RESEARCH ARTICLE

B. M. Sheliga · L. Riggio · G. Rizzolatti

Spatial attention and eye movements

Abstract We previously showed that when attention is allocated to the right or left of the fixation point, saccades directed to targets located above or below the fixation point deviate contralateral to the attention locus. In the present study, we examined how general this phenomenon is and whether the amount of saccade deviation depends on the location of attention with respect to that of the saccade target. Three experiments were carried out. In experiment 1 the location of the imperative stimulus was uncued. Its presentation exogenously directed attention to its location. In experiment 2 the location of the imperative stimulus was cued by a central cognitive cue. In this experiment attention was endogenously directed to the imperative stimulus location before its presentation (expectancy paradigm). In experiment 3 all stimulus boxes contained a possible imperative stimulus at the display presentation. A central cue, presented subsequently, indicated which of them had to be used for the saccade. In this experiment attention was endogenously directed to the imperative stimulus, but after its presentation (no-expectancy paradigm). The results showed that, regardless of how attention was directed to the imperative stimulus, the vertical saccades deviated contralateral to the attention location. The deviation was larger when attention was in the upper field and the saccade was directed upward ("same hemifield" condition) than when attention was in the upper field and the saccade was directed downward ("opposite hemifield" condition). The same relationship between the "same hemifield" condition and "opposite hemifield" condition was found when attention was in the lower field. Saccadic reaction times (SRTs) were shortest in experiment 2 and longest in experiment 3. In experiment 2, SRTs of the "same hemifield" condition were significantly longer than those of the "opposite hemifield" condition. Taken altogether, these results strongly support the notion that attention allocation in space leads to an activation of oculomotor circuits, in spite of eye immobility. The possible mechanisms responsible for saccade deviations and for greater saccade deviations when attention is in the same hemifield as the programmed ocular saccade are discussed.

Key words Spatial attention · Oculomotor system · Saccades · Human subjects

Introduction

Although shifts of attention are usually accompanied by overt eye and body movements, focal attention can also be aligned covertly, in the absence of movements of the head or eyes (for reviews see Posner 1980, Umiltà 1988). What are the relations between the covert and overt attention phenomena? Broadly speaking, two potential relationships have been suggested.

The first is that the two sets of phenomena, although linked, are basically independent. According to this point of view, attention is an independent supramodal function, subserved by anatomical circuits separated from the data processing systems (Klein 1980; Posner 1980; Rafal et al. 1989; Posner and Petersen 1990; Klein et al. 1992). Originally, the supramodal attentional system was thought of as an unitary system (e.g. Posner 1980; LaBerge and Brown 1989). More recent versions of the theory postulate the existence of at least two different attentional systems: a posterior system subserving spatial attention and an anterior system involved in the attentional recruitment and control of brain areas to perform complex cognitive tasks (Posner and Dehaene 1994).

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The second solution is that attention derives from the activity of those same circuits which process sensory data. There are no specific "attentional" circuits. As far as spatial attention is concerned, this is the consequence of the cooperative action of various pragmatic maps (oculomotor, for reaching, for walking). In man, because of the strong development of foveal vision and the neural mechanisms for foveation, a central role in spatial attention is played by maps that code space for programming eye movements. This proposal is known as the "premotor theory" of attention (Rizzolatti 1983; Rizzolatti and Camarda 1987; Rizzolatti et al. 1987, 1994; Umiltà et al. 1991, 1994).

Evidence in favor of the "premotor theory" derives from neurophysiological studies showing that those structures which are involved in spatial attention are also involved in motor programming (see references in Rizzolatti and Gallese 1988; Rizzolatti et al. 1994) as well as from psychological studies on attention orienting. These last studies showed that when subjects have to redirect attention across the horizontal or vertical meridian they have to pay an extra cost with respect to when they have to move attention within one visual quadrant. This "meridian effect" (Downing and Pinker 1985; Hughes and Zimba 1985, 1987; Rizzolatti et al. 1987; Tassinari et al. 1987; Umiltà et al. 1991; Reuter-Lorenz and Fendrich 1992) is hard to account for if attention is not related to motor programming, while it becomes an expected event if one accepts that oculomotor programming underlies attention orienting.

Recently, we reported three experiments which further support the premotor theory of attention (Sheliga et al. 1994). Subjects were asked to make vertical saccades toward a predetermined target, while their attention was allocated to different positions in space. In the first experiment, the stimuli triggering the ocular saccade (imperative stimuli) were visual signals presented at previously cued or non-cued locations. In the second and third experiments, the imperative stimuli were either visual signals, presented peripherally, or auditory signals presented centrally.

These experiments were based on the following rationale. If spatial attention involves an activation of oculomotor circuits, one should expect that the execution of an oculomotor response would be influenced by this activation. In contrast, if spatial attention is independent of eye movement programming, the oculomotor response should remain unmodified, regardless of whether spatial attention is allocated to one or another site.

The results showed that visual imperative stimuli determined a deviation of the vertical saccade contralateral to the hemifield in which they were presented. The degree of this deviation was greater, when the imperative stimulus was presented in the attended visual hemifield than in the opposite one. Furthermore, when the subjects paid active attention to a given spatial location, the saccade trajectory deviated contra-

lateral to the attention site, even when the imperative stimulus, triggering the saccade, was auditory and not lateralized. The deviation was therefore due to purely attentional factors.

The experiments described in the present article represent a continuation of the aforementioned investigation (Sheliga et al. 1994). The primary aim was to see how general is the effect of attention on deviations of ocular saccades. To this purpose, we studied the effect of focal attention on vertical saccades in three different attentional situations. In the first one, attention was allocated to the central fixation point. The imperative stimulus was then presented peripherally and the subject had to discriminate its shape in order to make the correct saccade. In this situation, the attention shift toward the imperative stimulus location was *exogenously* determined. In the second situation, a cue was presented before the imperative stimulus. The imperative stimulus was then presented in correspondence to the attended location. In this situation, the attention shift toward the imperative stimulus location preceded its appearance and was therefore *endogenously* generated. Note, however, that an exogenous orienting was also present at the moment of stimulus presentation. In the third situation, there was no abrupt presentation of the imperative stimulus. Potential imperative stimuli were present in the visual display before the presentation of the cue which, later, indicated which was the effective imperative stimulus. In this situation there was a *purely endogenous* orienting of attention, *without peripheral stimulus presentation*.

A second aim of the present experiments was to examine whether there were quantitative differences in the trajectory deviation according to spatial location of attention. In all three experimental situations the subjects, in order to solve the task, had to allocate attention to a box in the same hemifield (upper or lower) toward which the saccade was directed ("same hemifield" condition) or in the opposite one ("opposite hemifield" condition).

