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"Distribution in the Visual Field of the Costs of Voluntarily Allocated Attention and of the Inhibitory After-Effects of Covert Orienting"

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DISTRIBUTION IN THE VISUAL FIELD OF THE COSTS OF VOLUNTARILY ALLOCATED ATTENTION AND OF THE INHIBITORY AFTER-EFFECTS OF COVERT ORIENTING

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Abstract—By using a simple reaction time (RT) paradigm we have investigated the spatial distribution of the benefits and costs of voluntarily directed attention and of the inhibitory after-effects of covert orienting. In the first experiment subjects deliberately allocated attention to each one of five stimulus positions disposed along the horizontal meridian, while at the same time fixing their eyes on the central position. The separation in visual angle between the central position and the two nearest positions, one on the left and the other on the right, was 10°; that between the central position and the two most eccentric positions was 30°. By comparing RT to brief flashes of light presented at each position during directed attention with RT to identical flashes at the same position during diffuse attention (i.e. in a condition in which subjects paid equal attention to all five positions), it was possible to determine that benefits, that is RT decreases relative to the diffuse-attention condition, were strictly limited to the attended position. Costs, i.e. RT increases relative to the diffuse-attention condition, showed a more diffuse and complex spatial pattern. When attention was directed to one of the non-central positions, costs were apparent at the two contralateral positions and at the central position, but not at the ipsilateral position. When attention was directed to the central position, costs occurred at all other positions. This suggests a special role for the vertical meridian in delimiting the area of costs when one covertly orients towards the opposite right or left visual half field. Work of others and our preliminary evidence indicate that the area of costs is similarly limited by the horizontal meridian when one orients toward the opposite upper or lower visual field. In the second experiment we studied the inhibitory after-effect of covert orienting. Orienting to a light stimulus without moving the eyes to it may induce a short-lived facilitation of the speed of response to a second stimulus presented at the same position, but this facilitation is followed by a profound and prolonged RT retardation. By using a two-flashes paradigm we observed this RT retardation not only when the two stimuli appeared at the same position, but also when they occurred at different locations in the same altitudinal or lateral visual hemifield. There were no inhibitory after-effects when the two stimuli appeared on opposite sides of the vertical or horizontal meridian. Thus, as with the costs of voluntarily directed attention, the spatial spread of inhibitory after-effect of covert orienting was demarcated by the vertical or horizontal meridian. An attempt to provide a unitary interpretation for the similarity between the spatial distributions of the two different types of attentional effects is made by referring to directional constrains in motor readiness that are common to both situations.

INTRODUCTION

Many recent studies have addressed the problem of whether it is possible to allocate attention to a specific point in the visual field without foveating it. An experimental paradigm which has been favoured for its simplicity involves the measuring of simple reaction time (RT) to flashes of light presented at one of several extrafoveal locations in the visual field

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under three attentional conditions: in one condition the subject attends specifically to that location, in another condition he attends to a different location, and in yet another he attends equally to all possible stimulus locations [21]. The latter condition is called the neutral condition; decreases in RT at attended locations relative to the neutral condition are called benefits; and increases in RT at unattended locations over RT in the neutral condition, which are seen when attention is directed to a location different from that of the stimulus, are called costs. Significant benefits and costs at extrafoveal locations can be obtained while the foveae are locked on a fixation point until after the presentation of the stimulus, hence these changes in RT must be accounted for by changes in the receptivity for incoming visual signals that are totally independent of the orienting ocular response. This has led to the concept of a covert orienting mechanism that can shift attention over the visual field without requiring eye movements [10, 18, 19, 20, 21, 23].

In these experiments allocation of attention to a specific visual field position is usually induced by visually cuing the subject about the position for which the probability of stimulus occurrence is maximal. Visual cues for the generation of positional expectancies may be presented before the stimulus at or near the cued position, or they may occur far away from the cued stimulus position and signal it by means of a symbolic relation. It would seem reasonable that cues spatially linked with the stimulus position should be more effective than symbolic cues because they should automatically attract attention to the cued position [11]. However, it turns out that stimulation of a visual field location induces a long-lasting slowing of RT to stimuli subsequently presented to that location, and that this RT slowing is a consequence of a covert orienting to the first stimulus [1, 14, 16, 17, 19]. Thus, in addition to direct benefits and costs, there is an inhibitory after-effect of covert orienting. This has been attributed to a mechanism which biases the visual system toward collecting information from ever-changing regions of the visual field [16, 17, 19, 22].

Lately there has been a surge of interest in the spatial distribution of the benefits, costs and inhibitory after-effects of covert orienting. The simplistic idea that benefits are restricted to the attended position and costs affect equally all unattended positions has been disproved by much evidence bearing out a considerably more complex spatial pattern of such attentional effects. It is not clear if benefits can possibly spread away from the attended position, but there is general agreement that costs affect large portions of the visual field, although their distribution is far from homogeneous [5, 8, 9, 24]. There are indeed indications that the main meridians of the visual field may constitute boundaries or lines of major transitions in the spatial distribution of costs of selective attention.

Regarding the inhibitory after-effects of covert orienting, we saw that they also extended to large portions of the visual field which were bounded on the medial side by the vertical meridian [1, 3] and on the upper or lower sides by the horizontal meridian [3, 14]. These similarities between the spatial distribution of the costs of selective attention and the inhibitory after-affects of covert orienting have suggested to us that the general attentional field is anisotropic, with major changes in the distribution of attentional effects occurring at the vertical and horizontal meridians.

In the present paper we examine this possibility by describing two sets of different but related experiments. In the first set of experiments we have analysed the spatial pattern of the costs and benefits of voluntarily allocated attention, using a new paradigm which does not require the generation of positional expectancies. In the second set of experiments we have performed a more detailed evaluation of the spatial distribution of the inhibitory after-effects of covert orienting across the main meridians of the visual field.

