

Early and late inhibitions elicited by a peripheral visual cue on manual response to a visual target: Are they based on Cartesian coordinates?

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A non-informative cue (C) elicits an inhibition of manual reaction time (MRT) to a visual target (T). We report an experiment to examine if the spatial distribution of this inhibitory effect follows Polar or Cartesian coordinate systems. C appeared at one out of 8 isoeccentric (7°) positions, the C-T angular distances (in polar coordinates) were 0° or multiples of 45° and ISI were 100 or 800ms. Our main findings were: (a) MRT was maximal when C- T distance was 0° and minimal when C-T distance was 180° and (b) besides an angular distance effect, there is a meridian effect. When C and T occurred in the same quadrant, MRT was longer than when T and C occurred at the same distance (45°) but on different sides of vertical or horizontal meridians. The latter finding indicates that the spatial distribution of the cue inhibitory effects is based on a Cartesian coordinate system.

In a seminal paper, Posner and Cohen (1984) reported that a peripheral visual change can produce two opposite effects on Manual Reaction Time: facilitation or inhibition. These effects were found by measuring Manual Reaction Time (MRT) to a target stimulus occurring ipsi- or contralaterally to a cue that did not provide advance information about target location. Facilitation and inhibition occurred after short or long cue-target intervals, respectively. Facilitation was observed when the target occurred at the cue's position at an interval equal or shorter than 150 ms. This effect was short lived and was replaced by inhibition when the cue-target interval became longer

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than 300 ms. The early facilitation was considered to be due to an automatic and covert orienting of attention towards the cue's location, while the late inhibition (inhibition of return - IOR) was considered to be a process reflecting a reduced tendency to respond to a previously sampled source of stimulation.

It should be pointed out, however, that the facilitatory component of this bi-phasic process is not easily observed due to the overlap with an early inhibition that arises concomitantly with the facilitation (Carreiro et al., 1994; Gawryszewski et al., 1994a, 1994b; Riggio et al., 1998; Tassinari & Berlucchi, 1993; Tassinari et al., 1994). This early inhibition involves not only the classical forward masking effects (see Breitmeyer, 1984 for review) but also an inhibitory process that spreads to the whole cued hemifield (Berlucchi et al., 1989).

Two mechanisms have been proposed to explain the inhibition elicited by a non-informative cue. For both the effects elicited by unilateral (i.e., ipsilateral) or bilateral cues are critical. If the inhibition originated from a sensory process, unilateral and bilateral cues should produce identical inhibitory effects on a subsequent visual target. By contrast, if inhibition depended on the covert orienting of attention to the cue, it should occur with ipsilateral but not with bilateral cues. Using this rationale, Posner and Cohen (1984) reported comparable inhibitory effects using unilateral and bilateral cues, suggesting a sensory basis for the inhibition. The opposite was observed by Maylor (1985), supporting the role of covert orienting in producing the inhibition. These contrasting findings were explained by Tassinari and Berlucchi (1993) by showing that, at a short cue-target interval (200 ms), unilateral (ipsilateral) and bilateral cues produced the same inhibitory effect, but at a longer cue-target interval one (600 ms), only the unilateral (ipsilateral) cue had an inhibitory effect. It seems, therefore, that at least two types of inhibition are elicited by a non-informative cue: an early, sensory inhibition and a late attentional inhibition, which corresponds to the classical inhibition of return (IOR).

Because the facilitation (Posner & Cohen, 1984) occurred at short intervals between cue and target (less than 150 ms), whereas the inhibition occurred at longer cue-target intervals, it is reasonable to propose that the presence or absence of the early facilitation may depend on the temporal sequence of events. For instance, it has been shown (Carreiro et al., 1994; Gawryszewski et al., 1994a, 1994b, 2002b; Maruff et al., 1999; Riggio et al., 1998) that the onset and the offset of a non-informative visual cue have different effects on MRT to a visual target. The cue ONSET can elicit facilitatory or inhibitory effects on MRT to targets appearing ipsilaterally as compared to targets appearing contralaterally to the cue location. The facilitation is present at short cue-target intervals (100 ms) and the inhibition is present at longer intervals (800 ms). In contrast, the cue OFFSET elicits inhibition both at short and long cue-target intervals (Gawryszewski et al., 2002b).

As described before, comparing MRT to a target occurring after ipsi-, contra- and bilateral cues, it is possible to distinguish between sensory and attentional effects (Tassinari & Berluchi, 1993). An attentional effect must depend on an asymmetrical stimulation between the hemifields, which causes an attentional bias toward the stimulated hemifield. The attentional effect should be absent with a bilateral stimulation. In contrast, a sensory effect does not depend on an asymmetrical stimulation between the hemifields and should, therefore, be equal for a unilateral and a bilateral stimulation. Accordingly, using bilateral cueing to distinguish between sensory and attentional factors, we found that the ONSET of an ipsilateral cue elicits sensory facilitation at short (100 ms) cue-target intervals but attentional inhibition at long (800 ms) cue-target intervals. In contrast, the OFFSET of an ipsilateral cue elicits sensory inhibition at short and attentional inhibition at long intervals between cue offset and target onset (Gawryszewski et al., 2002b).