The results showed that regardless of how attention is moved, it determines a contralateral deviation of the trajectory of ocular saccade. The contralateral deviation was stronger in the condition "same hemifield" than in the condition "opposite hemifield". These new data are discussed in the framework of the premotor theory of attention.
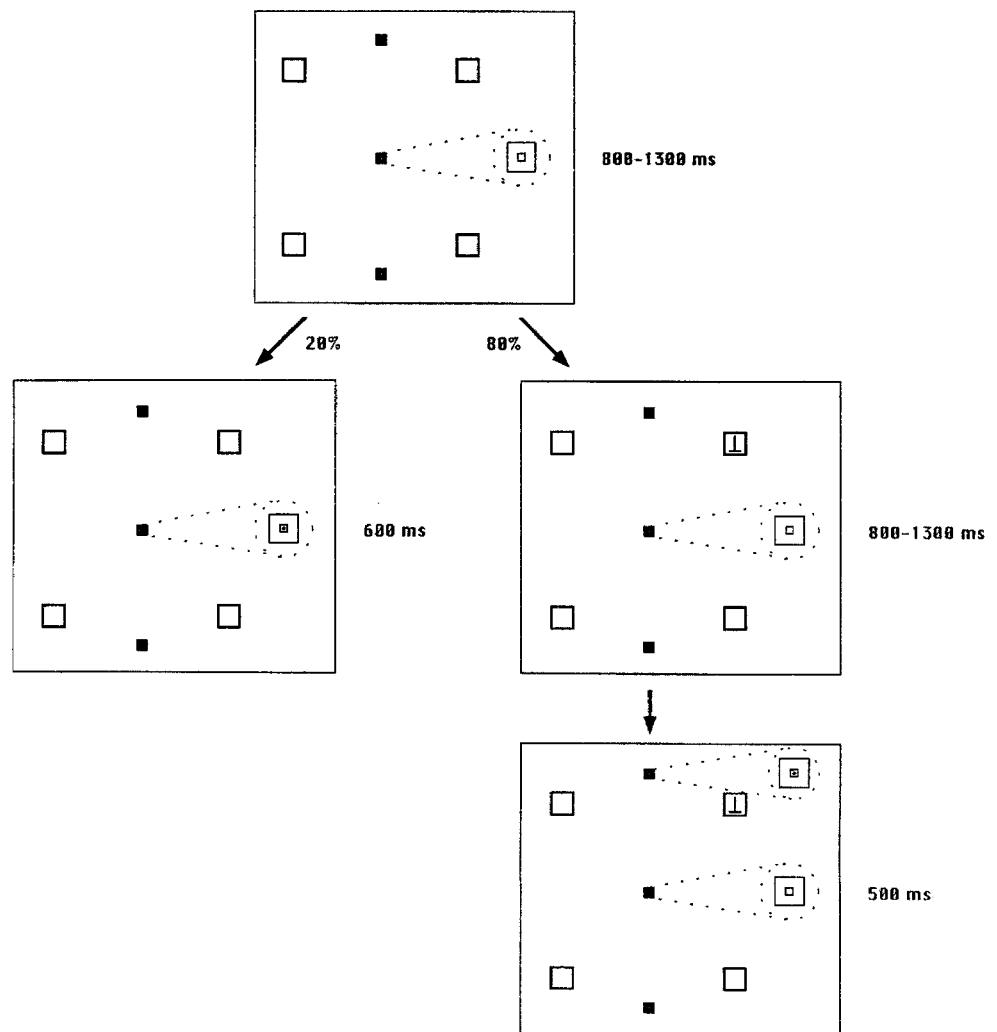
Methods

Subjects

General procedure

The experiments took place in a sound-attenuated room, dimly illuminated by a halogen lamp. A microcomputer IBM PC/AT 386 was used for stimulus generation and response recording. The subject sat in front of the computer screen with the head positioned on an adjustable head-and-chin rest and additionally restrained by the chair head-holder. The distance between the eyes and the screen was 57 cm. Eye movements were recorded using an infrared oculometer (Bach et al. 1983).

Every subject performed three experiments during three successive experimental sessions. All the experiments started with the presentation of the word "Ready" at the center of the screen. The subject, when ready, pressed and held a button, causing a visual stimulus display to appear on the screen.

The basic stimulus display is shown in Fig. 1 (upper panel). It contains three small (0.6° × 0.6°) and four large boxes (1.5° × 1.5°). One small box, "fixation" box, is located at the geometric center of the screen. The other two small boxes are positioned 8° (center to center) below and above the "fixation" box. They served as targets for ocular responses. Inside both the "fixation" and "target" boxes there is an additional tiny box (0.15° × 0.15°), where a dot could be presented during the trials (see below). The large boxes, "stimulus" boxes, are located at the angles of an imaginary square having the "fixation" box in its centre. The horizontal and vertical eccentricity of the "stimulus" boxes from the "fixation" box was 6°. The "stimulus" boxes indicate the possible positions in which the imperative stimulus could appear.

The imperative stimulus was the letter "T" (horizontal line 0.8°, vertical line 1.0°) which could be presented either normally oriented or inverted (Fig. 1, lower panels). Normally oriented and inverted Ts required ocular responses to the lower or upper "target" box, respectively.

Experiment 1: uncued imperative stimulus location

The stimulus display was that of Fig. 1. After a variable interval (800–1300 ms), during which the subject was instructed to fixate the central "fixation" box, one of the two following events occurred: (a) a dot appeared inside the "fixation" box (Fig. 1, left middle panel), (b) an imperative stimulus (a normal or inverted T) was presented inside one of the four "stimulus" boxes (Fig. 1, right middle panel). In the first case, the subject had to release the button within 600 ms after the dot presentation. There was no specific instruction to release the button as fast as possible. In the second case he had to make a saccade, as fast as possible, to the upper or lower "target" box according to the imperative stimulus orientation and to maintain fixation at that box until presentation of a dot inside it (Fig. 1, lower panel). The dot was shown 800–1300 ms after the imperative stimulus and remained on for 500 ms. The subject had to release the button during this time.

Fig. 1 Visual display and time sequence of events of experiment 1. Numbers on the right of each display panel indicate the duration of the presentation of the various displays. The central, "fixation" box of each panel and the upper "target" box of the bottom panel are also shown enlarged (the *dashed lines* and the *surrounding circles* show the enlarged representation) in order to provide a clear view of events occurring inside the box. For further explanations see text

Experiment 2: cued imperative stimulus location

Figure 2 illustrates the visual display of the experiment. After an interval of 800 ms following the pressing of the ready button, a directional cue was presented inside the "fixation box" (Fig. 2, second panel). The cue was an oblique, short, thin line ($0.2° \times 0.04°$). Its direction indicated in which of the four "stimulus" boxes the imperative stimulus was going to appear. The imperative stimulus was presented 800–1300 ms after the cue (Fig. 2, third panel). The subject was instructed to fixate the "fixation" box, then to direct attention to the cued "stimulus" box without breaking fixation, and, when the imperative stimulus occurred, to make a saccade, as fast as possible, to the upper or lower "target" box according to the imperative stimulus orientation. Finally, the subject had to maintain fixation at that "target" box until presentation of a dot inside it (Fig. 2, lower panel). The other instructions were as in experiment 1. Note that contrary to experiments 1 and 3 (see below), there was no condition in which the imperative stimulus (dot), requiring button release, was presented at the fixation point. This was done in order to allow the subject to allocate attention peripherally before the imperative stimulus presentation.

Experiment 3: imperative stimulus location cueing following imperative stimulus presentation

Unlike the other two experiments, in this experiment the imperative stimuli (normal and inverted Ts) were inside the four "stimulus" boxes at the moment of display presentation (Fig. 3, upper panel). After a variable time (800–1300 ms), during which the subject was instructed to maintain fixation, either a dot was presented inside the "fixation" box (Fig. 3, left middle panel) or a directional cue was shown inside this box as described in experiment 2 (Fig. 3, right middle panel). At the occurrence of the dot, the subject had to release the button within 600 ms following dot presentation. At the occurrence of the cue the subject had to direct attention to the cued box, discriminate the orientation of the T located inside it, and make a saccade as fast as possible to the "target" box indicated by the imperative stimulus orientation. The other instructions were as in experiment 1. The orientation of the Ts in the cued "stimulus" box was predetermined in such a way as to provide an overall equal number of trials for every stimulus position/direction of ocular response condition. The orientation of the Ts in the other three boxes was random.

In all experiments, successive trials were separated by a pause of approximately 2–3 s. At the end of the trial, the subjects were informed whether they had made errors and about the error type. This information was presented on the computer screen, after the display disappearance, together with the word "Ready".

Eye movements were recorded continuously from the moment of presentation of either the imperative stimulus (experiments 1 and 2) or cue (experiment 3). The sampling rate was 1000 Hz. Eye stability during the time interval preceding that moment was controlled by a "spatial window" of 1° in either orthogonal direction. In a previous experiment (Sheliga et al. 1994), we had demonstrated that horizontal presaccadic drifts do not account for the observed saccade deviations. In the present experiment we controlled for this variable in three subjects. To this purpose, we measured the position of the eyes 20 ms before the onset of the saccade and we compared this position to that of the eyes at the moment of cue and/or imperative stimulus presentation. We found no relation between the horizontal presaccadic drift and the saccade deviation.

Half of the subjects ran experiment 1 during the first session and experiment 2 during the second session. The order was reversed for the other half of the subjects. Experiment 3 was run during the third session.