EXPERIMENTS ON COSTS AND BENEFITS OF VOLUNTARILY ALLOCATED ATTENTION

Experiments on the selective allocation of attention to specified visual field positions have ordinarily employed pre-stimulus cues which provide information about the probability of stimulus occurrence at each given position. In the neutral condition the pre-stimulus cue signals that the probability of occurrence is the same for all possible positions. In the attentive conditions the probability of stimulus occurrence is high for the cued position (e.g. 80%) and equally low for all the other positions (e.g. the sum total of the probabilities of stimulus occurrence at these positions is 20%). If the stimulus does indeed appear at the high-probability position indicated by the cue, the positional expectancy and, presumably, the locus of selective attention coincide with the actual position of the stimulus; if on the contrary the stimulus appears at one of the low-probability positions, this is unattended because the cue has misdirected attention to the highly probable potential stimulus position [18, 20, 21, 23].

Three considerations suggest that this paradigm may be more complicated than it seems. First, although the primary task is a simple RT task, on each trial the subject must interpret the cue, and the difficulty of this interpretation may affect performance on the subsequent RT task. If, as it seems likely, the difficulty of the interpretation of directional cues is different from that of the interpretation of neutral cues, the comparison between RTs of the neutral and attentional conditions could be biased by this extraneous factor [12]. Second, there are many more RTs to attended than to unattended positions, and this may introduce unwanted sampling differences in the comparisons. Third, with different stimulus frequencies for attended and unattended positions, the better performance at attended positions may be attributed at least partly to probabilistic operant conditioning rather than to a conscious and wilful allocation of attention to a visual field position.

We have tried to overcome these complications in the analysis of voluntary allocation of visual attention by employing a different experimental paradigm in which pre-stimulus cues were eliminated and the probability of occurrence of the stimulus was equal for all possible positions, both in the neutral and in the attentive conditions. This paradigm has provided interesting results regarding the spatial distribution of voluntary attention in the visual field.

METHODS

Twelve normal right-handed adults, six males and six females, performed a simple visuomotor RT task during six experimental sessions which were run on separate days. All of them had experience with RT tasks. A light stimulus could appear in one of five positions along the horizontal meridian of the visual field. The source of the stimulus was any one of five light emitting diodes (LEDs, TIL 222) with round tips 5 mm dia. which could be lighted individually by a 15 mA square pulse of current of 5 msec duration, producing a gallium phosphide green flash of light with a luminance of 70 cd/sq. m. The LEDs were fastened to an arc perimeter 57 cm in radius, one LED in a central position being flanked on each side by two other LEDs at 10 and 30 cm.

Subjects sat with head position in a head- and chin-rest at the center of the perimeter so that the distance from the midpoint between their eyes and each LED was 57 cm. At this distance the visual angle between the central LED and each of the two nearest LEDs was 10°, and the visual angle between the central LED and each of the two farthest LEDs was 30°. The arc perimeter was attached to a white screen illuminated from above at a luminance of 0.15 cd/sq. m.

In each session there were six blocks of 50 trials each, and in each block ten stimuli were presented in each of the five positions in a completely random sequence. On each trial the light stimulus was preceded at an interval ranging randomly from one to three sec by an auditory tone peep, 50 msec in duration, delivered through earphones.

Subjects were instructed to fixate binocularly on the central LED upon hearing the warning signal and to respond bimanually by pressing one key with the right thumb and one key with the left thumb as soon as they saw a light flash in any of the five positions, while at the same time maintaining fixation on the central LED. The keys were positioned symmetrically on the sides of the subject at a convenient distance from two forearm rests. RT was measured to the nearest msec from the onset of the stimulus to the closing of a switch by the key-press.

At the beginning of each of the six blocks within a session subjects read on a computer screen a standard instruction either to pay selective attention to a specified stimulus position or to attend equally to all five positions throughout the block. With the standard background illumination the five LEDs were clearly visible, in central as well as in peripheral vision, even when not activated. In each session there was one block allotted to selective attention to each of the five stimulus positions, the remaining block serving for the condition of "diffuse" attention. The subjects understood that ocular fixation on the central LED was to be maintained throughout each trial in all atttentional conditions. The block order was completely counterbalanced across sessions and across subjects according to a Latin square design. The intertrial interval within each block was about 3 sec, and there was a few minutes' intermission between blocks.

In order to ensure that fixation was maintained, the position of the subjects' eyes was checked continuously by closed-circuit television. Subjects knew that on each trial the stimulus could occur with equal probability at each of the five positions, and the only reinforcement they received for complying with the attentional instructions was provided by seeing the results for each block on a computer print-out immediately after the end of the block itself.

Responses shorter than 150 msec and longer that 300 msec were discarded and the trial was repeated later in the sequence. At the end of the six sessions each subject had provided 120 RTs (60 for each hand) for each position, both when that position was attended to specifically and in the diffuse attention condition.Further, he or she had provided 480 RTs (240 for each hand) for each position while attention was directed to one of the other four positions. The presentation of the stimuli, the collection of RTs and the on-line and off-line analyses of the data were performed with a small general-purpose computer.

RESULTS

Most subjects indicated that they complied with the instruction to attend selectively to a specific position by trying to increase their speed of response to stimuli in that position. None of them reported that he or she tried to slow down responses to stimuli in unattended positions. The intensity of the stimuli being well above threshold, omissions of responses were extremely rare and were unrelated to any specific condition or position. RT anticipations and retardations were also exceptional and showed no systematic pattern in relation to conditions and/or positions.

Median RT was computed across sessions for each hand of each subject for each position in each of six conditions. The six conditions for each position resulted from the sum of four unattended conditions (during which responses to that position were made while attending selectively to each of the four other positions), one attended condition (during which responses to that position were made while it was being attended to), and one diffuse-attention condition (during which all five positions were equally attended to). Since preliminary inspections of the data revealed no systematic intermanual differences, the means of the medians for the two hands were employed in the analyses reported hereunder.

Figure 1 shows RT as a function of stimulus position and attentional condition. The points in the attended-condition curve and in the diffuse-attention condition curve are means across subjects of the appropriate individual median values. The points of the non-attended-condition curve were arrived at by first computing in each subject the means of the medians of the single four unattended conditions, and then by taking the means of these values across subjects.