These results suggest that the inconsistent findings about facilitation and inhibition elicited by a non-informative visual cue can be explained by considering that cue onset has a facilitatory effect (or no effect), whereas cue offset has an inhibitory effect on a target occurring in the cued hemifield (see Gawryszewski et al., 2002b; Maruff et al., 1999 and Tassinari et al., 1994, for an analysis of the effect of cue and target duration). Moreover, since classically IOR arises at cue-target intervals longer than 200 ms (Posner & Cohen, 1984; Klein, 2000), the presence of an inhibition at shorter intervals indicates that cue offset elicits an early inhibition that is different from IOR. Other investigators, using different experimental paradigms, have also proposed the existence of at least two different types of inhibition elicited by a peripheral cue: an early (stimulus-related) inhibition and a late (attentional or response-related) inhibition (Tassinari & Berlucchi, 1993; Umiltà et al., 1991).

The spatial distribution of the inhibitory effects elicited by a non-informative cue has been studied by several authors (Berlucchi et al., 1989; Gawryszewski et al., 1994a, 2002a; Tassinari et al., 1987) and the main findings are: (i) the inhibition is maximal when the target appears at the cue position; (ii) the inhibition decreases with cue-target distance and (iii) the vertical and horizontal meridians act as barriers that limit the spreading of inhibition, which can extend to the whole cued hemifield. Berlucchi et al. (1989), for instance, found that a 5 ms cue occurring at 1° from fixation inhibits MRT to a target occurring at 30° in the ipsilateral hemifield (29° cue-target distance) as compared to a target occurring at 1° in the contralateral hemifield (2° cue-target distance). This spatial distribution of the inhibitory effect indicates that the cue-target absolute distance is not the main factor to determine the inhibitory effect. The important point that needs to be stressed is, therefore, that the inhibitory effect is only present if the cue and the target are located on the same side of the vertical (or horizontal) meridian. A similar finding was observed for ocular responses. Saccadic RT to a peripheral target (10°) occurring after an ipsilateral parafoveal (2°) or peripheral (10°) cue is longer than after a contralateral parafoveal (2°) or peripheral (10°) cue

(Guimarães-Silva et al., 2004). The similar spatial distribution of the inhibitory effect produced by the cue, observed for manual and ocular responses (Berlucchi et al., 1989; Guimarães-Silva et al., 2004), suggests that the postulated functional link between covert and overt orienting of attention (Rizzolatti et al., 1987) is valid both for peripheral and parafoveal cues. Note that this is also true regardless of the effector because the spatial distribution of the inhibitory effect is equivalent with eye movement and key-press responses.

Behavioral and electrophysiological studies suggested the involvement of the Superior Colliculus (SC) with the inhibition elicited by a non-informative cue (Rizzolatti et al., 1974; Sapir et al., 1999; Simion et al., 1995; Wurtz et al., 1980a, 1980b). Considering the sensory and the motor representations in the SC, there is a clear division of the visual space: stimuli located in the left hemifield activate the right SC, which generates eye movements towards the left hemifield (and vice-versa for the left SC). In contrast, stimuli located in the upper part of the left hemifield activate neurons in the medial region of the right SC and stimuli located in the lower part of the left hemifield activate neurons in the lateral part of the right SC (the same is true for the left SC). In short, for stimuli located along the horizontal dimension, there is a discontinuity in the visual representation on the SC at the border between the two hemifields (vertical meridian) because the left hemifield is represented in the right SC and the right hemifield in the left SC. By contrast, for stimuli located along the vertical dimension, there is no discontinuity in the visual representation of the upper and the lower part of the visual space. Moreover, the sensory and motor representations in each SC follow a Polar Coordinate system, in which each position in the visual space is coded using its eccentricity and direction (see Sparks, 1986, 2002; Sparks & Mays, 1990 for reviews). However, it is worth to note that, in the primate oculomotor system, the neurons in the paramedian pontine reticular formation (PPRF) and in the mesencephalic reticular formation are involved in the generation of horizontal and vertical components, respectively, of saccadic eye movements. Thus, at the premotor level of eye movement programming, the movement of the eye is defined by Cartesian coordinates. (see Sparks, 2002; Moschovakis & Highstein, 1994; Moschovakis, 1996 for reviews).

Masino and Knudsen (1990, 1993) results on the barn owl's tectum opticum have led to their proposal that a system based on orthogonal coordinates might be a general property of the intermediate stages in motor hierarchies. Evidence for an abstract system intermediate to the sensory and motor processes that control orienting movements has also been obtained from: (a) recordings of eye and head movements produced by electrical stimulation of brainstem tegmental regions in cats and monkeys (Fukushima, 1987; Moschovakis, 1996); (b) psychophysical experiments with human arm and hand pointing movements (Soechting & Flanders, 1989); (c) deficits in body orienting of brain-lesioned frogs (Masino & Grobstein, 1989a, 1989b). Finally, we have demonstrated that voluntary covert orienting of attention towards a spatial position involves the computation of two orthogonal vectorial

components along the vertical and horizontal axes (Gawryszewski et al., 1992; Gawryszewski & Carreiro, 1996).