Each session consisted of 20–25 initial practice trials, a series of eye movement calibration trials, and 160 (experiment 2) or 200
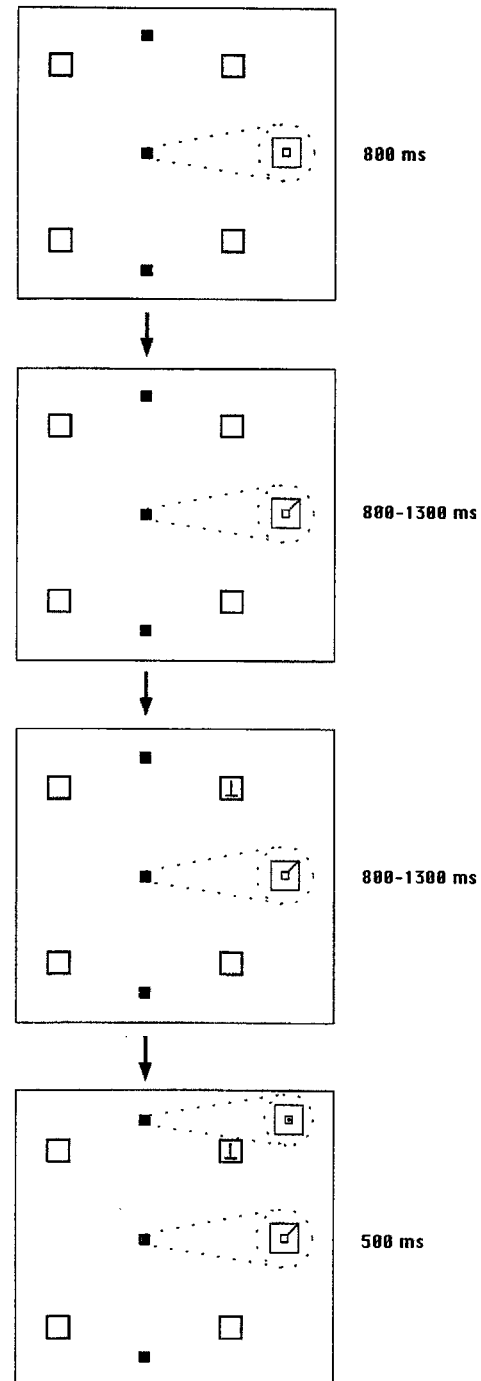

Fig. 2 Visual display and time sequence of events of experiment 2. Conventions as in Fig. 1

(experiments 1 and 3) correct experimental saccade trials. Error responses were rerun. In experiments 1 and 3, 160 trials required ocular response toward the "target" boxes, and 40 trials a manual response to the dot presented inside the "fixation" box. Thus any stimulus-response combination – location of the imperative stimulus (four possible locations)/direction of ocular response (up or down) – was tested 20 times in each experiment. The presentation order of the various stimulus-response combinations was random. All sessions were subdivided into four or five blocks of 40 correctly performed trials with some minutes of rest between the blocks.

Fig. 3 Visual display and time sequence of events of experiment 3. Conventions as in Fig. 1
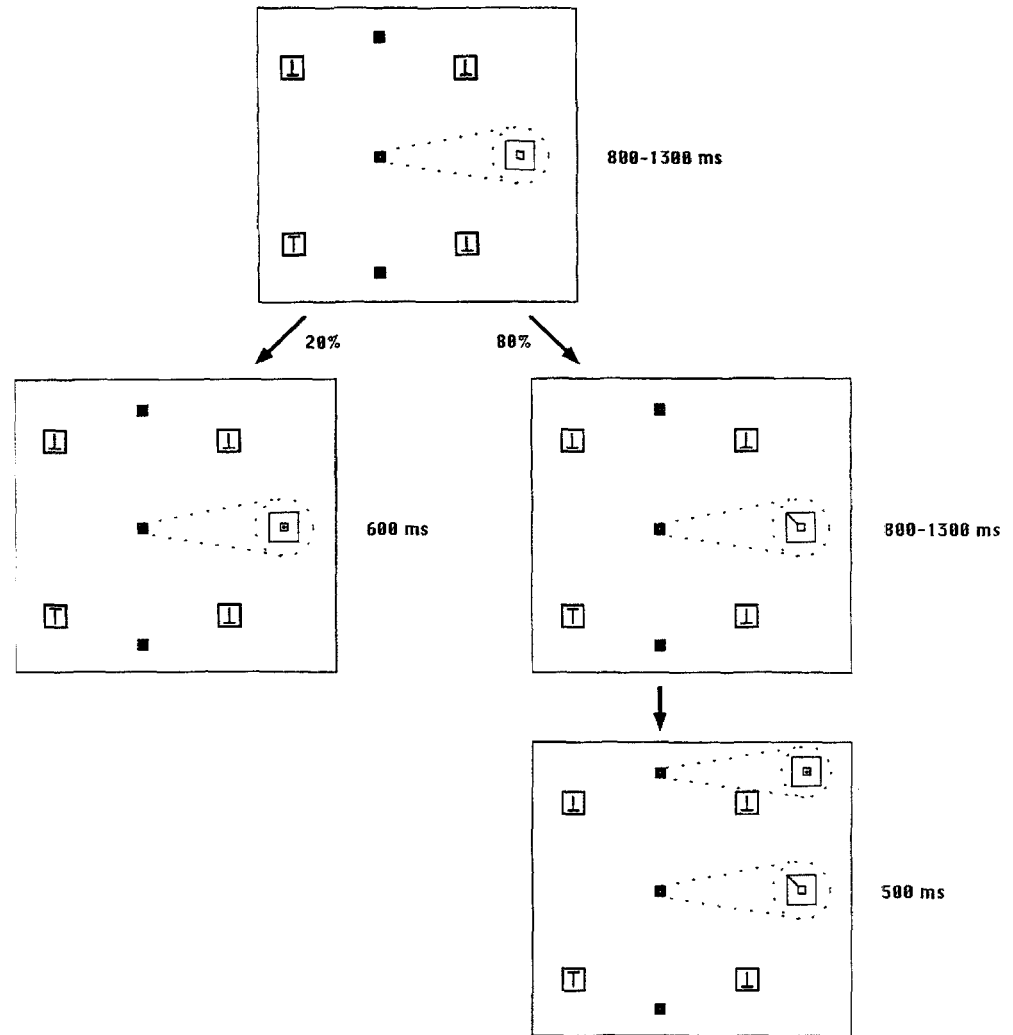
Data collection and analysis

Saccadic reaction time and saccadic kinematic parameters

In each trial the two orthogonal (x and y) components of eye movements were recorded on a magnetic disc. Off-line filtering (11-point moving average) was performed for quantitative data analysis.

Saccade detection was based on a velocity criterion. The beginning of the saccade was defined as the first point of a series of ten at which the eye velocity exceeded $30°/s$. The end of the saccade was the point at which the eye velocity dropped below $30°/s$. The onset of the saccadic eye movement with respect to the moment of imperative stimulus (experiments 1 and 2) or cue (experiment 3) presentation gave the saccadic reaction time (SRT).

Horizontal saccade deviation from a straight vertical trajectory (average deviation – AD) was calculated as follows. The values of the x-component of the saccades were measured from the moment of the saccade onset for 10 ms, with a sampling rate of 1000 Hz. The value of the x-component at the moment of the saccade onset was used as the reference value. The differences between the current values of the x-component and the reference value were summed and the sum of differences divided by the number of the performed summations. For more details see Sheliga et al. (1994).

Error handling

Five types of errors were controlled on line. Two of them were related to button release: (a) release before the dot occurrence and (b) late release, i.e., release 500–600 ms following dot presentation. Three types of errors arised from subjects inappropriate ocular respondes. They were: anticipations, retardations, and "opposite direction" errors. Anticipations were SRTs shorter than 80 ms (see Werban-Smith and Findlay 1991). Retardations were SRTs longer than 600 ms (700 ms for experiment 3). Finally, "opposite direction" errors were saccades directed opposite to the direction indicated by the imperative stimulus. Trials with errors were not stored, but their number and type recorded.

The accuracy of the saccades was checked during off-line analysis. Saccades with amplitudes lower than 4° or larger then 12° were rejected. Saccades directed toward visual imperative stimuli were the last type of error responses. They were also eliminated during the off-line analysis.

