

POSSIBLE RECODING OF VISUAL SPACE IN COVERT ORIENTING TASKS

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INTRODUCTION

Experimental evidence and everyday experience about visual cognition and action indicate that observers tend to partition the visual field in relation to its main meridians passing through the fixation point. The central vertical meridian normally provides the distinction between left and right, and the central horizontal meridian normally provides the distinction between up and down. This oculocentric frame of reference is open to influences not only from headcentric and bodycentric components of spatial coding (5), but also from the momentary deployment of attention in the visual field. The focus of visuospatial attention can be voluntarily dissociated from the line of sight (14), and in some cases at least it is this focus, rather than the fixation point, that functions as the nodal point of the reference system for segmenting space into its lateral or altitudinal halves. Cases of visuospatial recoding based on the direction of the attentional focus have been described, for example, in spatial stimulus-response compatibility tasks, where compatibility effects have been determined by the right or left positions of the stimuli relative to the attentional focus rather than the fixation point (e.g. 11, 12).

In previous papers we have described a visuomotor reaction time (RT) task which produces different effects on different sides of the vertical meridian. Simple manual RT for detecting a light target, henceforth called S2, at an extrafoveal location is increased if that location has recently received another light stimulus, henceforth called S1. Following Posner et al. (16), this effect has been called inhibition of return (e.g. 1, 17, 22), and attributed by Posner and Cohen (15) to a local inhibition that serves to redirect attention to other locations, thus favoring a balanced exploration of the entire visual field. We have additionally described a smaller but very robust inhibitory effect from extrafoveal S1s remote from extrafoveal S2s, but occurring on the same side of the vertical or horizontal meridians (ipsilateral inhibition). More precisely, RT to S2s preceded by S1s in the same hemifield is systematically longer than RT to S2s preceded by contralateral S1s at stimulus-onset-asynchronies (SOAs) that vary from 0 to over 3 sec (2, 23-28). Ipsilateral inhibition is usually demonstrated with S1s that do not predict the

* The senior author dedicates this paper to Professor Arnaldo Arduini on the occasion of his retirement, with gratitude for the physiological training received from him nearly forty years ago.

location of the following S2s, and is largely independent of the S1-S2 distance. Since the task is to be performed with the line of sight locked onto a fixation mark, observers have to resist the natural tendency to foveate S1, and we believe that it is this oculomotor inhibition toward the side of S1 that interferes with the emission of other motor reactions to subsequent S2s from the same side (2, 23-28). Reactions to S2s from the other side do not suffer from this spreading inhibition and may even benefit from dishinhibition, in accord with the reciprocal innervation principle applying to opposite turning tendencies (28).

Another possibility is that the detection of both S1 and S2 requires that the focus of attention be moved to their respective locations, and that after S1 the focus is recentered in preparation for an S2 that can occur unpredictably on either side. On the assumption that movements of focus of attention are in some ways associated with the mechanisms for moving the eyes (e.g. 1, 3, 7, 17-22), subsequent movements against the recentering direction would be disadvantaged compared to movements in the same direction as the recentering direction (22). If, for example, S1 occurred on the right, and the recentering movement would thus be from right to left, a subsequent S2 on the right would call for an inversion of the direction of the recentering movement, whereas a left S2 would not.

The question we ask in this paper is whether an ipsilateral inhibition effect might occur when ipsilateral and contralateral are defined with reference to an attentional focus dissociated from the fixation point. Suppose that the focus of attention is initially centered on the midpoint of a multi-location display restricted to one visual hemifield. The locations that lie on the same side of the attentional focus (and the display midpoint) are now defined as ipsilateral, and those that lie on opposite sides are defined as contralateral. If the focussing of attention on the lateralized display results in a recoding of visual space, ipsilateral inhibition may persist to the extent that the directional effects assumed to underlie it are translated from the fixation point to the display midpoint. A further aspect to be considered is whether this spatial recoding, if it occurs at all, involves only the control of the movements of covert attention, or whether it also in some way affects the oculomotor control itself.