The aim of this study is to test the hypothesis that the spatial distribution of the inhibitory effects elicited by a non-informative cue follows rules similar to those described by Masino and Knudsen (1990, 1993) for owl head movements, by Soechting and Flanders (1989) for human pointing movements and by Gawryszewski and Carreiro (1996) for voluntary covert orienting of attention. Moreover, we will compare the spatial distribution of the inhibitory effects observed for short - 100 ms and long - 800 ms cue-target intervals. In short, in this work, we studied the spatial distribution of the inhibitory effects elicited by a non-informative cue on MRT to a visual target. The main issue is to determine if the spatial distribution of the inhibitory effect is best described on the basis of a Cartesian coordinate system (in which positions are defined by vertical and horizontal vectorial components) or on the basis of a Polar coordinate system (in which positions are defined by vectors of a given direction and amplitude). The results of the present study may also be important with reference to the pre-motor hypothesis of visual attention (Rizzolatti et al., 1987). If the spatial distribution of the inhibitory effects conforms to the rules discovered by those previous studies (Gawryszewski et al., 1987, 1992, Rizzolatti et al., 1987), then, it would corroborate the premotor hypothesis. However, if this hypothesis were proved false, this would not dispute the premotor hypothesis but would show that the neural mechanisms involved in the inhibitory effects of a visual non-informative cue have properties different from those identified for the voluntary orienting of attention and from those proposed by Masino and Knudsen (1990, 1993) for "an abstract system intermediate to sensory and motor processes that control orienting movements".

METHOD

Participants. Eight right-handed subjects (2 males and 6 females) voluntarily participated in the experiment. They were students of Universidade Federal Fluminense, were right-handed according to the Edinburgh Inventory (Oldfield, 1981), had normal or corrected visual acuity, and, except for the two co-authors, were ignorant of the purpose of the study.

Apparatus and stimulus display. The participants were tested in a sound-attenuated room under dim ambient light. They sat in front of a 14-inch video monitor, with their head positioned on a chin-and-front rest and with their eyes positioned at approximately 57 cm from the screen. The timing of the presentation of visual stimuli and the recording of key pressings were performed by a IBM-PC microcomputer running customized software written in MEL1.0 language (Psychology Software Tools, Pittsburgh, PA, USA). The visual display was empty except for a fixation cross located at its geometric center. The luminance of the screen and of the cross were 0.3 and 11.5 cd/m², respectively. The stimulus luminance was 11.5 cd/m² and the response to the

imperative stimulus was recorded by pressing a micro-switch with the right index finger.

Procedure. The subjects were instructed to fixate a cross, not to respond to a cue (0.8° empty circle), and to respond to a visual target (0.4° filled circle) by pressing a micro-switch using the right index finger. Each trial began with the presentation of a fixation cross, which was followed after 1150 ms by a non-informative cue. That is, the cue did not provide any information concerning the target position. The cue appeared for 50 ms and the target occurred 100 or 800 ms after cue offset at the previous cue location or at several distances from it (Figure 1). The cue and target eccentricities were 7° and their angular directions were: 22.5°; 67.5°; (upper-right quadrant); 112.5°; 157.5° (upper-left quadrant); 202.5°; 247.5° (lower-left quadrant); 292.5°; 337.5° (lower-right quadrant). The combinations between cue and target locations were equiprobable, so that, the angular distances between cue and target were: 0°, 45°, 90°, 135°, 180°, 225° (-135°), 270° (-90°) or 315° (-45°) (Figure 1B). In order to reduce the number of combinations between cue and target positions, the subjects were divided into two groups. For each group, the cue appeared in eight positions and the target appeared in four positions (Figure 1A). We considered the groups to be equivalent, because, for both, the target could be unambiguously classified as a right, upper, left, or lower stimulus and the cue-target distances were the same.

Subjects attended four sessions (one for training and three for collecting data) of 320 trials each, divided in blocks of 80 trials. MRT shorter than 100 ms and longer than 1000 ms were considered anticipations and misses and these trials were repeated. At the end of each session, 64 medians of 5 correct RTs for each combination of target location (right; upper; left; lower), cue-target distance (0, 45, 90, 135, 180, 225 (-135), 270 (-90) or 315 (-45)) and cue-target interval - ISI (100/800 ms) were calculated. For subsequent analysis, we averaged MRT medians obtained in each of the above combinations in the last three sessions.

RESULTS

Correct RTs were submitted to three repeated-measures analyses of variance (ANOVAs).