Two trends are immediately evident from the figure. First, in all attentional conditions RT was shortest at the central position (fixation point), intermediate at the two intermediate positions, and longest at the two lateral positions, with no apparent differences between corresponding right and left positions. This well known increase in RT with the eccentricity of the stimulus is regarded as an expression of the gradual decrease in the photopic sensitivity of the retina as one moves from the fovea toward the periphery [7], and provides good indirect evidence that our subjects maintained fixation in all attentional conditions.

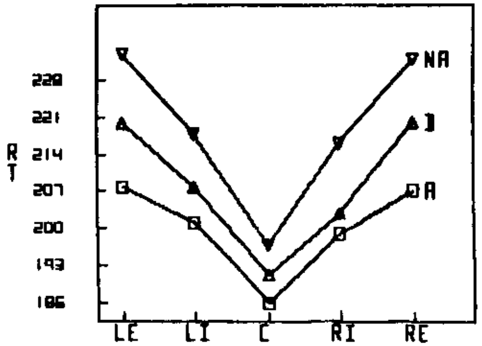

FIG. 1. Benefits and costs of voluntary selective attention. Reaction time (RT) is shown as a function of stimulus position (LE = left external position; LI = left internal position; C = central position; RI = right internal position; RE = right external position) and attentional condition (A = attention directed to stimulated position; NA = attention directed to positions other than the stimulated position; D = diffuse attention, i.e. attention equally distributed among the five positions).

Second, benefits, measured as differences between RT in the diffuse attention condition and RT in the attended condition, and costs, measured as differences between RT in the non-attended condition and RT in the diffuse attention condition, were both present and approximately mirror-symmetrical at each of the five positions. Again, the results for the right positions were not distinguishable from those for the left positions. Since subsequent statistical analyses confirmed the absence of right–left differences, these will not be considered further.

Analysis of variance with attentional conditions and location of the stimuli as factors showed highly significant *Fs* for both factors as well as for their interaction ($P < 0.001$ in each case). *Post-hoc* comparisons by paired t-tests showed that the benefit, taken as the difference between diffuse and attended conditions, was significant generally (8.1 msec, $P < 0.001$), as well as for each single position ($P < 0.02$ in all cases). However, the benefit was smallest for the central position (mean 4.3 msec), intermediate for the intermediate positions (mean 5.7 msec), and largest for the lateral positions (mean 12.2 msec). The increase in benefits from the central position to the intermediate positions fell short of significance ($P < 0.1$), while the increase in benefits from the intermediate positions to the lateral positions was amply significant ($P < 0.01$).

The main cost of 10.5 msec was also highly significant ($P < 0.001$) and significant costs were observed at all positions ($P < 0.01$ in all cases). However the mean cost of 5.9 msec at the central position was significantly smaller than either the mean cost of 10.9 msec at the intermediate positions ($P < 0.02$) or the mean cost of 12.5 msec at the lateral positions ($P < 0.02$). The difference between the two latter costs was insignificant ($P = 0.4$).

Figure 2 shows a break-down of RTs to stimuli in unattended locations according to the relative positions of the stimulus and the locus of attention. For simplicity the data regarding both the responses made to stimuli in the central position, or to the stimuli in the other positions when selective attention was directed to the centre, were excluded from the figure. Costs can again be assessed as differences against the diffuse-attention condition. Thus the magnitude of the costs for the four non-central positions can be related to whether the locus of the stimulus and the locus of selective attention were on the same side of the fixation point,

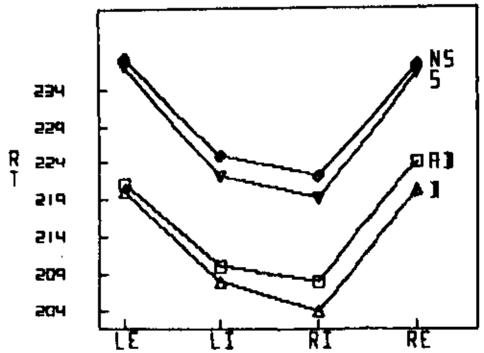

FIG. 2. Break-down of costs of voluntary selective attention. For each of the four non-central positions (LE, LI, RI, RE, see previous figure) RT is shown as a function of the positional relationship between the attended location and the locus of the stimulus. AD = attended location and locus of stimulus are in adjacent positions in the same hemifield; S = attended location and locus of stimulus are in symmetrical positions across the vertical midline; NS = attended location and locus of stimulus are in non-symmetrical positions across the vertical midline. D shows, for comparison, RT in the diffuse-attention condition. Note that only the S and NS RTs are increased compared to the D RTs.

or on opposite sides of the fixation point, either in the symmetrical or the non-symmetrical disposition. When attention was directed to the other position in the same hemifield the costs appeared minimal or non-existent, and in fact RTs were not significantly longer than corresponding RTs in the diffuse-attention condition (the mean difference was 2.7 msec and was not significantly different from zero, $P>0.1$).

The costs represented in Fig. 2 were therefore accounted for entirely by costs suffered when attention was directed to a position on the other side of the fixation point, and there was no difference between symmetrical and asymmetrical dispositions of locus of stimulus and locus of attention. Further, there was no significant difference between any of the positions in terms of these cross-midline costs.

The data not shown in Fig. 2 indicated that paying selective attention to the central position induced significant costs in all other positions (mean 11.1 msec, $P=0.001$), with costs at the lateral positions being significantly greater than costs at the intermediate positions (13.4 vs 8.8 msec, $P=0.05$). Conversely, when selective attention was allocated to the eccentric positions there was at the central position a significant mean cost of 6.0 msec ($P=0.001$). When attention was directed to the lateral positions the costs was 7.8 msec, while it was 4.2 msec when attention was directed to the medial positions. The difference between these two costs was almost significant ($P=0.07$).