METHODS

Subjects. - Six female and six male students or staff of the University of Verona, ranging in age from 23 to 40 years, took part in the experiment. They were all right handed, had normal or corrected-to-normal vision, and were naïve about the purpose of the study.

Apparatus. - The experiment was carried out in a sound attenuated room with a background illumination of 0.1cd/m^2 provided by two red bulbs. The stimuli were projected on a white tangent screen by means of a computer controlled GE Imager 300 video projector. A permanent display consisted of a central 1° by 1° red cross and four red 1° by 1° square boxes aligned along the horizontal direction through the cross center. In one condition the four boxes were positioned to the right or left of the cross, so that the distance between their centers was 8° , and the center of the medialmost box lay at a distance of 4° from the cross center. In another condition a 2° long vertical segment (marker) was added in the center of the unilateral display of four boxes.

These two types of display will be called unilateral, as opposed to a third condition involving a bilateral display in which the four boxes were symmetrically positioned with respect to the central cross, two on the right and two on the left. The distance between the centers of the two boxes on each side was 8° , and the distance between the cross and the center of the medialmost box on each side was 4° (near bilateral display) or 20° (far bilateral display). The various types of display are shown in Fig. 1, where it can be noticed that the eccentricity of the boxes in the two types of bilateral display matched the eccentricity of the boxes in the unilateral display.

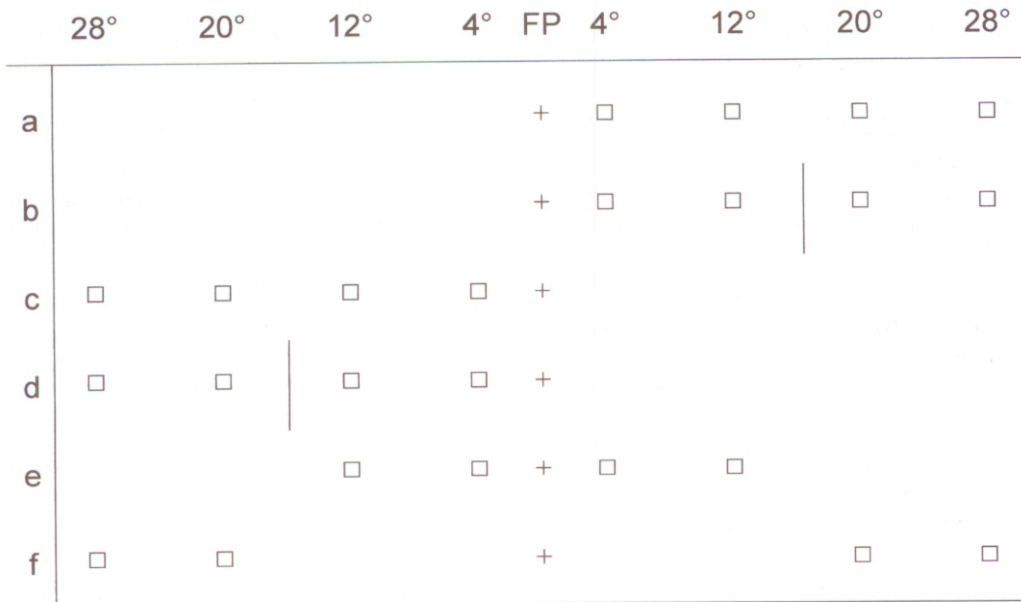


Fig. 1. - Stimulus positions in the bilateral display and in the right and left unilateral displays, with and without the central marker.

a and c = right and left unilateral displays without marker; b and d = right and left unilateral displays with marker; e = near bilateral display; f = far bilateral display.

Green 0.5° by 0.5° solid squares with a luminance of 15 cd/m^2 could be projected for 16 msec in the center of any of the four boxes to serve as either S1 or S2 stimuli. Acoustic stimulation was provided by delivering binaural 400 Hz tone bursts, having a duration of 200 msec and a moderately suprathreshold intensity, via a headphone.