The aim of ANOVA 1 was to compare MRT when cue and target occurred at the same position (SP) with MRT when they appeared at different positions (DP - mean of the other 7 MRT). The factors were target field (right; upper; left; lower), cue-target spatial relationship (SP vs. DP) and ISI (100/800 ms). ANOVA 1 showed that both ISI ($F(1,7)= 62.694, p < .001$) and cue-target spatial relationship ($F(1,7)= 66.198, p < .001$) were significant sources of variance. In addition, the interaction between the factors cue-target spatial relationship and ISI ($F(1,7)= 68.575, p < .001$) was significant. A post-hoc analysis using the Newman-Keuls method showed that, for an ISI of 100 ms, when the target occurred at the cued position, MRT (402 ms) was longer

than MRT (289 ms) when cue and target occurred at different positions. The same was true for the 800 ms ISI (287 and 248 ms for SP and DP, respectively). Thus, the interaction was due to a greater inhibition (113 ms) after an ISI of 100 ms than after an ISI of 800 ms (39 ms). This effect of ISI on inhibition magnitude has been described previously (Berlucchi et al., 1989; Breitmeyer, 1984; Tassinari et al., 1987) and is probably due to sensory inhibitory mechanisms, such as visual masking, that have faded away with an ISI of 800 ms.

ANOVA 2 was designed to test the cue inhibitory effects when the target occurred at distances different from 0° on the same or different side of the vertical and/or horizontal meridian. (Figure 2). The factors were target field (right; upper; left and lower), cue-target angular distance (45, 90, 135, 180, 225 (-135), 270 (-90) or 315 (-45)) and ISI (100 or 800 ms). Two factors, ISI ($F(1,7)= 14.256, p= .007$) and cue-target distance ($F(6,42)= 19.589, p < .001$), were significant sources of variance. MRT for 100 ms ISI (288 ms) was longer than for 800 ms ISI (247 ms). This 41 ms difference can be due to a better motor preparation for the 800 ms cue-target interval and/or to a stronger inhibition at 100 ms ISI. The interaction between ISI and cue-target-distance was not significant. This indicates that the spatial distributions of the cue inhibitory effects do not vary with ISI. In other words, the spatial distribution of the early (100ms) and the late inhibitory (800ms) effects are similar, and except when the target occurred at the cued position (see above), the difference between the early and the late inhibitory effect will be around 41 ms. The main effects due to cue-target distance are illustrated in Figure 2.

We can observe that: (a) MRT is minimal when cue-target distance is equal to 180° (259 ms); (b) MRT increases as cue-target angular distance decreases and, (c) the magnitude of inhibition (MRT delay) is influenced not only by angular distance between cue and target locations but also depends on whether cue and target are located in the same or in different quadrants. More specifically, a post-hoc analysis showed that MRT for a 45° distance (281 ms) is longer ($p < .05$) than MRT observed for any other distance. The same holds when we compare MRT for a -45° distance (275 ms) with MRT for the other distances. Finally, MRT for the $\pm 90^{\circ}$ distances (268 and 269 ms) are longer than that for the 180° distance (259 ms). These results show that for the inhibition produced by the cue, it is possible to distinguish distance and meridian effects, as was proposed by Rizzolatti et al. (1987) for the covert orienting of attention.

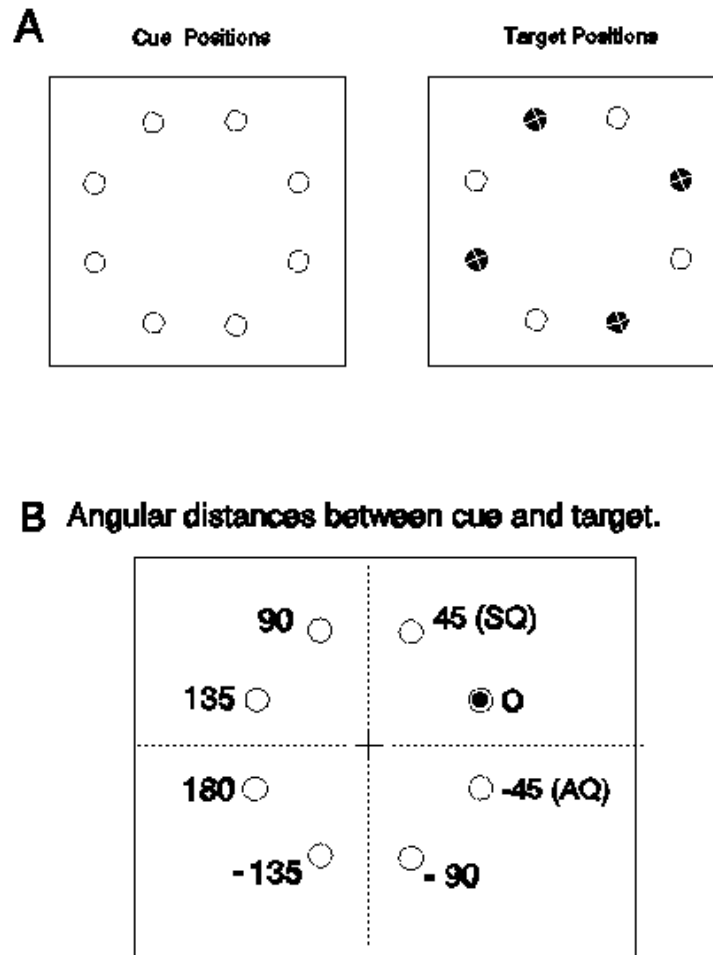


Figure 1. A- Cue and target positions. The cue and target directions varied from 22.5° to 337.5° and their eccentricities were 7° . For the target, four positions (black - 22.5° to 292.5°) were used in four subjects (Group I) and the cue-target distance was measured using trigonometric convention. The other four positions (white - 67.5° to 337.5°) were used in the other four subjects (Group II) and the distance was measured in clockwise direction. B- Cue-target angular distances for a target occurring, for example, at 22.5° . (SQ- same quadrant, AQ- adjacent quadrant).