Figure 3 provides an overall graphic representation of the results. Cumulative frequency distribution curves were constructed for RT for each position for the attended condition, the diffuse-attention condition and each of the four non-attended conditions by taking the means across subjects of the first, 10th, 25th, 50th, 75th, 90th and last percentiles of the respective RT samples. The five columns in the figure represent stimulus positions, from lateral left to lateral right, whereas the five rows represent the attentional conditions for each of the positions, from lateral left at the top to lateral right at the bottom. Each graph in a column allows a visual comparison between the pertinent curve, identified by the vertical marks, and

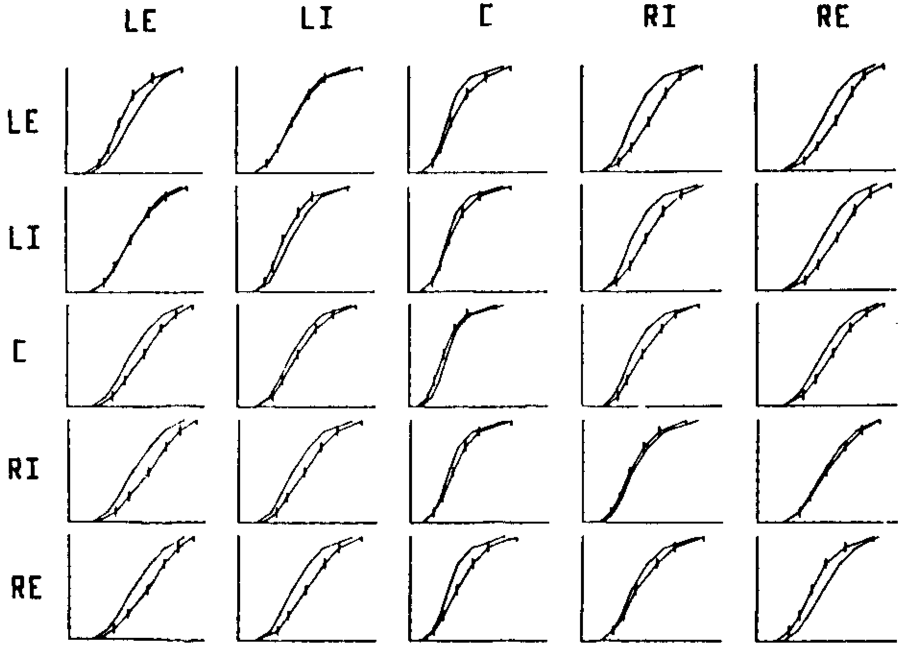

FIG. 3. Overall effects of voluntary selective attention. Cumulative frequency distribution curves for each position (columns) in each selective-attention condition (rows). The cumulative percent frequencies are plotted on the ordinates from 0 to 100%, and RT is plotted on the abscissae. The portion of the abscissae between the origin and the right end corresponds to the range 150–300 msec. For each diagram in a column the critical curve, identified by 6 vertical strokes that mark the 10th, 25th, 50th, 75th, 90th and 100th percentiles, can be compared with the standard reference of the diffuse attention condition (unmarked curve).

a standard provided by the curve for that position in the diffuse-attention condition. The standard for comparison is obviously the same in each column.

The figure highlights in graphic form the most important aspects of the results. First, it is clear that for each of the five positions benefits involved a leftward shift of the whole curve (i.e. toward shorter RTs) relative to the standard, and costs involved a rightward shift of the whole curve (i.e. toward longer RTs). Thus, the decrease of median RT associated with the allocation of attention to the locus of the stimulus, and the increase of median RT associated with the allocation of attention to unstimulated positions, were not merely due to an increased relative frequency of short RTs in the first case and an increased relative frequency of long RTs in the second case, because the changes affected the whole RT range, significant differences with the diffuse-attention conditions being observed from the 10th percentiles onwards. Moreover, Fig. 3 also reiterates that benefits increased with stimulus eccentricity; that costs resulting from attention being directed toward a non-central position affected the central and contralateral positions, but not the ipsilateral position; and that paying selective attention to the central position induced costs at all other positions, especially the most eccentric ones.

DISCUSSION

The results show that visual attention can be allocated to foveal or extrafoveal sites in the visual field by an effort of will which need not be cued on each trial and does not require to be reinforced by different frequencies of stimulus occurrence at attended and unattended positions. The clear and meaningful pattern of costs and benefits which emerges from the results is in contrast with previous reports [23] indicating that a "blocked" paradigm does not bear out the effects of directed attention. We feel on the contrary that the present blocked paradigm is advantageous for its simplicity, and the results can contribute to the analysis of voluntary allocation of attention to points in space.

The main point to be discussed here concerns the spatial distribution of the effects of selective attention. In this discussion we will at first refer to costs and benefits as behavioural effects, measured as differences from the diffuse-attention condition, without considering their possible neural bases. The spatial distribution is markedly different for costs and benefits. Benefits are limited to the locus of attention and are greater for the more eccentric positions, whereas costs are much more diffuse and virtually independent of eccentricity. When attention is directed to an eccentric position, costs affect both the central position and, to an equal degree, the two positions on the opposite side of the vertical midline. When attention is directed to the central position, costs become apparent at all the other positions. With attention allocated to either of the eccentric positions, the other position on the same side of the midline shows neither benefits nor costs.

The present results on the spatial distribution of costs and benefits can be compared and contrasted with those of other similar studies [5, 8, 9, 24] using pre-stimulus cues to direct attention on each trial, as well as different frequencies of stimulus presentation at attended and unattended positions. The finding that with our interstimulus separations of 10 or 20° benefit was exclusively restricted to the locus of attention confirms Downing and Pinker [5] who used shorter interstimulus separations (about 2.5°) and found a very limited spread of benefits from the cued position. Rizzolatti *et al.* [24] used a horizontal array of stimulus locations positioned 6° above or below the central horizontal meridian and having an interstimulus separation of 4°; they also found that benefits of directed attention were strictly confined to the cued position. Hughes and Zimba [8, 9], at variance with the present and other studies cited above, did not find benefits of directed attention, and therefore their studies provide only data on the spatial pattern of costs at unattended locations.

There is a remarkable agreement among all these studies on the fact that costs do not affect all unattended positions to the same extent, but are particularly prominent for unattended positions contralateral to the stimulated position. In keeping with Downing and Pinker [5] and with Hughes and Zimba [8, 9], we found that costs were uniform throughout the hemifield contralateral to that of the stimulus, and in fact when our subjects attended to either location on one side of the fixation point, the spatial extent of costs began at the fixation point and extended to the most eccentric lateral position. The lack of costs observed ipsilaterally to the attended position in our experiment confirms Hughes and Zimba [8, 9] and is in partial agreement with Downing and Pinker (5), whereas Rizzolatti *et al.* [24] found costs also in the hemifield ipsilateral to the attended location. However, such costs were vastly smaller than those seen in the other hemifield.