Statistical evaluation of data

SRTs, saccade horizontal deviation, and saccade y-component velocity data were subjected to multivariate analyses of variance

(MANOVAs). MANOVA was used in order to avoid assumptions about the intercorrelations among levels of the within-subject factors (sphericity assumption). Wilke's Lambda statistics were used. MANOVAs were performed using median values. A logarithmic transformation was performed upon SRT data before subjecting them to MANOVA. All the performed MANOVAs had four within-subject factors: (a) *Experiment* (1, 2 or 3) (b) *Direction* (upward or downward direction of the saccades), (c) *Field* (trajectory of the saccade in the same or opposite upper-lower field as the imperative stimulus location), and (d) *Side* (left or right field location of the imperative stimuli).

Results

Error analysis

Releasing of the button before dot presentation was rarely observed: this type of error occurred in 1.8% (range 0–7.5%), 1.1% (0–2.8%), and 1.6% (0.4–4.5%) of trials in experiments 1, 2 and 3, respectively. Retardations, anticipations as well as accuracy errors of the saccadic responses were also rather rare: their rates were 0.7% (range 0–2.5%), 0.9% (0–4.6%), and 3% (0–9.4%), respectively, in experiment 1; 0.9% (range 0–2.9%), 2.4% (0–9.6%), and 4.5% (0–10.9%), respectively, in experiment 2; 7.2% (range 0.3–18.2%), 0.5% (0–2.2%), and 3% (0–15.2%), respectively, in experiment 3. Saccades toward the imperative stimuli were observed in 0.6% (range 0–2.6%), 0.9% (0–4%), and 2.3% (0–9.9%) of trials in experiments 1, 2, and 3, respectively.

"Opposite direction" errors were the errors most frequently observed. They occurred in 6% (range 1.9–10.6%), 7.1% (1.8–14.6%), and 19.2% (11.4–32.2%) of trials in experiments 1, 2, and 3, respectively. A MANOVA revealed a significant main effect of Experiment ($F(2, 8) = 25.3$, $P < 0.001$), indicating that "opposite direction" errors were more numerous in experiment 3 than in the other two experiments. The three-way interaction Experiment × Field × Side was also significant ($F(2, 8) = 16.4$, $P < 0.002$). This was due to the fact that in experiment 3 the occurrence of imperative stimuli in the left hemifield led to a higher rate of directional errors when the imperative stimulus was in the same (upper or lower) hemifield as the target of the desired ocular response ("same hemifield" condition), than when the imperative stimulus and the target of the saccade were in the opposite (upper and lower) fields ("opposite hemifield" condition).

Saccadic reaction time

The main factors Experiment ($F(2, 8) = 62.6$, $P < 0.001$) and Direction ($F(1, 9) = 80.0$, $P < 0.001$) were significant. Bonferroni t-test revealed faster SRTs in experiment 2 – cued imperative stimulus location – (340 ms), than in experiment 1 – uncued imperative stimulus location – (370 ms), and faster SRTs in exper-
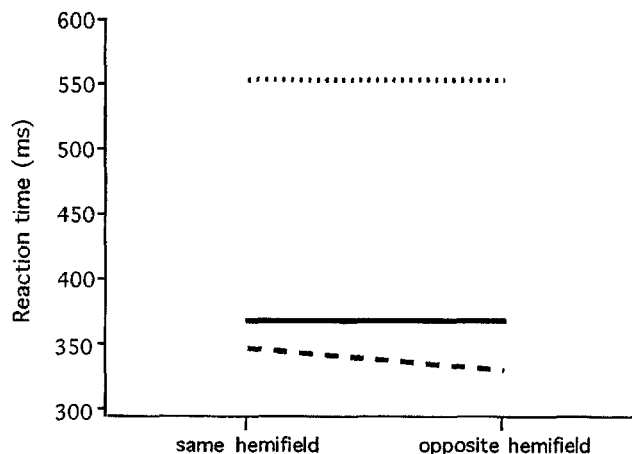
Fig. 4 Saccadic reaction times of experiment 1 (*thick continuous line*), experiment 2 (*thick interrupted line*), and experiment 3 (*dashed line*) as a function of Field. In experiment 2, the saccadic reaction times were slower when the imperative stimulus was presented to the same hemifield (upper or lower) towards which the subsequent saccade was directed ("same hemifield" condition) than when the imperative stimulus was presented to the hemifield opposite to the one towards which the subsequent saccade was directed ("opposite hemifield" condition)

iment 1 and experiment 2 than in experiment 3 – imperative stimulus location cueing following imperative stimulus presentation (555 ms). Downward-directed saccades were slower than those directed upwards (433 ms vs 410 ms).

Significant was also the interaction Experiment × Field ($F(2, 8) = 6.04$, $P < 0.03$). In experiment 2, SRTs were slower if the imperative stimulus was located in the hemifield (upper or lower) where the ocular response was subsequently directed ("same hemifield" condition, 348 ms), than when the imperative stimulus location and the desired ocular response were in opposite hemifields ("opposite hemifield" condition, 331 ms). Figure 4 illustrates the interaction.

Saccade horizontal deviation

As described in Methods, saccade horizontal deviation was analyzed using AD values. Two main factors – Side

Fig. 5A, B Experiment 2: saccadic responses to presentation of visual imperative stimuli (subject F.O.). **A** Upward saccades following inverted "T" presentation. Four situations are illustrated: the imperative stimulus was presented in the left upper box (A_1), right upper box (A_2), left lower box (A_3), and right lower box (A_4). *Left panels* saccadic trajectories, *calibration marks* = 1°. *Right panels* mean horizontal deviation of saccades for the condition indicated in the corresponding left panel. *vertical dashed lines* vertical trajectories with 0° deviation. *abscissa* horizontal deviation (positive numbers correspond to a deviation to the right, negative numbers to a deviation to the left), *ordinate* time elapsed from the moment of saccade initiation. **B** Downward saccades following normally oriented "T" presentation. Imperative stimulus presentation in the left upper box (B_1), right upper box (B_2), left lower box (B_3), and right lower box (B_4). Other conventions as in **A**