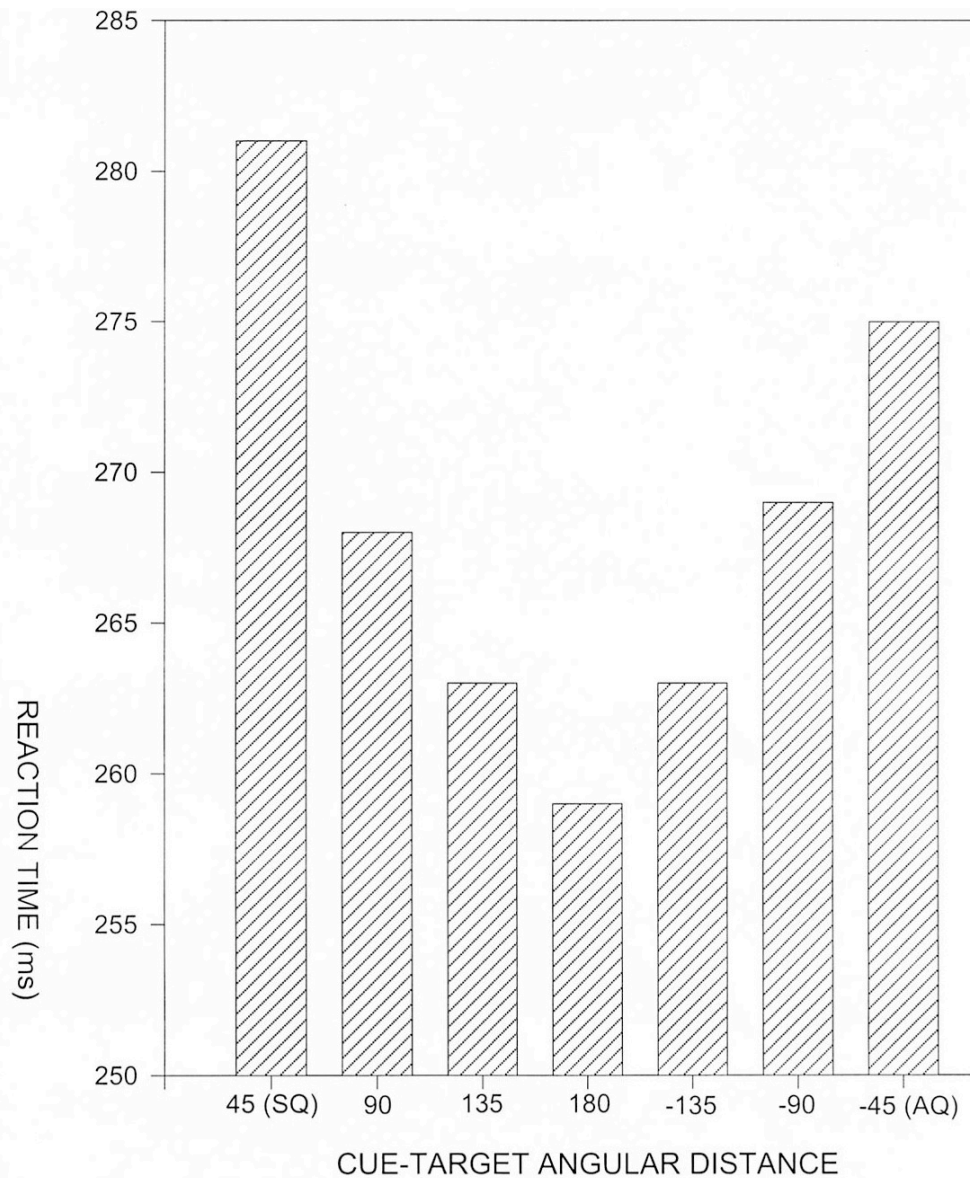


Figure 2. Effects of cue-target angular distance on Manual Reaction Time (MRT) to a visual target. MRT is shortest when cue and target appear at opposite positions (180°) and MRT inhibition increases as cue and target distance decreases. (SQ- same quadrant, AQ- adjacent quadrant).