In connection with the above discrepancies, it must be stressed that a given pattern of behavioural costs and benefits does not necessarily reflect a unique pattern of brain activity. For example, in the present experiment the absence of behavioural costs and benefits in the adjacent position in the ipsilateral field may have resulted from a mutual neutralization of antagonistic brain processes potentially leading to behavioural costs and benefits. In other words, the absence of a difference between RT in the diffuse-attention condition and RT with attention directed to the adjacent ipsilateral position is no proof that the neural processing of information from that position is the same in the two conditions.

With regard to the possible neural basis of costs and benefits, the role of the vertical midline in bounding the area of visual field affected by costs, or in marking the border between an area of low costs and an area of high costs, can be discussed in relation to the fact that the vertical midline is also the line of separation between the right visual field, which projects to the left cerebral hemisphere, and the left visual field, which projects to the right hemisphere. However, as demonstrated by Rizzolatti *et al.* [24] and by Hughes and Zimba [9], any interpretation of the spatial distribution of costs based on the split of the representation of the visual field between the two hemispheres is either incomplete or downright wrong. They showed that a spatial distribution of costs analogous to that seen across the vertical meridian can also be observed in experiments using a vertical array of stimuli across the horizontal meridian. We also have preliminary evidence that the same pattern of results as described here can be found with five stimulus positions aligned along the vertical meridian. In these conditions it is the horizontal meridian that marks the limit of the cost area, and there is no interhemispheric cleft corresponding to the horizontal meridian in the neural representation of the upper and lower visual fields. Further, although secondary or tertiary visual cortical areas in the monkey may contain separate representations of the upper and lower visual fields, the visual field representation in the primary visual cortex is continuous at the horizontal meridian [27]. The relationship between these anatomo-functional subdivisions in the visual cortex and the spatial distribution of attention deserve further investigation.

The possible functional significance of the horizontal and vertical meridian as lines of division between visual field areas characterized by different attentional costs has been discussed by Rizzolatti *et al.* [24] and by Hughes and Zimba [9]. Our aim is to show that the main meridians of the visual field are also involved in partitioning the visual field with respect to the inhibitory after-effects of covert orienting.

EXPERIMENTS ON THE INHIBITORY AFTER-EFFECTS OF COVERT ORIENTING

The speed of detection of a simple flash of light in an extrafoveal region of the visual field is markedly influenced by previous stimulation of that point [1, 14, 16, 17, 19]. Although intuitively prior stimulation should act as a positional cue, and therefore it should decrease RT to stimuli subsequently presented in that position [11], it is now clear that simple RT to stimuli occurring in one region of the visual field is strongly prolonged after previous stimulation of the same region. Facilitatory effects of a first stimulus on RT to a second stimulus may appear if the two stimuli are separated by no more than 100 msec [16, 17, 19], and thus might be due merely to temporal summation, but if the interstimulus interval is longer (up to 1.5 sec) RT to the second stimulus is markedly slowed down.

There is strong evidence that this RT retardation by prior stimulation is at least partially independent of retinal processes such as local adaptation, and totally independent of response biases such as motor inhibition or probability guessing [16, 17, 19, 26]. Local adaptation of the retina may contribute to RT retardation at relatively short interstimulus intervals (less than 500 mec), but not at longer interstimulus intervals [26]. Instead, the effect appears to be caused by a selective inhibition of the orienting reaction toward a point of the visual field that has been the target of an immediately preceding orienting reaction.

The form of the effect with which we have been concerned can be termed inhibitory after-effect of covert orienting. A typical experiment consists in presenting subjects with pairs of successive flashes of light, and the two flashes in a pair can appear one on the right and the other on the left of a fixation point, or both can appear successively at the same location, either on the right or on the left. The subject has to make a quick manual response to the second flash, and the dependent variable is the RT of such response, while the independent variable is the positional relation of the two flashes in the visual field. Usually no overt response is required to the first flash, but obviously the subject has to detect it in preparation for responding to the second flash, and it seems plausible that such a detection must involve a covert orientation toward the locus of the first flash. The orientation is covert because fixation must be maintained throughout each trial, and no eye and/or head movement is allowed in the interval between the first and the second flash.

In accord with previous studies [1, 14, 16, 17, 19] we have found in experiments of this kind that if the two flashes appear at the same position, RT is longer than when the two flashes appear at different positions. The definition of such effect as an "inhibitory after-effect of covert orienting" is justified by the following considerations.

That the effect is due to an inhibition of the response to the second of two spatially coincident flashes, rather than to a facilitation of the response to the second of two contralateral flashes, is shown by comparing the two RTs with a standard reference such as RT to the first flash. If the subject responds to both flashes in a pair, RT to the second of two spatially coincident flashes is longer than mean RT to the first flash, while RT to the second of two mutually contrateral flashes does not differ from it [26].

That the inhibitory effect requires covert orienting to the first stimulus is shown by prior bilateral stimulation. If inhibition is due to a covert orienting to one side which for some time acts against reorienting to the same side, a bilateral stimulus should not be inhibitory on subsequent orienting responses because it should not induce a lateral orientation. Indeed, RT to a flash in one lateral position, say on the right, is considerably slowed when the flash is preceded by another flash in the same position, but is not retarded (at least for interstimulus intervals beyond the duration of the local retinal adaptation) when the flash is preceded by two simultaneous flashes, one on the right and the other on the left, similar to when it is preceded by a single flash on the left [16, 26]. Further, procedures which lead to the habituation of the orienting response, such as repeated stimulation, tend to suppress the inhibitory after-effect of prior stimulation of the same visual field position. Thus, when subjects respond to each flash in a sequence of flashes presented at random on the right or the left, RT to a given flash in a sequence does not appear to be influenced by the position of the previous flash, since it is the same regardless of whether the previous stimulus had occurred in the same or in the opposite position [26].