Procedure. - The subjects sat in an armchair in front of the screen, with the head positioned in a headrest so that the distance between the eyes and the cross was 171 cm. Each trial of the task started with the auditory tone burst which prompted the subject to fixate on the central cross. After an interval varying randomly between 2 and 3 sec a green square was presented in one of the four boxes (S1), followed by another green square (S2) in the same or a different box at an SOA that could take one of four values: 200, 600, 1500 or 4000 msec. The subject's right or left hand was comfortably placed on a response key fastened to the corresponding side of the armchair. Pressing the key could stop an electronic msec counter that was started by the computer at the onset of S2. Subjects were instructed to press the key with their right or left thumb as soon as they saw S2 while maintaining fixation, and their RT was recorded by the

computer. No overt reaction was to be made to S1, but since S1 and S2 were physically identical, subjects had to detect S1 in order to identify S2 as the target for the manual response. The occurrences of S1 and S2 in the four boxes were completely and independently randomized so that the position of S1 did not predict that of S2. Each subject participated in nine experimental sessions, each of which included three blocks of 64 trials. The three blocks in a session corresponded to the three experimental conditions identified by the three kinds of display, namely the unilateral display without the vertical marker (UDW), the unilateral display with the vertical marker (UDM) and the bilateral display (BD). Subjects were told that while they had to maintain fixation throughout each trial in each experimental condition, the occurrence of S1 and S2 in the four locations of each display would be randomized independently for the two stimuli. They were additionally told that both S1 and S2 of unilateral displays would consistently occur on the same side, so that it would be convenient for them to covertly orient attention to that side. Finally, they were told that the vertical line in the UDM condition would provide a landmark for facilitating covert orientation to the midpoint of the unilateral display. The 64 trials in each block exhausted all possible combinations between the four positions of S1, the four positions of S2 and the four S1-S2 SOAs, which were presented in a variable randomized order. The order of the three conditions was changed from session to session and counterbalanced across subjects. In previous experiments of this kind we failed to find differences between the right and left visual fields, or the right or left hand. Thus six subjects were consistently presented with UDs in the right field, and six were consistently presented with UDs in the left field; and six subjects consistently used the right hand for responding and the other six used the left hand. Finally, six subjects were presented with the near BD and six with the far BD. The three variables, field, hand and box eccentricity in the BDs were counterbalanced across subjects according to a Latin square design. Responses faster than 150 msec or longer than 500 msec were discarded as anticipations and misses, and replaced later in the sequence. Fixation maintenance was monitored via a videocamera, and trials contaminated by eye movements were also rejected and rerun. A third cause for aborting and repeating trials was given by key-pressing responses to S1, which were detected by the computer. In all cases the number of rejected trials was so small as to justify the disregard of this variable.

Data analysis. - Each subject provided nine RTs for each of the combinations between the position of S1, the position of S2 and the SOA in each of the three experimental conditions. In each subject RTs were grouped in order to assess the effects of 1) the SOA, 2) the condition and 3) the positional relationship between S1 and S2. RT grouping for analyzing the last factor was effected in accord with our previous studies: at each SOA and for each kind of display we divided trials according to whether S1 and S2 went to the same location (SP trials), or to locations on the same side of the display midpoint (SF trials), or to locations symmetrically (SYM) or asymmetrically (ASYM) placed on the two sides of the display midpoint. Means from these various RT groups were entered into repeated-measures analyses of variance (ANOVAs) with subjects considered as a random source of variation.

RESULTS

The results are presented in synthetic form in Figures 2, 3 and 4 and can be summarized as follows. The BD condition completely replicated the ipsilateral inhibitory effect reported with similar bilateral displays in our previous studies (2, 23-28). Namely, RT was longest when the position of S1 and S2 coincided (the same point effect, SP), intermediate when S1 and S2 appeared in different locations on either side of the fixation point (the same field effect, SF), and shortest when the locations of S1 and S2 were contralateral (the opposite field effect, OF). The two UD conditions exhibited an overall advantage for RT over the BD condition, but only at the three longest SOAs.