Finally, in ANOVA 3, we test directly the presence of a meridian effect by comparing MRT to cue-target distances of 45° (same quadrant) and -45° (adjacent quadrant). The factors were target field (right; upper; left and lower), quadrant (same; adjacent) and ISI (100 or 800 ms). Two factors, ISI ($F(1,7)=14.178$, $p=.007$) and quadrant ($F(1,7)=8.392$, $p=.022$), were significant sources of variance. MRT for 800 ms ISI (258 ms) was shorter than for 100 ms ISI (297 ms). When cue and target occurred in the same quadrant, MRT (281 ms) was longer than MRT (275 ms) when cue and target occurred on different sides of horizontal or vertical meridians (adjacent quadrant).

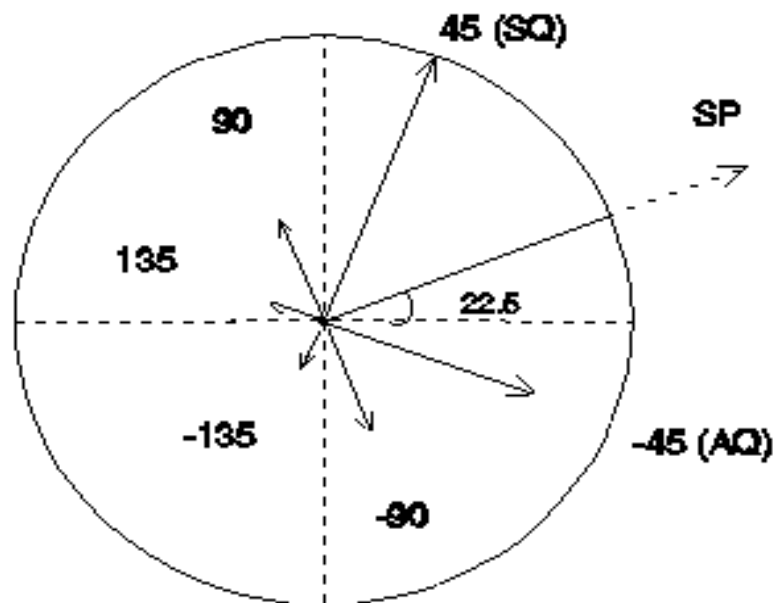


Figure 3. Cue-target angular distance and inhibition of Manual Reaction Time (MRT) to a visual target. The 22.5° target position was chosen as reference. The inhibition (vector amplitude = difference between MRT at each distance and MRT for a cue-target distance of 180°) is maximal when cue and target appear in the same position (SP- 85 ms, out of scale), decreases with cue-target distance, but is still significant for a 90° and for a -90° cue-target distance, when the cue and the target are in the upper hemifield or the right hemifield, respectively. The circle radius corresponds to a difference of 22 ms. (SQ-same quadrant, AQ- adjacent quadrant).

DISCUSSION

Our main findings are illustrated in a Polar diagram in Figure 3, where one arbitrary target position (22.5°) was chosen as representative of all target positions and the magnitude of the inhibition is represented by vector amplitude. The inhibition was measured by calculating the difference between MRT observed for each cue-target angular distance and MRT observed when the target occurred at 180° from cue position. It can be seen that: (a) when an imperative stimulus is preceded by a non-informative cue occurring at the same location, there is maximal inhibition. This inhibition is responsible for a response delay of 121 ms for a 100 ms ISI and a response delay of 50 ms for a 800 ms ISI. The difference between the early (ISI=100ms) and late (ISI=800ms) inhibitions is probably due to a visual masking inhibitory effect, which is maximal at short ISI, decreases as ISI increases and, usually, is null at 800 ms ISI (see Breitmeyer, 1984 for review); (b) the inhibition spreads to other positions located in the same hemifield (that is, to other positions located on the same side of the vertical or horizontal meridians), and, although it decreases with increasing cue-target distance, it is significant even when cue and target are $\pm 90^\circ$ apart. It is important to note that there is no interaction between cue-target distance and ISI. Thus, the spatial distributions of the early and late inhibitions are similar; (c) the magnitude of inhibition is influenced not only by angular distance between cue and target locations but also depends on whether cue and target are located in the same or in different quadrants.

The presence of greater inhibition when cue and target are located in the same quadrant as compared to when they occur at the same distance but in different quadrants strongly suggests that cue and target positions are computed on a Cartesian coordinate system and that the meridian effect is based on the coincidence, or lack of coincidence, of the horizontal and vertical components of an attentional vector having its origin at the fixation point. This is shown in detail in Figure 4. In agreement with other authors (Tassinari et al., 1987), we believe that, when a cue appears at one position, besides the visual masking effects (Breitmeyer, 1984), it elicits an orienting of the eyes toward its position. This eye movement has to be voluntarily inhibited. According to our hypothesis, the cue position or, more specifically, the motor representation of cue position, is computed with reference to two perpendicular axes: one vertical and the other horizontal. In our example, when the cue appears at one position in the upper-right quadrant, it is necessary to inhibit an eye movement directed up and to the right. If the cue appears at one position located in the lower-right quadrant, then an eye movement down and to the right must be inhibited. Using this approach, it is easy to understand why the response to a target located in the upper-right quadrant will be more inhibited in the former case (when cue and target are located in the same quadrant) than in the latter case, in which the vertical component of cue position is directed downwards and the vertical component of target position is directed upwards.