A_1

A_2

A_3

A_4

B_1

B_2

B_3

B_4
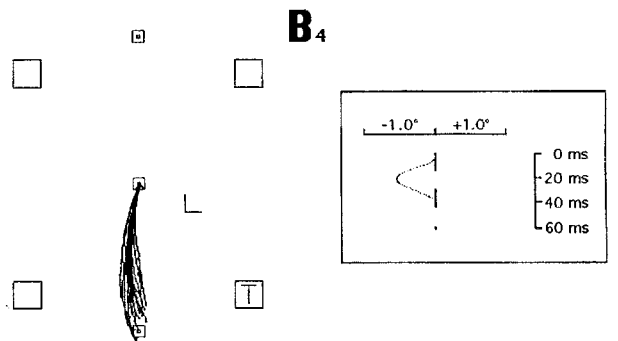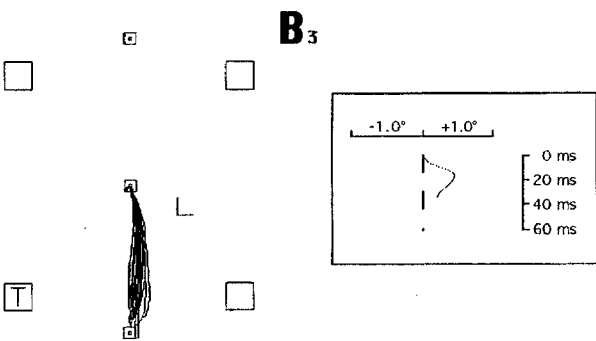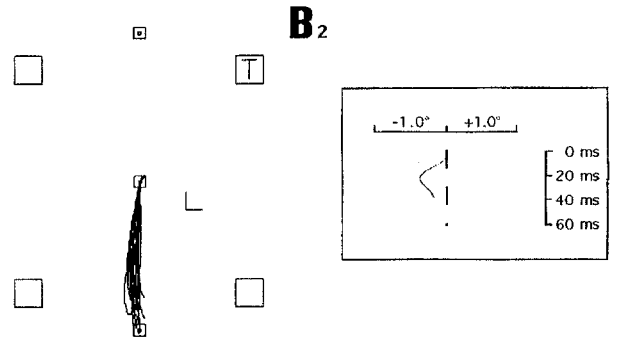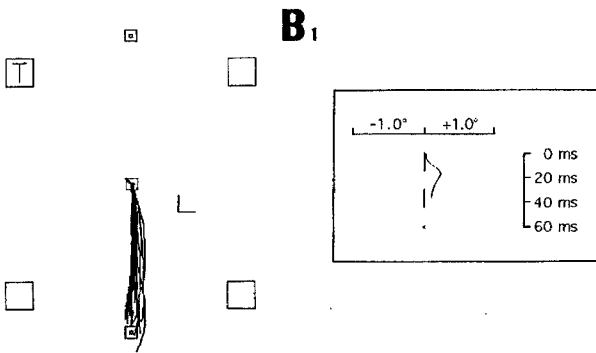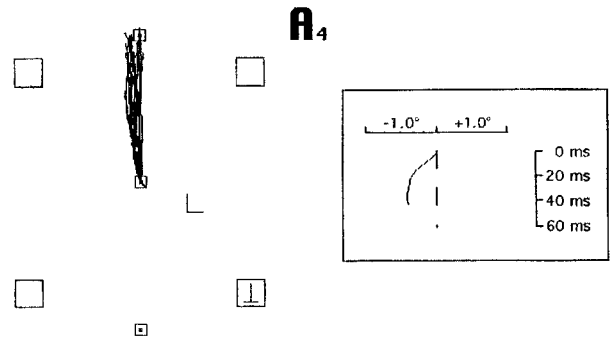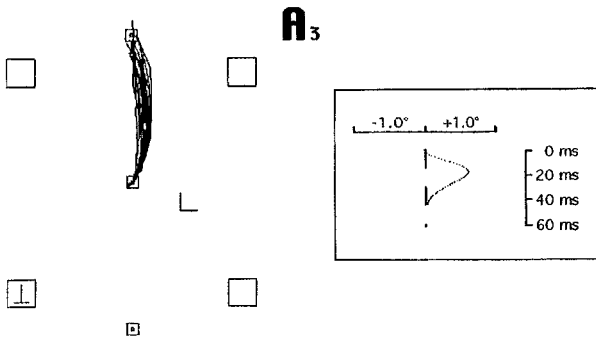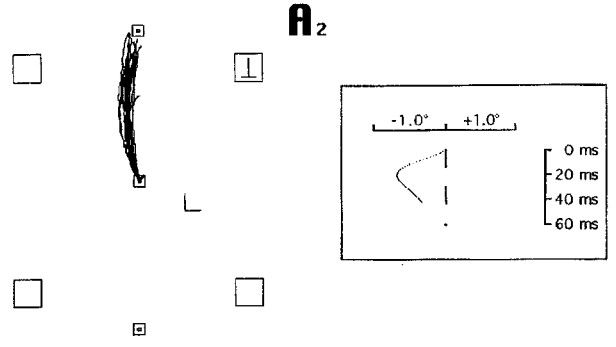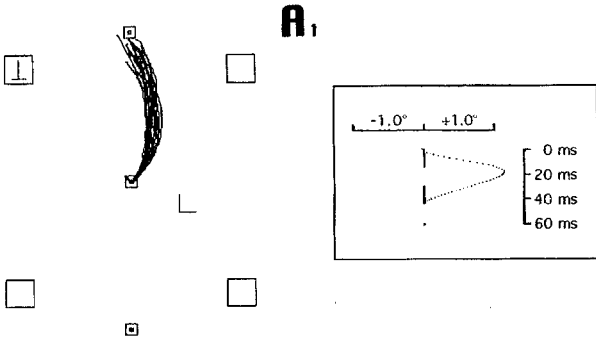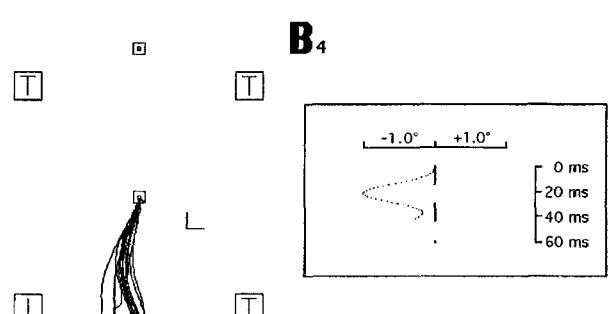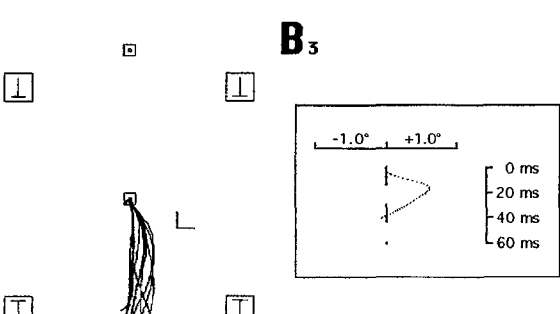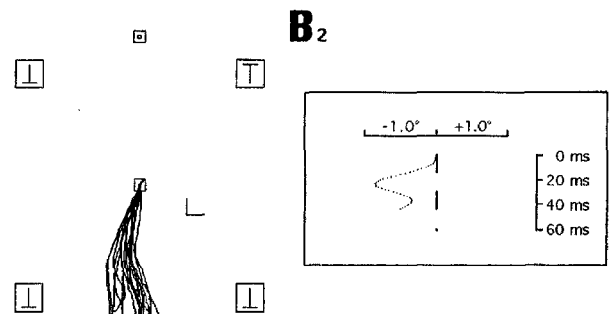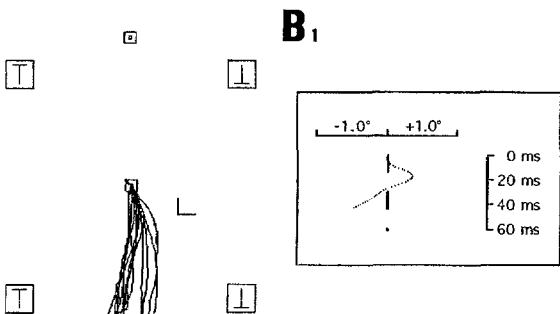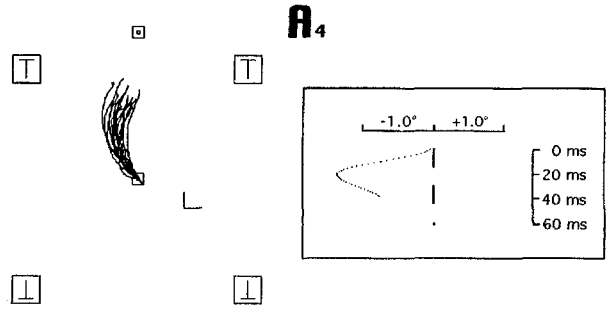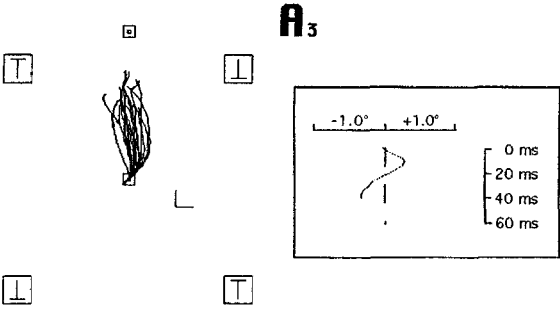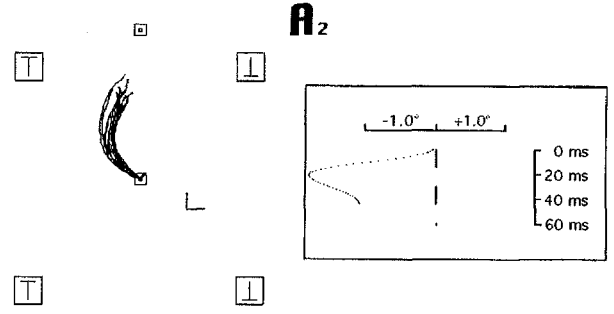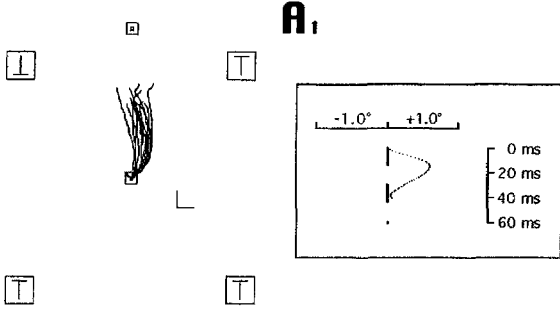
$(F(1, 9) = 87.2, \quad P < 0.001)$, Experiment $(F(2, 8) = 6.42, P < 0.05)$ – and four two-way interactions – Field $\times$ Side $(F(1, 9) = 23.0, P < 0.001)$, Experiment $\times$ Side $(F(2, 8) = 7.76, P < 0.05)$, Side $\times$ Direction $(F(1, 9) = 18.7, P < 0.005)$, and Field $\times$ Direction $(F(1, 9) = 15.4, P < 0.005)$ – were significant.
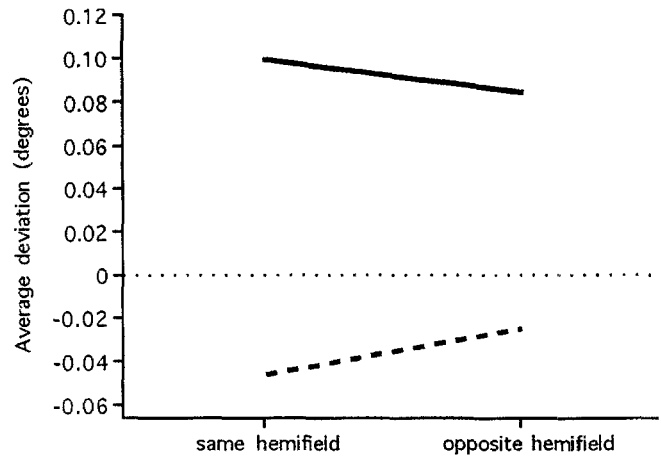
The effect of Side was due to the fact that saccades deviated to the left (0.035°) when the imperative stimulus was located in the right visual hemifield and to the right (0.093°) when the imperative stimulus was located in the left hemifield. Figures 5 and 6 illustrate these effects in experiments 2 and 3, respectively.