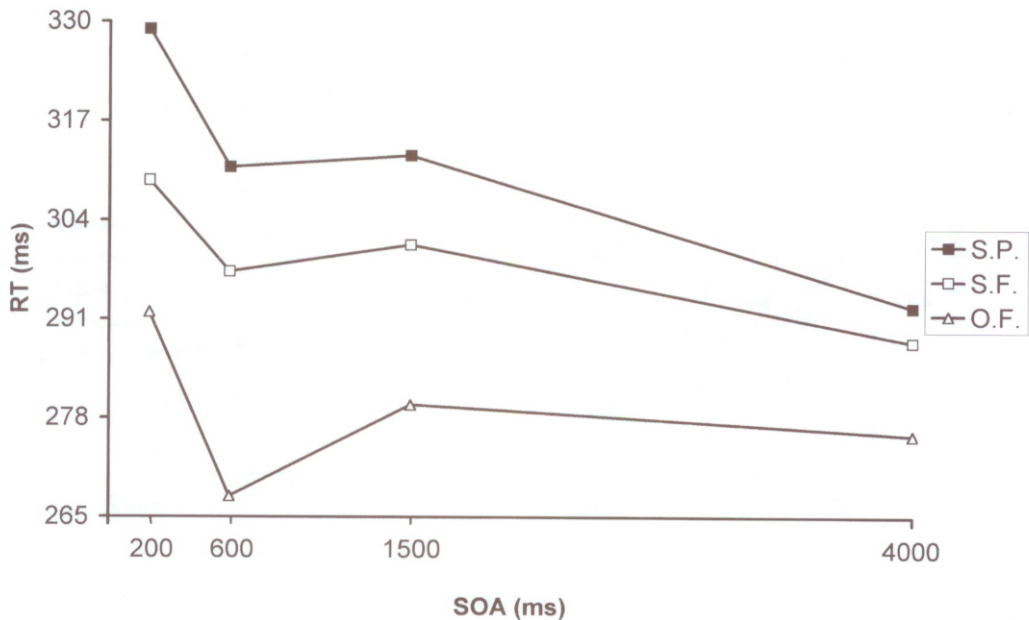


Fig. 2. - Reaction time as a function of the S1-S2 positional relation and S1-S2 SOA in the bilateral display condition.

SP = S1 and S2 at the same location; SF = S1 and S2 at ipsilateral locations; OF = S1 and S2 at opposite locations. For simplicity, RTs to S2s symmetrically and asymmetrically opposite to S1s are collapsed in the OF combination.

Both UD conditions yielded significant effects akin to the ipsilateral inhibitory effect of the BD condition, i.e. RT to S2s following S1s on the same side of the display midpoint was longer than RT to S2s opposite to S1s relative to the display midpoint. These effects however were much smaller in size than the corresponding effects in the BD condition, and were slightly but significantly greater with the marker than without. Further, at the 200 msec SOA in both UD conditions RT was the same for S2 targets not coinciding with S1, regardless of their position relative to the display midpoint. Statistical validation of all these effects was provided by the following ANOVAs in which orthogonal contrasts were performed with Bonferroni-corrected paired t-tests.

In an ANOVA with SOA (four levels), S1-S2 positional relation (four levels), and condition (three levels), all sources of variation proved significant except for the SOA/condition interaction which fell just short of significance [$F(6,66) = 2.2$, $p = .053$]. RT decreased significantly with SOA [$F(3,33) = 5.5$, $p < .005$] and varied significantly with the condition [$F(2,22) = 7.7$, $p < .005$]. BD RT was significantly longer than both UDM RT [$t(11) = 2.5$, $p < .04$] and UDW RT [$t(11) = 4.6$, $p = .001$], and UDM RT was significantly longer than UDW RT [$t(11) = 2.7$, $p = .02$]. The significance of the S1-S2 positional relation [$F(3,33) = 99.9$, $p < .0001$] reflects the fact that SP RT was significantly slower than SF RT