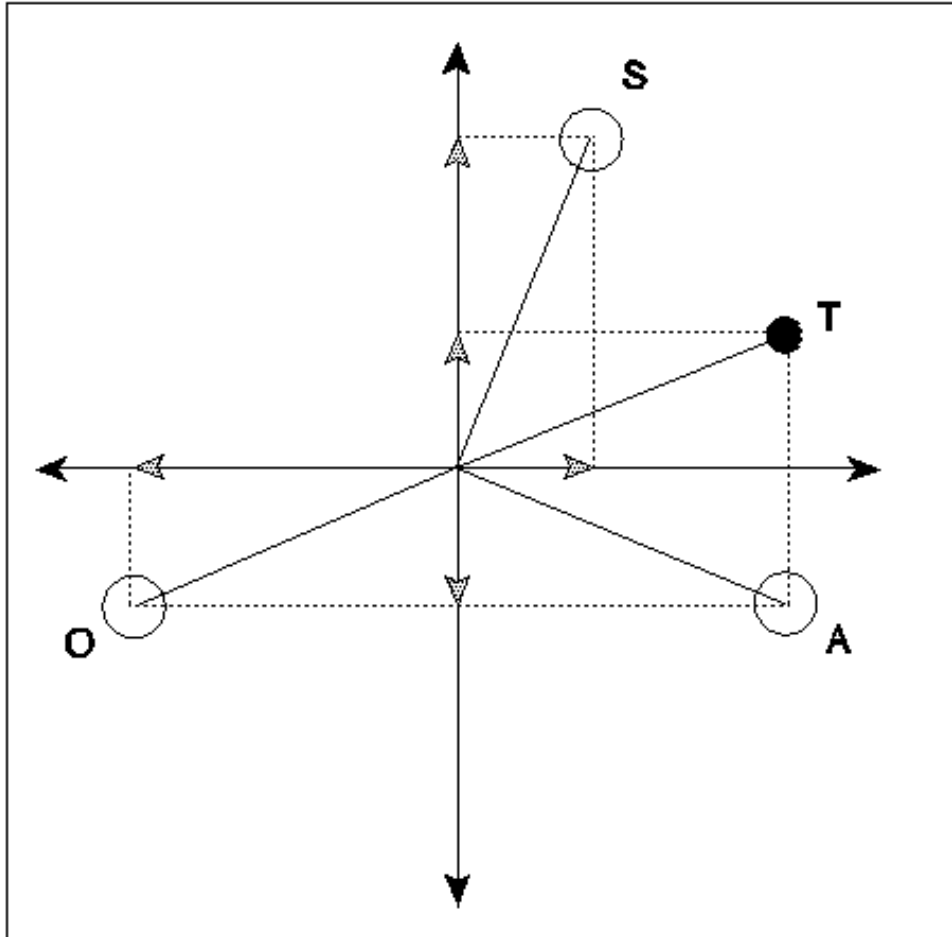


Figure 4 - Cartesian coordinates of cues occurring in opposite (O), adjacent (A), or same quadrant (S) of a subsequent target (T).

These results are similar but symmetric to those found using covert orienting of attention (Gawryszewski & Carreiro, 1996). In that work, we used central cues to covertly orient attention to peripheral positions. The costs for targets occurring at unattended positions were measured by calculating the difference between MRT for each angle between cued and target positions (directions) and MRT when the target occurred at the attended position. Using MRT when the target appeared at the expected position (0°) as baseline, we found that: 1) MRT increased 13 ms when the target occurred at an angle of 45° from the expected position (direction) but in the same quadrant; 2) MRT increased 30 ms when the target occurred at an angle of 45° from the expected position (direction) but in an adjacent quadrant,

indicating a meridian effect of about 17 ms in relation to a reorienting of attention across the vertical or the horizontal meridian; and 3) MRT increased about 60 ms when the target occurred at an angle of 135, 180 or -135° from the expected position (direction).

The presence of a greater cost when the target appeared at 45° from the cue position and in an adjacent quadrant as compared to when it occurred at 45° but in the same quadrant renders it difficult to explain an attentional process based on Polar coordinates. On the other hand, if attention is computed on a Cartesian coordinate system, the difference between a target appearing in the same or in an adjacent quadrant is easy to explain. In agreement with other studies (Gawryszewski et al., 1987; Rizzolatti et al., 1987, 1994), we believe that, when one expects a visual stimulus at one position, a motor program for a saccade towards this position is prepared. Our data strongly suggests that this motor representation is computed on a Cartesian coordinate system (Gawryszewski & Carreiro, 1996). For instance, when a cued position is in the upper-right quadrant, an ocular motor program specifying an eye movement up and to the right overt eye movement is prepared. When the target appears at another position located in the same quadrant, what is needed is only an adjustment in the parameters of a set of eye movements whose general programming has been already made (the same muscles will be contracted but with different degrees of activation due to a change on the amplitudes of the horizontal and vertical vectorial components). In contrast, if the target appears in the lower-right quadrant, it will be necessary to reverse the direction of the vertical vectorial component, which means programming contraction of a completely different set of muscles. This change in motor program is more time-consuming and it is the origin of meridian effect. Finally, if the target appears in the lower-left quadrant, it will be necessary to reverse the direction of both the vertical and the horizontal vectorial components, thus producing a greater cost.