We have shown that the inhibitory after-effect of covert orienting does not affect solely the position of the first stimulus, but may extend to a whole half of the visual field. Since this spatial distribution of the inhibitory after-effect of covert orienting has much in common with that of costs of voluntarily directed visual attention, we will describe an experiment aimed at assessing the spatial coordinates of RT inhibition by prior stimulation.

METHODS

Six right-handed normal male adults served as subjects. They sat in front of a white screen with their head in a head- and chin-rest facing a bar which supported four LEDs identical to those of the previous experiment. The distance between the eyes and the midpoint of the bar was 57 cm, and the LEDs were positioned symmetrically two on one side and the other two on the other side of this midpoint at a distance of respectively 10 and 30° of visual angle from it. The bar could be oriented horizontally or vertically by rotating it around its midpoint. Subjects could fixate on the midpoint of the bar, and in such case the stimulus array lay on the central vertical meridian of their visual field if the bar was vertical, or on the central horizontal meridian of the visual field if the bar was horizontal. Otherwise they could fixate on a point 10° above or below the midpoint of the bar when this was horizontal, or on a point 10° to the right or the left of the midpoint of the bar when this was vertical. In these cases a horizontal array of stimuli crossed the central vertical meridian of the visual field 10° above or below the fixation point, and a vertical array of stimuli crossed the central horizontal meridian 10° to the right or left of the fixation point.

Each subject performed a simple RT task in each of the six conditions of fixation. A block of 64 trials was assigned to a specific fixation condition, and on each trial the subject was to fixate binocularly on a specified fixation point upon hearing a standard auditory warning signal delivered through earphones. After an interval ranging randomly from 1 to 3 sec a flash of 5 msec duration and 70 cd/sq. m luminance was presented in one of the four positions, without requiring an overt response of the subject. After a further interval, which could last 0.2, 0.6, 1.5 or 5 sec a second identical flash was presented at one of the same four positions, and the subject had to press a key with his right or left thumb as fast as possible upon seeing it.

In a block of 64 trials, both flashes appeared 16 times in each of the four positions, and there was one trial for each of all possible combinations between the position of the first flash, the position of the second flash and the interstimulus interval. The order of these combinations within each block was completely random, so that it was impossible for the subject to predict either the position of the second flash from that of the first, or the duration of the interstimulus interval.

Subjects attended on a total of 8 sessions, each consisting of two blocks. The condition of fixation was the same for each session, but subjects performed with one hand in one block and with the other hand in the other block. The hand order was counterbalanced across sessions and across subjects. There was one session for each of the four conditions of eccentric fixation (i.e. when fixation was to the right or left of a vertical bar, or above or below a horizontal bar) and two sessions for each of the two conditions of central fixation (i.e. when subjects fixated the midpoint of the horizontal or vertical bar). The order of fixation conditions was completely counterbalanced across subjects. In total, each subject provided 128 RTs for each of the four eccentric-fixation conditions, and 256 RTs for each of the two central-fixation conditions. Half of these trials were performed with the right-hand and half with the left.

Subjects were instructed to maintain fixation on each trial from the warning auditory signal until after performing the response, and the position of their eyes was continuously monitored by television. RTs were measured to the nearest msec from the onset of the second flash in a pair to the closing of a switch by the key-press. RTs shorter than 150 msec or longer than 990 msec were rejected and the trial was repeated later in the sequence. Trials on which subjects responded during the interstimulus interval were also discarded and repeated at the end of the block.

The presentation of the stimuli, the measure and collection of RTs and the data analyses were performed automatically by means of a general purpose computer.

RESULTS

The description of the results is made simpler if we ignore possible differences between right and left hands, right and left fields and upper or lower fields. This is justified because there was no significant difference between the hands and between the lateral fields, whereas a systematic advantage for RT of the lower over the upper field could be accounted for entirely by retinal factors [7], and had no impact on the spatial distribution of the inhibitory after-effect.

The spatial pattern of the inhibitory after-effect can be analysed in a general way by considering that in all conditions of fixation the second flash could occur at the same location as the first flash, or at a different location on the same side of either the vertical or horizontal meridian, or in one of two locations on the opposite sides of the vertical or horizontal meridian. The pattern of results depicted in the figure can be generalized to all positions in all fixation conditions.

Figure 4 shows the means across the four positions and across subjects of RT to flashes preceded by a flash in the same position (SP), by a flash in the other position on the same side of the vertical or horizontal meridian (SF), or by a flash on the opposite side of the meridians (OF; since it made no difference whether the opposite flash was in one or the other position, RTs for contralateral combinations have been collapsed in Fig. 4). In all fixation conditions, at the first three interstimulus intervals SP RT was clearly slower than OF RT. The SP-OF difference is of course the classical inhibitory after-effect which on statistical analysis (analysis of variance and *t*-tests) proved to be significant at each of the first three interstimulus intervals, whereas it had disappeared at the 5 sec interstimulus interval. The means across fixation conditions of the SP-OF differences were 57.7 msec at the first interstimulus interval (different from zero at the $P<0.001$ level by a one-sample *t*-test), 36.5 msec at the second interstimulus interval ($P<0.001$), 19.3 msec at the third interstimulus interval ($P=0.01$) and 6 msec at the fourth interstimulus interval (n.s.)

The novel result in Fig 4 is the presence of an inhibitory after-effect of SF combinations, that is when the two stimuli in a pair were on different locations on the same side of the horizontal or vertical meridians. As indicated in the four graphs of Fig. 4, at the first three interstimulus intervals RT of SF combinations was clearly longer than RT of OF combinations, and the SF-OF difference showed a time course similar to that of the SP-OF difference. The means across fixation conditions of the SF-OF differences were 15.7 msec at the first interstimulus interval ($P=0.01$), 19.0 msec at the second interstimulus interval ($P<0.001$), 8.3 msec at the third interstimulus interval (n.s., but $0.10>P>0.05$) and 4 msec at the fourth interstimulus interval (n.s.). The SP-OF difference was significantly greater than the SF-OF difference at each of the three first interstimulus intervals (paired *t*-tests of differences, $P=$ or <0.005 in each case).

