleman, D. J., Newsome, W. T. and Van Essen, D. C. Anatomical and physiological asymmetries related to visual areas V3 and VP in macaque extrastriate cortex. *Vision Res.* **26**, 63-80, 1986.
4. De Renzi, E. *Disorders of Space Exploration and Cognition.* John Wiley, New York, 1982.
5. Downing, C. J. and Pinker, S. The spatial structure of visual attention. In *Attention and Performance XI*, M. I. Posner and O. S. M. Marin (Editors), pp. 171-187. Erlbaum, Hillsdale, New Jersey, 1985.
6. Eriksen, C. W. and Hoffman, J. E. Some characteristics of selective attention in visual perception determined by vocal reaction time. *Percept. Psychophys.* **11**, 169-171, 1972.
7. Haines, R. F. and Gilliland, K. Response time in the full visual field. *J. appl. Psychol.* **58**, 289-295, 1973.
8. Hillyard, S. A. Electrophysiology of human selective attention. *Trends Neurosci.* **8**, 400-405, 1985.
9. Hughes, H. C. and Zimba, L. D. Spatial maps of directed visual attention. *J. exp. Psychol. Hum. Percept. Perform.* **11**, 409–430, 1985.
10. Hughes, H. C. and Zimba, L. D. Natural boundaries for the spatial spread of directed visual attention. *Neuropsychologia* **25**, 5-18, 1987.
11. Johnston, W. A. and Dark, V. J. Selective attention. *A. Rev. Psychol.* **37**, 43–75, 1986.
12. Jonides, J. Towards a model of the mind's eye movements. *Can. J. Psychol.* **34**, 102-112, 1980.
13. Jonides, J. Voluntary versus automatic control over the mind's eye's movement. In *Attention and Performance IX*, J. Long and A. Baddeley (Editors), pp. 187–203. Erlbaum, Hillsdale, New Jersey, 1981.
14. Kinsbourne, M. The mechanism of hemispheric control of the lateral gradient of attention. In *Attention and Performance V*, P. M. A. Rabbitt and S. Dornic (Editors), pp. 81–97. Academic Press, London, 1975.
15. Marzi, C. A. Transfer of visual information after unilateral input to the brain. *Brain Cognit.* **5**, 163-173, 1986.
16. Matelli, M., Olivieri, M. F., Saccani, A. and Rizzolatti, G. Upper visual space neglect and motor deficits after section of the midbrain commissures in the cat. *Behav. Brain Res.* **10**, 263-285, 1983.
17. Maylor, E. A. Facilitatory and inhibitory components of orienting in visual space. In *Attention and Performance XI*, M. I. Posner and O. S. M. Marin (Editors), pp. 89-104. Erlbaum, Hillsdale, New Jersey, 1985.
18. Maylor, E. A. and Hockey, R. Inhibitory component of externally controlled covert orienting in visual space. *J. exp. Psychol. Hum. Percept. Perform.* **11**, 777–787, 1985.
19. Myers, J. L. *Fundamentals of Experimental Design.* Allyn & Bacon, Boston, 1979.
20. Posner, M. I. Orienting of attention. *Q. J. exp. Psychol.* **32**, 3-25, 1980.
21. Posner, M. I. and Cohen, Y. Components of visual orienting. In *Attention and Performance X*, H. Bouma and G. G. Bouwhuis (Editors), pp. 531–556. Erlbaum, Hillsdale, New Jersey, 1984.
22. Posner, M. I., Nissen, M. J. and Ogden, W. C. Attended and unattended processing modes: the role of set for spatial location. In *Modes of Perceiving and Processing Information*, H. L. Pick and I. J. Saltzman (Editors), pp. 137–157. Erlbaum, Hillsdale, New Jersey, 1978.
23. Posner, M. I., Rafal, R. D., Choate, L. S. and Vaughan, L. Inhibition of return: neural basis and function. *Cognit. Neuropsychol.* **2**, 211–228, 1985.
24. Posner, M. I., Snyder, C. R. R. and Davidson, B. J. Attention and the detection of signals. *J. exp. Psychol. Gen.* **109**, 160-174, 1980.
25. Posner, M. I., Walker, J. A., Friedrich, F. A. and Rafal, R. D. How do the parietal lobes direct covert attention? *Neuropsychologia* **25**, 135–145, 1987.
26. Possamai, C. A. Relationship between inhibition and facilitation following a visual cue. *Acta Psychol.* **61**, 243–258, 1986.
27. Remington, R. W. Attention and saccadic eye movements. *J. exp. Psychol. Hum. Percept. Perform.* **6**, 726–744, 1980.
28. Rizzolatti, G. and Camarda, R. Neural circuits for spatial attention and unilateral neglect. In *Neurophysiological and Neuropsychological Aspects of Spatial Neglect*, M. Jeannerod (Editor), North-Holland, Amsterdam, 1987.
29. Rizzolatti, G., Camarda, R., Grupp, L. A. and Pisa, M. Inhibitory effect of remote visual stimuli on visual responses of cat superior colliculus: spatial and temporal factors. *J. Neurophysiol.* **37**, 1262-1275, 1974.

30. RIZZOLATTI, G., RIGGIO, L., DASCOLA, I. and UMILTA', C. Reorienting attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention. *Neuropsychologia* 25, 31–40, 1987.
31. SCHILLER, P. H. The superior colliculus and visual function. In *Handbook of Sensory Physiology*, J. M. BROOKHART and V. B. MOUNTCASTLE (Editors), Vol. 3, *Sensory Processes*, Part 1, I. DARIAN-SMITH (Editor), pp. 457–505. American Physiological Society, Bethesda, MD, 1984.
32. SKRANDIES, W. The upper and lower visual field of man: electrophysiological and functional differences. In *Progress in Sensory Physiology*, D. OTTOSON (Editor), Vol. 8, pp. 1–93. Springer, Berlin, 1987.
33. SPERRY, R. W. Neurology and the mind-brain problem. *Am. Sci.* 40, 291–312, 1952.
34. TASSINARI, G., AGLIOTI, S., CHELAZZI, L., MARZI, C. A. and BERLUCCHI, G. Distribution in the visual field of the costs of voluntarily allocated attention and of the inhibitory after-effects of covert orienting. *Neuropsychologia* 25, 55–71, 1987.
35. VAN ESSEN, D. C., NEWSOME, W. T., MAUNSELL, J. H. R. and BIXBY, J. L. The projection from striate cortex (V1) to areas V2 and V3 in the macaque monkey: asymmetries, areal boundaries, and patchy connections. *J. comp. Neurol.* 244, 451–480, 1986.
36. WURTZ, R. H. and ALBANO, J. E. Visual-motor function of the primate superior colliculus. *A. Rev. Neurosci.* 3, 188–226, 1980.
37. WURTZ, R. H., RICHMOND, B. J. and JUDGE, S. J. Vision during saccadic eye movements. III. Visual interactions in monkey superior colliculus. *J. Neurophysiol.* 43, 1168–1181, 1980.