The significance of the Experiment factor is explained by the interaction Experiment $\times$ Side. When the imperative stimulus was presented to the left visual hemifield, there was a stronger rightward deviation of the saccadic trajectory in experiment 2 than in experiments 1 and 3 (0.104° vs 0.083° and 0.091°, respectively). The Bonferroni t-test showed that only the difference between experiments 2 and 1 was significant $(t(9) = 5.66, P < 0.05)$.

Of particular interest is the interaction Field $\times$ Side. This interaction resulted from the fact that the deviation contralateral to the imperative stimulus was greater in the "same hemifield" than in "opposite hemifield" condition. When the required saccade was directed downward, the contralateral deviation was greater when the imperative stimulus was located in the lower hemifield than when it was located in the upper hemifield. Conversely, when the required saccade was directed upwards the contralateral deviation was larger if the imperative stimulus was located in the upper hemifield. This result is illustrated in Fig. 7 (see also Figs. 5 and 6; compare A1 vs A3, A2 vs A4, B1 vs B3, and B2 vs B4).

The interaction Side $\times$ Direction resulted from a greater contralateral deviation of saccades directed upward with respect to those directed downward. Pos-hoc analysis showed, however, that the difference between saccade deviations was significant only when the imperative stimulus was located in the left hemifield.

Fig. 7 Mean horizontal saccade deviation following left imperative stimulus presentation (*continuous line*) and right imperative stimulus presentation (*interrupted line*) as a function of Field ("same hemifield" condition vs "opposite hemifield" condition). Negative values of horizontal deviation correspond to a leftward deviation, positive values to a rightward deviation. Note that the contralateral saccade deviation is greater in "same hemifield" condition than in "opposite hemifield" condition whether the imperative stimulus is presented to the left or to the right visual hemifield

Finally, the interaction Field $\times$ Direction was due to the fact that the difference between the deviation of upward and downward saccades was larger in the "opposite hemifield" condition than in the "same hemifield" condition $(t(9) = 3.92, P < 0.05)$.

Saccade y-component

MANOVA showed that only the main factor Direction $(F(1, 9) = 56.1, P < 0.001)$ and the interaction Side $\times$ Direction $(F(1, 9) = 22.4, P = 0.001)$ were significant.

Downward saccades were faster (273°/s) than upward saccades (212°/s). The Side $\times$ Direction interaction was significant because upward saccades were slightly faster when the imperative stimulus was presented to the left hemifield (215°/s) than when it was presented to the right hemifield (208°/s). The opposite was true for the downward saccades (270°/s vs 275°/s).

SRT/AD relationships

In order to evaluate whether there was a relation between the degree of saccade deviations and the length of the SRTs, we used the following procedure. For each experiment, we calculated the median values of SRTs in the eight basic stimulus-response combinations (four positions of the imperative stimulus $\times$ two directions of saccades). Trials of each stimulus-response combination were subdivided into two groups. Group 1 (g1) consisted of the trials having SRTs smaller than the median value of the examined stimulus-response combination; group 2 (g2) included the trials having SRTs larger than

Fig. 6A, B Experiment 3: saccadic responses following active (endogenous) orienting to visual imperative stimulus (subject B.N.) **A** Upward saccades following discrimination of inverted "T" inside the cued "stimulus" box. Four situations are illustrated: the imperative stimulus was located in the left upper box (A_1), right upper box (A_2), left lower box (A_3), and right lower box (A_4). *Left panels* saccadic trajectories, *calibration marks* = 1°. *Right panels* mean horizontal deviation of saccades for the condition indicated in the corresponding left panel. *vertical dashed lines* vertical trajectories with 0° deviation. *abscissa* horizontal deviation (positive numbers correspond to a deviation to the right, negative numbers to a deviation to the left), *ordinate* time elapsed from the moment of saccade initiation. **B** Downward saccades following discrimination of normally oriented "T" inside the cued "stimulus" box. Imperative stimulus presentation in the left upper box (B_1), right upper box (B_2), left lower box (B_3), and right lower box (B_4). Other conventions as in **A**

the median. All ADs of each combination were then attributed to either g1 or g2. Two median values of AD for each group were calculated, the first measuring the saccade deviation in the trials with short reaction time (g1), the second for those with long reaction time (g2). The AD medians of the eight conditions of each experiment were then averaged and the resulting two means, ADg1 and ADg2, used for statistical analyses (three paired t-tests, one for each experiment).

No significant difference was found between ADg1 and ADg2 in experiments 1 and 2 (0.059° vs 0.055°; $t(9) = 0.88$, n.s. for experiment 1 and 0.072° vs 0.066°; $t(9) = 1.62$, $P = 0.14$ for experiment 2). In contrast, in experiment 3, ADg1 was smaller than Adg2 (0.062° vs 0.071°; $t(9) = 2.57$, $P = 0.03$), thus indicating that saccades having short SRTs deviated contralateral to the side of the imperative stimulus less than the saccades with long SRTs.

Discussion

The present study confirms our previous findings showing that spatial attention modifies the trajectories of ocular saccades (Sheliga et al. 1994). If a subject's attention is focussed on a stimulus in the right hemifield, vertical saccades, directed to a target located above or below the fixation point, deviate to the left. In contrast, if attention is focussed on a stimulus in the left hemifield, the saccades deviate to the right. The contralateral deviation is observed both when attention is attracted passively by an abrupt stimulus presentation (experiment 1) and when it is moved actively (experiments 2 and 3).

In addition, the present data show that: (1) the contralateral deviation of vertical saccades is greater when the visual stimulus triggering the saccade is in the same (upper or lower) hemifield as the target for the saccade than when the visual stimulus and target for the saccade are in opposite hemifields; (2) when the location of the incoming stimulus is cued, SRTs are longer when the imperative stimulus is located in the same hemifield towards which the saccade is directed than when the imperative stimulus is located in the opposite hemifield; and (3) when cueing follows the imperative stimulus, the contralateral deviation is larger for saccades having longer SRTs than for saccades having shorter SRTs.