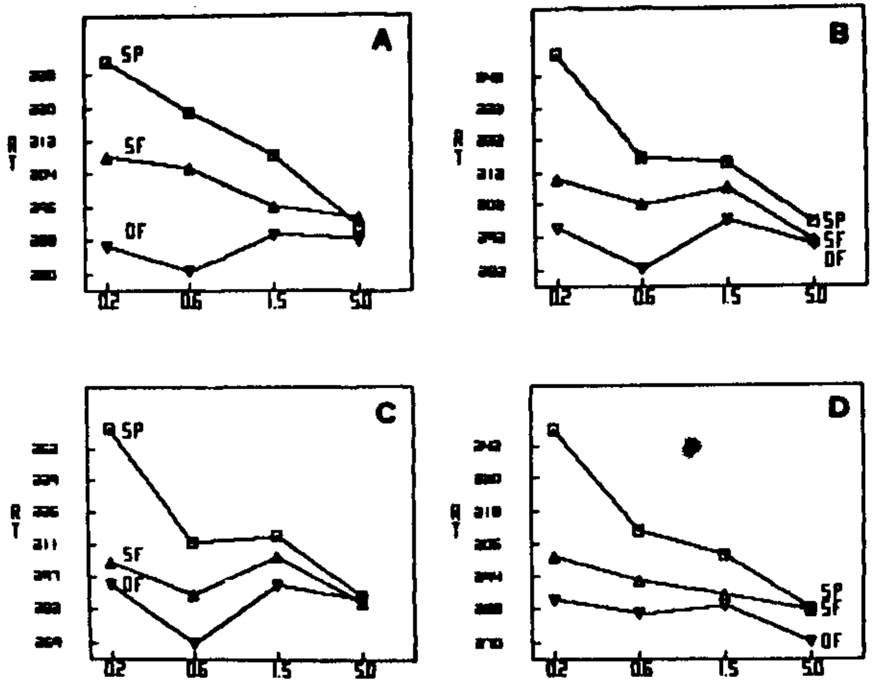

FIG. 4. Effect of prior stimulation on simple RT to a flash. RT to the second flash (msec) is shown as a function of the interval between the first and the second flash (sec) and the positional relationship between the two flashes. SP = the two flashes occurred at the same point; SF = the two flashes occurred in different positions in the same lateral or altitudinal field; OF = the two flashes occured in opposite lateral altitudinal fields, the symmetrical and non-symmetrical positions being pooled. In A the stimulus array was aligned with the horizontal meridian; in C it was aligned with the vertical meridian; in B the stimulus array was horizontal, but it was 10° above or below the fixation point (pooled conditions); in D the stimulus array was vertical but it was 10° to the right or the left of the fixation point (pooled conditions).

Thus, the inhibitory after-effect of covert orienting was not limited to the site of the first stimulus, but also affected, although to a smaller degree, the other position on the same side of the fixation point in the central-fixation conditions, or on the same side of the vertical or horizontal meridian in the eccentric-fixation conditions. Analysis of variance showed that the different fixation conditions did not differ from each other in terms of magnitude of either the SP or the SF inhibitory after-effect at all interstimulus intervals, since all the pertinent interactions were totally insignificant. It was as though both main meridians delimited the area of the visual field within which prior stimulation induced a retardation of RT to subsequent stimuli.

This delimiting action of the main meridians on the inhibitory after-effect became even more evident when we considered RTs to stimuli presented to the positions at 10° from the meridians and preceded by a stimulus at the other position in the same field, or in the corresponding position on the opposite side. In either case the physical separation between the stimuli was 20°, but the RTs of SF combinations, pooled over the three first interstimulus intervals, were significantly slower than RTs of OF combinations in all fixation conditions (mean differences 11.3, 18.7 and 9.9 msec for the three first interstimulus intervals). This proves that the inhibitory after-effect occurred when the two stimuli were separated by the vertical or horizontal meridian rather than by a given distance in the visual field.

DISCUSSION

The relevance of these results to the present paper lies in the complementarity between the spatial distribution of the inhibitory after-effects of covert orienting and that of the costs of voluntarily directed attention. In both cases the visual field areas showing the effects are limited by functional partitions which coincide with the main meridians of the visual field. This similarity invites speculations about the possibility of an identical or partially shared neural basis for the two types of effects.

There is little support for the hypothesis that the functional barriers which impede the spatial spread of attentional effects may coincide with discontinuities in the representation of the visual field over the cortex. According to traditional neurological thinking one such discontinuity may be at the vertical meridian, since the anatomical organization of the optic pathways provides for the representation of the right and left visual fields in different hemispheres. However, interhemispheric connections of visual cortical areas have been shown to link up the half-field representations of both hemispheres, thereby ensuring a continuous representation of the visual field in each of them [2]. Further, it has already been mentioned that the present and other studies [3, 9, 14, 24] indicate that major changes in attentional effects occur not only at the vertical but also at the horizontal meridian, and there is no evidence that at least in the primary visual cortex the representation of the upper visual field is disjoint from that of the lower visual field.

Another hypothesis is that the abrupt cessation at the vertical and horizontal meridians of both costs of directed attention and inhibitory after-effects of covert orienting may have to do with the inhomogeneous representation of visual space in cerebral space [5]. Regions of the primary visual cortex representing two adjacent points in the central visual field are farther apart than visual cortical regions representing two distant points in the peripheral visual field [4]. Attentional effects may encounter difficulties in crossing the representation of the vertical and horizontal meridians at the fovea simply because this involves moving over long cortical distances [5]. The discontinuous distribution of attentional effects in physical space might actually correspond to a continuous distribution in cortical space [5, 9].

However, RIZZOLATTI *et al.* [24] have shown that the barrier function of the vertical and horizontal meridians in the spatial distribution of the effects of selective attention is fully expressed in visual field regions far away from the fovea, where the cortical distances between the representations of points across the meridians are comparatively short. Our present findings suggest that the spread of the inhibitory after-effect of covert orienting is similarly limited in a continuous fashion by the vertical meridian laterally, and by the horizontal meridian altitudinally, thereby denying any special role of the cortical representation of the fovea in this functional organization. Further, we have recently observed that the magnitude of the inhibitory after-effect of prior stimulation at 30° from the fovea in the same hemifield was the same regardless of whether the second stimulus was presented at 2 or 10° from the fovea. Obviously the spread of the inhibitory after-effect cannot be related either to physical or to cortical distance.