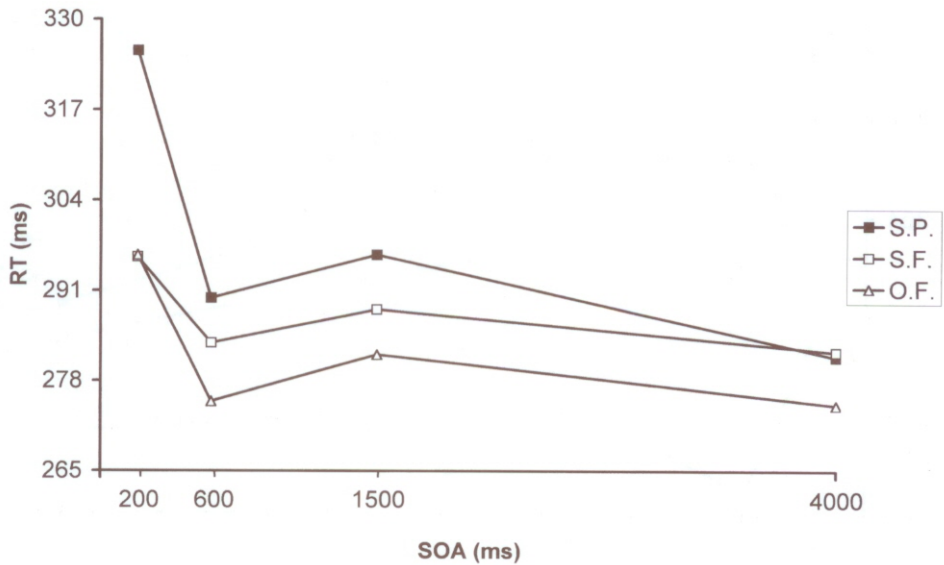


Fig. 3. - Reaction time as a function of the S1-S2 positional relation and S1-S2 SOA in the unilateral display condition with marker.

SP = S1 and S2 at the same location; SF = S1 and S2 at locations ipsilateral to the display midpoint; OF = S1 and S2 at locations on opposite sides of the display midpoint. For simplicity, RTs to S2s symmetrically and asymmetrically opposite to S1s are collapsed in the OF combination.

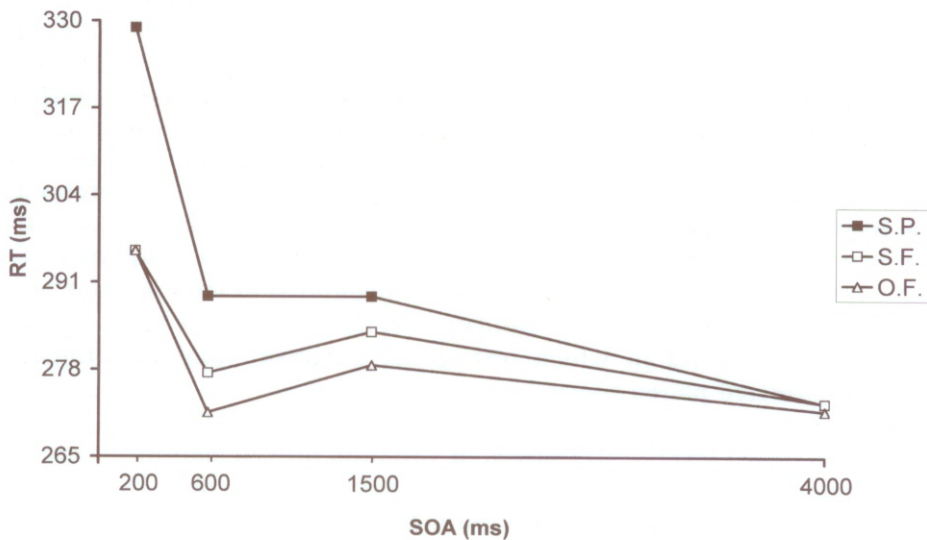


Fig. 4. - Reaction time as a function of the S1-S2 positional relation and S1-S2 SOA in the unilateral display condition without marker.

SP = S1 and S2 at the same location; SF = S1 and S2 at locations ipsilateral to the display midpoint; OF = S1 and S2 at locations on opposite sides of the display midpoint. For simplicity, RTs to S2s symmetrically and asymmetrically opposite to S1s are collapsed in the OF combination.