At this point, it is worth noting that single unit studies in cats (Rizzolatti et al., 1974) and monkeys (Judge et al., 1980; Wurtz et al., 1980b) have shown inhibition of neuronal response with the same features as those found behaviorally. Thus, the early inhibition can represent the behavioral expression of the single neuron response inhibition observed in the primary visual cortex (Judge et al., 1980) and superior colliculus (SC) (Wurtz et al., 1980b) of monkeys. In both regions, the response of neurons to an effective visual stimulus is attenuated by previous stimulation at the same locations. Moreover, SC neurons also show response attenuation by previous stimulation of locations remote from the receptive field if both stimuli occurred in the same hemifield with a 0-100 ms interval between conditioning and test stimulus. In contrast, the late inhibition can be related to the response attenuation described in the cat's SC by Rizzolatti et al. (1974). This response attenuation is more likely to be linked to attention since it shows habituation. It can be induced by a remote ipsilateral stimulus but not by a contralateral one and, in contrast to the inhibition described in monkeys (Wurtz et al., 1980b), it was observed with an inter-stimulus interval of up to 1s.

It is important to note that our results did not show any difference between the spatial distribution of early and late inhibitory effects. This suggests that the 41 ms delay found between MRT for 100 and 800 ms ISI (at cue-target distances bigger than from 0°) is related, mainly, to motor preparation and that the sensorial and the attentional factors elicited inhibitory effects with similar spatial distributions.

CONCLUSIONS

Experimental paradigms similar to those just described before have also been employed in behaving monkeys for studying the neural mechanisms involved in overt and covert orienting of attention. In some neural structures (for instance, SC, pulvinar, posterior parietal cortex), it was observed an enhancement of the response to a visual stimulus flashed in the receptive field of a neuron when the stimulus became relevant to the animal (see Colby, 1991; Wurtz et al. 1980a, 1980b and Gattass & Desimone, 1996 for reviews). In the SC, it was also found that an irrelevant stimulus inhibits the response to a subsequent stimulus occurring in the receptive field of a neuron (Wurtz et al., 1980a, 1980b). In other regions, the main effect of the orienting of attention seems to be an active inhibition of unattended locations rather than a facilitation of attended ones (see Desimone & Duncan, 1995 for review).

Based on physiological, pharmacological and behavioral studies, several authors suggest that the SC can be involved in the overt and covert orienting of attention to one spatial location. For instance, Rizzolatti et al. (1994) proposed that the facilitatory effects of covert orienting of attention can be due to a modulation of the collicular excitability by a circuit involving cortical oculomotor areas, the caudate nucleus and the pars reticulata of the substantia nigra (SNr). The voluntary orienting of attention to a spatial position will activate cortical oculomotor areas, which will activate the caudate. The latter, in turn, will inhibit SNr neurons, reducing the tonic inhibition mediated by nigro-collicular connections. Since all these connections are topographically organized, the final effect will be an activation of premotor neurons of intermediate and deep collicular layers, which can lead to the "enhanced" response to a visual target that was observed in collicular superficial layer neurons. This "enhancement" effect is spatially selective and could be responsible for the faster responses when the target appears at the expected position.

The same circuit could be involved in the inhibition observed after the occurrence of a non-informative peripheral cue. In this case, the peripheral cue would automatically activate a collicular local motor program for a saccade in the direction of the stimulated position. This local program, however, must be counteracted by a central program in the opposite direction because of the instructions to not move the eyes towards the peripheral cue. The central program should cause a bias against eye movements (and attentional shifts) that share direction with the local program and, possibly, a bias in favor of eye movements (and attentional shifts) in the opposite direction. In addition, a

masking effect and the early inhibition described previously would also delay the response to a target occurring in the same hemifield of a non-informative visual cue.

Finally, from single-unit recordings it has been well established that at a premotor level, the saccadic system is organized in a Cartesian coordinate system (see Moschovakis & Highstein, 1994 for a review). At this peripheral level, the paramedian pontine reticular formation and the mesencephalic reticular formation are responsible for the generation of the horizontal and vertical components of saccades, respectively (Moschovakis & Highstein, 1994). Thus, it is possible that the spatial distributions of both the facilitatory effect due to voluntary orienting of attention (Gawryszewski & Carreiro, 1996) and the early and late (IOR) inhibitory effects due to a non-informative visual cue (see present paper) reflect the Cartesian coordinate system used in the last steps of saccadic eye movement programming. Similar orthogonal coordinate systems were observed for other motor systems leading Masino and Knudsen (1990, 1993) to propose the existence of an "abstract system intermediate to sensory and motor processes that control orienting movements".

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