A third hypothesis is that the segmentation of the attentional visual field by the vertical and horizontal meridians is more the result of the organization of motor control in visual space than of the organization of the visual input. This will be dealt with at some length in the following General Discussion.

GENERAL DISCUSSION

The basic assumption is that selective attention to a spatial location is simply an "operational adjustment of the brain" [25] which biases the organism to emit motor reactions to stimuli in that location. Which reaction is eventually emitted depends on the actual stimulus constellation, as well as on the specific intentions, cognitive sets and goals of the organism at that moment. However, its execution is always bound to start from a state of organization of the nervous system which favours motor responses to stimuli in the attended location. The privileged responses include all potential reactions to the stimuli appearing in the target location, ranging from those that are naturally linked to the stimulus, such as an orienting reaction of the head and eyes towards it, to innumerable others that may be produced on the spur of the moment. More specifically, the brain generates a state of selective motor readiness which results in a general facilitation of all motor outputs potentially triggered or guided from the target area, to the disadvantage or exclusion of motor reactions to other stimulus locations.

Motor responses to stimuli in non-attended locations obviously do not become impossible, but their execution requires a readjustment of the ongoing pattern of neural organization. The promptness, speed and ease with which such responses are performed will ultimately depend on the feasibility of the readjustment of the preparatory motor set, which in turn is proportional to the degree of similarity and compatibility between the required new pattern of neural organization and the one that must be replaced.

We submit that the above concepts can help in the interpretation of the segmentation of the visual field by the vertical and horizontal meridians seen in the two experiments reported here. We believe that when they were deliberately paying attention to a specific point in the right visual field, the subjects of our first experiment simply made themselves ready to respond motorically to a flash in that point. This motor set conflicts with other reaction possibilities in varying degrees. Conceivably an essential element in the brain adjustment underlying the preparation to respond to a given point on the right is the specification of the direction "right" as opposed to "left", and this element is shared by the whole class of preparatory sets for responding to all possible points in the right field.

If a stimulus is presented at an unattended position in the right visual field, i.e. on the same side of the vertical meridian as the attended location, the readjustment needed for responding is relatively minor because the essential directional element is already present in the ongoing brain pattern of activity and therefore need not be corrected. The costs for RT in these conditions have indeed been found to be small [24] or downright absent [5, 8, 9 and present paper], the discrepancy between the results being probably ascribable to differences in accessory factors such as the intensity, size and eccentricity of the stimulus, the separation between the attended location and the site of the stimulus, and so forth.

If however the stimulus appears in the left field, i.e on the other side of the vertical meridian relative to the attended location, or on the vertical meridian itself, the corresponding neural adjustments must involve at least a complete reversal or cancellation of the previous directional bias, and as a result the emission of the response is retarded. Hence the marked costs for RT consistently found for stimuli presented across the vertical midline from the attended location [5, 8, 9, 24 and present paper], and in this study also for stimuli presented on the vertical midline. Exactly the same argument applies to the results concerning the allocation of attention to the upper or lower visual field, where the horizontal meridian is the origin of the two opposed directional specifications.

This interpretation is akin to that of RIZZOLATTI *et al.* [24], except that it does not postulate the necessity for a hypothetical internally movable beam of attention to be aligned with the source of the stimulus before any response can be emitted.

The interpretation of the experiment of the spatial distribution of the inhibitory after-effect of covert orienting is less direct, but it may follow a similar line of reasoning. The current meaning of "covert orienting" in experimental psychology is "orienting to a point in space without moving the eyes to it". Since turning the eyes to the target of orienting is a natural component of the orientation reaction, covert orienting requires that such eye movement be actively suppressed. This suppressive action is bound to have consequences for more general motor adjustments.

Suppose that you have been instructed to suppress your natural reaction to look at a stimulus suddenly appearing at an extrafoveal location in your visual field, and that one such stimulus occurs in your right hemifield. At some level in your neural pathways for oculomotor control you will have to generate a central command that counteracts the natural orienting reaction and vetoes the eye movement to the right. If you have also been instructed to make a manual response to the same or to a slightly later stimulus at the same position, for some time your general motor set will contain two instructions that are contradictory with respect to direction. The vetoing command opposes movements to the right, whereas the manual response depends on a motor predisposition to react to the right.

The neural controls involved in this motor set are linked to different muscular effectors—ocular in one case, manual in the other—but it is known that simultaneous motor activities of different effectors are rarely independent from one another since they are constrained by preexisting patterns of synergy [13].

It seems likely that the performance of hand responses to a stimulus in a given direction should be optimal when directional commands for hand and eyes are congruent, while it should deteriorate when the eyes receive motor commands that are directionally opposite to those controlling the hand response. The hypothesis that ocular and manual responses are integrated within a single spatial frame of reference is supported by recent work [6, 15].

In our experiment on voluntarily allocated attention the directional conflict between maintenance of fixation and the execution of the manual response was of little concern, since it was present in all conditions and thus could hardly affect the differences between attended, non-attended and neutral conditions, which therefore were entirely determined by selective attention. However, it is our assumption that in the double-flash experiment our subjects oriented toward the first flash in a pair because they had to detect it rapidly, but did so covertly because they were asked to maintain fixation. This means that they avoided looking at the first flash by generating a motor instruction that counteracted the orienting eye reaction, thus biasing the entire motor system against reacting to stimuli in that direction. A second stimulus appearing in that direction would therefore be responded to less rapidly than a stimulus appearing in the opposite direction, because the motor set required for responding to the latter stimulus would not conflict directionally with the command to the oculomotor system. The fact that RT slowing is greater when the position of the second stimulus coincides with that of the first stimulus than when both stimuli appear in different positions on the same side of the midline may depend at least partly on local adaptation in the retina [26].

The assumption of a conflict between oculomotor and hand-motor commands would account for the advantage for RT of contralateral over ipsilateral stimulus combinations not only with stimuli in the right and left fields, but also with stimuli in the upper and lower visual fields. If this hypothesis is correct, the long time course of the manual RT effect should of course correlate with the duration of the postulated command vetoing the ocular orienting reaction.

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