[$t(11) = 8.8, p > .001$], SF RT was significantly slower than both SYM RT [$t(11) = 8.0, p < .001$] and ASYM RT [$t(11) = 6.8, p < .001$], while the two latter RTs did not differ from each other [$t(11) < 1$]. The significance of the interaction between condition and the S1-S2 positional relation [$F(6,66) = 15.0, p < .0001$] is attributable to the fact that the differences between SP RT and SYM-ASYM RT (averaged for simplicity) and between SF RT and SYM-ASYM RT occurred in all three conditions, but were significantly greater in the BD condition than in the UDM condition [respectively: $t(11) = 5.1, p < .0001$; $t(11) = 3.8, p < .005$] and the UDW condition [respectively: $t(11) = 6.5, p < .0001$; $t(11) = 5.1, p < .0001$]. The significance of the interaction between SOA and the S1-S2 positional relation [$F(9,99) = 6.2, p < .0001$] is accounted for by the fact that the difference between SP RT and SF RT became insignificant at the longest SOA [$t(11) < 1$]. The significance of three-way interaction [$F(18,198) = 1.9, p < .02$] is best accounted for by the presence at the 200 msec SOA of a significant difference between SF RT and SYM-ASYM RT in the BD condition [$t(11) = 3.1, p = .01$], and the absence at the same SOA of such difference in the UDM and UDW conditions [$t < 1$ in both cases].

It has been mentioned in the Methods that the eccentricity of the stimuli in the BD condition was balanced with that in the two UD conditions between but not within subjects. To make sure that the intrasubject partial differences in stimulus eccentricity did not account for the significant RT differences between the BD condition and the two UD conditions, only the RTs that each subject yielded to S2s in the two locations shared by the three conditions were retained and entered into an ANOVA with condition (three levels) as the only factor. Condition proved again significant [$F(2, 22) = 8.4, P < .005$], BD RT being significantly greater than UDW RT [$t(11) = 7.6, p < .001$] and UDM RT [$t(11) = 2.7, p = .02$]. Therefore the difference between the BD condition and the two UD conditions revealed by the first ANOVA was found also when stimulus eccentricity was eliminated as a possible factor. In this ANOVA the two UD conditions did not significantly differ from each other.

A final test was aimed at assessing whether ipsilateral inhibition could simply be interpreted as a spread of inhibition from the S1 location that decayed with distance. To this purpose, we compared RTs to S2s preceded by contralateral near and contralateral far S1s in a subset of data. The complete lack of a significant difference [$t(11) < 1$] militates against an inverse relation between inhibition and distance from S1, suggesting that ipsilateral inhibition was restricted to one side of the display midpoint.

DISCUSSION

The first issue to be considered is whether our subjects did covertly attend to the unilateral displays. When observers expect a stimulus that can randomly occur anywhere in a multi-location stimulus array, they detect it at best when attention

is overtly or covertly aligned with the stimulus direction (14, 15). In the bilateral display condition of our experiment, observers might choose to split attention between the two sides (3), if this is at all feasible (10), or to attend covertly to either the right or left in order to anticipate the arrival of S2. In the first case, obviously no S2 stimulus would enjoy the observer's undivided attention. In the second case, because of the unpredictability of the side of S2, orienting of attention would be opposite to stimulus direction on half of the trials on average. In both cases there are thus reasons for expecting unfavorable consequences for response speed. By contrast, with unilateral displays, the observers' complete foreknowledge of the stimulus side would reasonably lead them to orient covertly to that side, either continuously throughout a trial, or after S1 and before S2. Orienting to the right or left would thus always be in the general direction of the stimuli, with expectable benefits for response speed. A faster RT with unilateral than bilateral displays would therefore argue for such a directed allocation of attention by our subjects. The results do indeed bear out a significant RT advantage for unilateral displays that cannot be accounted for by differences in the eccentricity of the stimuli, and therefore can reasonably be attributed to the suggested attentional factor. Since the advantage for unilateral over bilateral displays arose after the 200 msec SOA, it seems likely that on average subjects did not hold attention to the side of the display during the entire trial, but oriented toward it after the occurrence of S1. Umiltà et al. (29) assessed that 300 msec are necessary for a rather precise covert orientation from fixation toward a location in one visual hemifield.