The following discussion will be focussed mainly on these three points. In particular, we will examine how the mechanisms responsible for ocular deviations, discussed in our previous articles (Rizzolatti et al. 1994; Sheliga et al. 1994), can accommodate the new data.
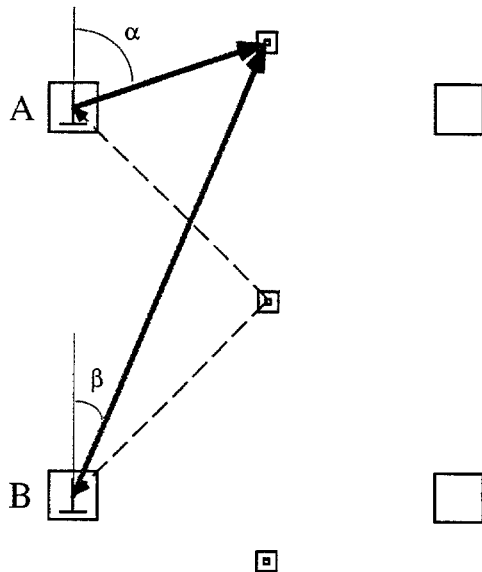
Saccadic deviation

An advantage of our experimental paradigm with respect to traditional manual reaction time experiments

consists in the fact that the studied responses – the ocular saccades – are spatially structured: they have direction and amplitude. By measuring these parameters, we found that when the imperative stimulus was in the hemifield (lower or upper) where the saccade had to be made ("same hemifield" condition), the deviation contralateral to the stimulus was larger than when the imperative stimulus and the target of the saccade were located in opposite hemifields ("opposite hemifield" condition).

We previously proposed two mechanisms which may explain the attention-determined saccade deviations (Sheliga et al. 1994). We named them remapping and suppression mechanisms, respectively. The idea of a remapping mechanism derives essentially from the findings of Duhamel et al. (1992) showing that visual neurons in the lateral intraparietal area (LIP) of the macaque monkey shift their receptive fields before an eye movement. The direction and amplitude of this shift was such as to anticipate the retinal consequences of the intended movements (see also Segraves and Goldberg 1987). According to the remapping mechanism hypothesis, the presentation of an imperative stimulus, as well as the mere stimulus expectancy, determines a shift of space representation towards the stimulus location in the oculomotor centers. A left stimulus, be it presented or expected, demands a saccade to the left and causes a shift of the space representation to the left. A right stimulus causes a shift in the opposite direction. When, eventually, the command to move the eyes is issued, the eyes are physically on the fixation point, but for the oculomotor system they are shifted toward the stimulus. The oculomotor system computes, therefore, erroneously the remapped eye position. This error is responsible for the contralateral deviation.

The remapping mechanism can easily account for the difference in the saccade deviation between the "same hemifield" and "opposite hemifield" conditions observed in the present experiments. This is graphically illustrated in Fig. 8, where two conditions are shown. In the first, the imperative stimulus is presented in the upper left stimulus box (A), in the second it is presented in the lower left stimulus box (B). In both cases the required response is an upward saccade toward the "target" box. The two movement vectors which the remapped fovea has to perform in order to reach the target, are shown by the two thick arrows joining A and B with the target box, respectively. With respect to the vertical axis, the angle formed by the vector starting in A is larger than the angle formed by the vector starting in B ($\alpha > \beta$). As consequence, the contralateral saccadic deviation in A, i.e., in the "same hemifield" condition, should be greater than in B, "opposite hemifield" condition. This is exactly what was found experimentally. It is important to stress, however, that the remapping hypothesis postulates a shift of the remapped fovea towards the stimulus location,

Fig. 8 Graphical representation of the remapping hypothesis accounting for the difference in the amount of saccadic deviation between the "same hemifield" and "opposite hemifield" conditions. Two situations are illustrated: in the first the imperative stimulus is presented in the left upper "stimulus" box (*A*), in the second it is presented in the left lower "stimulus" box (*B*). In both cases the imperative stimulus demands an upward saccade. The presentation of the imperative stimulus in *A* or *B* causes the remapping of the internal representation of the fovea toward the two locations (*dashed line vectors*). The movement vectors, which the remapped fovea has to perform in order to reach the "target" box, are shown by *two thick line vectors* joining the two "stimulus" boxes with the "target" box. The angle formed by the vector starting in *A* is larger than the angle formed by the vector starting in *B* ($\alpha > \beta$). As a consequence, the contralateral saccade deviation to reach the target should be greater in the "same hemifield" condition than in the "opposite hemifield" condition

but not its having reached the location. It predicts, therefore, different saccade deviations when attention is allocated to different spatial locations, but not the exact value of these deviations.

In addition to saccade horizontal deviations of different magnitude, the schema of Fig. 8 suggests also a difference in the saccade amplitude according to the position of the remapped fovea. Namely, the saccade amplitudes should be shorter when the remapped fovea is in A than when it is in B. This effect was not found. The lack of differences in the saccade amplitude could be due to an "in flight" correction due to a visual feedback from the target or, alternatively, to the fact that, since the required amplitude of the saccade was the same during all trials, its values were computed by the oculomotor system before the trials, regardless of the remapped fovea location. We are inclined to think that this latter interpretation is correct. First, if there was a late "in flight" amplitude correction, the peak velocity of the saccade should be higher in B than in A, because of an initial programming of a greater amplitude saccade. This was not found. Second, in a preliminary study the location of the "target" boxes was made less predictable, so that they could appear in two

locations, one close and one far from the fixation point. In this experimental condition both amplitude and velocity were larger when the remapped fovea was in location B than when it was in location A.

An alternative mechanism which may explain the attention-determined saccade deviation is the so-called suppression mechanism. According to this mechanism, the occurrence of the imperative stimulus is accompanied by an inhibition of orienting responses toward the side of the imperative stimulus presentation. The inhibition is determined by the instructions to keep the eyes still and not foveate toward the imperative stimulus. As a consequence, the cortical command to move the eyes vertically in response to this stimulus, finds a different excitability state in the ipsilateral and contralateral superior colliculus (SC) and in the two frontal eye fields (FEF). It is this difference in oculomotor center excitability which determines the observed contralateral saccade deviation.

How can this mechanism explain the "field" effect? If one conceives the suppression mechanism as a diffuse inhibition of the SC responsible for the orienting reaction, it is obvious that the differential effects on saccade trajectory of stimuli in the "same hemifield" and "opposite hemifield" conditions cannot be accounted for by the suppression mechanism. However, a diffuse SC inhibition is not a necessary assumption of the suppression hypothesis. Physiological evidence indicates that stimuli presented outside the classical neuron's receptive field, but not far from it, can have a strong inhibitory effect on neuron responses in the oculomotor centers. This effect was found in the SC of the cat and monkey (Rizzolatti et al. 1974; Wurtz et al. 1980) and, more recently, in a behaviorally more complex situation by Schall in the FEF of the monkey (Schall and Hanes 1993). These findings suggest that the imperative stimulus produces, concomitantly with the excitation of neurons spatially related to it, an inhibition of the oculomotor neurons located near its locus of presentation. Thus, when the imperative stimulus is presented to the upper visual field, the inhibition should primarily affect the upper visual field representation, whereas when the imperative stimulus is presented to the lower visual field, the lower visual representation should be more affected. As a consequence, the saccade deviation contralateral to the imperative stimulus should be larger in the "same hemifield" condition than in the "opposite hemifield" condition because the inhibition of the SC due to the inhibition of orienting responses summates to the inhibition caused by the imperative stimulus presentation, and this last inhibition is stronger near the locus of the imperative stimulus presentation than far from it. It is important to stress that, while this version of the suppression hypothesis explains well the results of the first two experiments (in which the imperative stimulus was phasically presented), it explains less well the results of the third experiment, where the imperative stimulus was in the

field of vision from the beginning of the trial. As far as we know there are no physiological data on neuron activity in such a behavioral situation. The presence of an inhibitory mechanism related to the imperative stimulus is, therefore, in the case of the third experiment purely hypothetical.