The long RT found in all conditions and at all SOAs with the SP effect (S1-S2 combinations at the same location) is in keeping with many similar results usually designated in the psychological literature as inhibition of return (e.g. 1, 17, 22), in accord with Posner et al. (16). Posner and Cohen (15) attributed the effect to a sensory inhibition arising at the site of a recent visual stimulation, while other researchers have invoked additional factors associated in one way or another with covert orienting and/or oculomotor control (1-3, 6, 8, 9, 17, 22-28). The main focus of this paper was not on the SP effect, but rather on the ipsilateral inhibition or same field effect, i.e. the disadvantage for ipsilateral S1-S2 combinations relative to contralateral combinations, ipsilateral and contralateral being defined with respect to the display midpoint, as specified in the Introduction. The results provide an affirmative answer to the question of whether ipsilateral inhibition would persist with stimulus displays completely lateralized to one hemifield, though a few qualifications are in order because of the very small size of the effect compared with that typically found with bilateral displays. On one hand this would seem to indicate that the major factors of ipsilateral inhibition have to do with opposite rightward and leftward oculomotor tendencies originating from the vertical meridian of the visual field (2, 6, 23-28). On the other hand, the ipsilateral inhibition observed with unilateral displays was statistically significant, and thus putatively accountable for by movements of the focus of attention within the unilateral display, as explicated in the Introduction. The small size of ipsilateral inhibition with unilateral displays may simply be due to the subjects' failure to

attend to the display midpoint on a number of trials. Ipsilateral inhibition was indeed significantly greater with the marked unilateral display, which was supposed to help subjects focus attention onto the display midpoint, than with the unmarked unilateral display, where probably the focussing of attention was more imprecise. The assumption that ipsilateral inhibition required the centering of the focus of attention on the unilateral displays is strongly supported by the results at the 200 msec SOA, indicating the absence of both the ipsilateral inhibition and the attentional advantage for the unilateral over the bilateral conditions.

All these considerations suggest that the ipsilateral inhibition observed with unilateral displays may be indicative of a recoding of visual space, contingent on the centering of covert attention on the midpoint of such displays, and similar to that reported in spatial compatibility tasks (11, 12). Whether such visual space recoding affects only the control for covert shifts of attention, or whether it involves a recoding of the spatial frame of reference for oculomotion as well, cannot be decided on the basis of the present evidence. It is known, however, that neurons in the supplementary eye field of macaques can code eye movements in an object-centered manner, whereby the neuronal discharge is selectively related to eye movements toward the right or left side of an object independent of whether the eye movement is directed toward the oculocentric right or left (13). These findings suggest that the oculomotor system ought to be able in some degree to distinguish between relative right and left stimulus directions in our unilateral displays, regardless of the fact that for each unilateral display these directions were all to the right or to the left of the line of sight. If this is so, the suppression of an oculomotor reaction toward an S1 in a unilateral display may have different effects depending on whether S1 occupies a right or left location in the display, even though the general direction of the suppressed reaction would be the same in both cases. It is clear that more experimental evidence is needed for assessing the combined or separate effects of oculomotor tendencies and covert movements of the attentional focus on visual RT to fully lateralized stimulus displays.

SUMMARY

Reaction time to lateralized light targets is longer if targets are preceded by light stimuli in the same visual hemifield compared to when they are preceded by light stimuli in the opposite visual hemifield. The effect is probably caused by interactions between implicit oculomotor tendencies and covert shifts of attention. We show here that a similar, but much smaller, ipsilateral RT inhibition can be observed when all stimuli are presented in a display completely lateralized to one hemifield, where ipsilateral and contralateral are defined with respect to the midpoint of the display. The persistence of ipsilateral inhibition with unilateral stimulus displays can be accounted for by a recoding of visual space predicated on the centering of covert attention on the display midpoint rather than on the fixation point. The recoding seems to affect the control of covert attention and perhaps oculomotor control as well.

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