Saccadic reaction times

The present findings showed that the SRTs of experiment 2 differed from those of the other two experiments in two respects. First, in experiment 2 they were significantly faster than in both experiment 1 and experiment 3. Second, only in experiment 2 were the SRTs in the "same hemifield" condition significantly longer than those in the "opposite hemifield" condition. Before discussing the possible reasons for these differences, let us briefly consider the cognitive processes occurring in the three experiments.

All the experiments began with attention located on the fixation point. In experiment 1 at the imperative stimulus presentation, the following processes started: (a) an automatic orienting of attention toward the imperative stimulus, (b) the suppression of an overt orienting reaction toward the stimulus, (c) the discrimination of the imperative stimulus, (d) the programming of a voluntary saccade toward the target location. In experiment 2, the subjects were cued as to where in the display the imperative stimuli were going to appear. Thus, in addition to the four processes occurring in experiment 1 there was a fifth one: following cue presentation, the subjects actively (endogenously), oriented their attention to the location of the impending imperative stimulus. In experiment 3, the imperative stimulus was present in the display from the beginning of the trial. Therefore the automatic orienting of attention, determined by the imperative stimulus presentation, was absent in this experiment. The processes taking place in this experiment were: (a) a voluntary orienting toward the imperative stimulus, (b) the imperative stimulus discrimination, (c) a programming of the saccade toward the location indicated by the imperative stimulus.

From this brief review of the processes occurring during the three experiments, it appears clear that what differentiates experiment 2 from the others is that only in this experiment were the subjects able to predict the imperative stimulus location and focus their attention on it before stimulus presentation. This expectancy of the imperative stimulus was absent in experiments 1 and 3, instead in these experiments attention moved toward the imperative stimulus after its appearance, either as a result of its presentation (experiment 1) or as a consequence of a cue indicating where in the display the effective imperative stimulus was located (experiment 3). Expectancy can easily explain the rapidity of SRTs in experiment 2. Since in this experiment

attention was at the imperative stimulus location when the imperative stimulus was presented, no time was spent shifting attention to it from the fixation point. An additional factor that may have contributed to the rapidity of the SRTs in experiment 2 is that this experiment was the only one devoid of the dual task requirements present in experiments 1 and 3. Note, however, that in none of these experiments was there a requirement for fast manual responses. We are inclined, therefore, to think that dual task effect played only a minor role, if any, in delaying the experiment 1 and 3 SRTs.

Expectancy is also most likely responsible for the fact that in experiment 2, the SRTs in the "same hemifield" condition were longer than those in the "opposite hemifield" condition. According to the premotor hypothesis of attention (Rizzolatti et al. 1987; Umiltà et al. 1991, 1994) stimulus expectancy in a spatial location is due to the setting of an oculomotor program toward that location. If this is accepted, the experimental situation of experiment 2 can be described as characterized by the simultaneous presence of two motor programs, one underlying expectancy and a second one predetermined by the verbal instructions to generate saccades toward the target. We propose that the difference between "same hemifield" and "opposite hemifield" SRTs is due to the interference between these two concomitant motor programs, with the corollary assumption that motor program interference is greater when the similarity between them is closer.

The main point of our proposal, i.e., that two tasks that have to be executed simultaneously or in rapid serial order interfere (except in particular conditions, see Allport et al. 1972) one with another is beyond dispute (Welford 1952; Kahneman 1973; Keele 1973; Pashler and Johnston 1989; McCann and Johnston 1992; Pashler 1992). Thus, the presence in experiment 2 of two motor tasks, one internally generated, the other determined by the imperative stimulus, must produce interference.

There is also evidence in the literature, albeit less rich, in favor of the second point of our proposal, i.e., that the degree of interference is influenced by the similarities of motor tasks. In a number of dual task studies in which one task involved mostly one cerebral hemisphere, Kinsbourne showed that speech produces lateralized interference on activities of the right, but not the left hand (see Kinsbourne and Hiscock 1983 for review). He proposed that the verbal-manual interference is a special case of a conflict between two activities that are close in "functional cerebral space". Thus, speech interferes more with right than left hand activities because the speech areas are functionally closer to cortical areas that program right hand movements (Lempert and Kinsbourne 1985).

Evidence of a selective interference between left hemisphere tasks and the capacity of this hemisphere, but not of the right hemisphere, to translate a visual stimulus in an elementary manual response was

demonstrated by Rizzolatti and colleagues (1982). They measured simple reaction times to lateralized unstructured visual stimuli while subjects were carrying out a concomitant left hemisphere task. They found that during verbal cognitive tasks (counting backward) and praxic tasks (complex hand tapping) there was a significant disadvantage for the left hemisphere in responding to stimuli, regardless of the responding hand. They concluded that during praxic or speech activity simple motor responses mediated by the left hemisphere were delayed because they shared common neural substrates with verbal and praxic left hemisphere centers.

In addition to evidence from lateralized studies showing that interference is greater if the two tasks are functionally closer, data from stimulus-response compatibility experiments (Fitts and Seeger 1953; Fitts and Deininger 1954) indicate that it is more time-consuming to inhibit a response similar to that which has to be executed than another one less similar to it. For example, Kornblum tested subjects in a two-choice reaction time experiment in which the stimuli were two lights (presented to the left and to the right of the fixation) and the responses consisted in depressing the appropriate one of two keys (Kornblum 1965). In the "ipsilateral condition" of the experiment, the response was made with either the index or the middle finger of the right hand; in the "contralateral condition" the response was made with either the index finger of the left hand or the middle finger of the right hand. It was found that the mean reaction times for the "ipsilateral condition" were 28 ms and 16 ms longer than for the "contralateral condition" for the middle and index finger data, respectively. Although these data on the interference between motor programs, by no means prove the validity of our explanation of the results of experiment 2, nevertheless they clearly provide good evidence in favor of its plausibility.

An important question which arises at this point is why the amount of saccadic deviation observed in "same hemifield" condition is larger than that observed in "opposite hemifield" condition in all three experiments, while in the case of SRTs this "hemifield" effect is found only in experiment 2. Our interpretation is that the deviation phenomena depend on the activity of the oculomotor mechanisms related to the orienting toward a stimulus present in the display as well as on those related to stimulus expectancy (Sheliga et al. 1994), whereas the "hemifield" effect on SRTs depends exclusively on mechanisms underlying stimulus expectancy. A distinction between expectancy and exogenous orienting mechanisms have been made on a number of grounds. For example, exogenous orienting is not sensitive to a secondary verbal-memory task, that disrupts endogenous orienting (Jonides 1981). Exogenous orienting is poorly sensitive to interruption by subsequent visual events (Muller and Rabbitt 1989). Exogenous orienting is faster than the endogenous one

(Yantis and Jonides 1984; Muller and Findlay 1988; Spencer et al. 1988; Muller and Rabbitt 1989) and when caused by an uninformative cue produces not only a facilitatory effect (Posner and Cohen 1984), but also a subsequent inhibition (inhibition of return: Posner and Cohen 1984; Maylor 1985; Maylor and Hockey 1985; Possamai 1986; Tassinari et al. 1987; Berlucchi et al. 1989). Expectancy produces the so-called vertical meridian effect, i.e., an extra cost that subjects pay when attention crosses the horizontal or vertical meridian (Downing and Pinker 1985; Hughes and Zimba 1985, 1987; Rizzolatti et al. 1987; Tassinari et al. 1987; Umiltà et al. 1991; Reuter-Lorenz and Fendrich 1992). Such an extra cost is not observed with exogenous orienting (Egly and Homa 1991; Umiltà et al. 1991; Reuter-Lorenz and Fendrich 1992; Henderson and Macquistan 1993).

It is very likely that exogenous orienting and expectancy are mediated by different neural circuits. Exogenous orienting relies mostly on structures, such as the SC or the FEF, which transform visual stimuli into oculomotor commands. When instructions prevent overt orienting, it is still the activity of these centers which give salience to the presented stimuli. Evidence in favor of a role of the SC in exogenous orienting was provided by Rafal et al. (1989). Expectancy, in contrast, appears to be based on the activity of centers such as the caudate nucleus and the substantia nigra, pars reticulata (SNr), that tonically modulate the activity of the SC (Hikosaka and Wurtz 1983a, b; Hikosaka et al. 1989a,b). When a stimulus is expected in a given location, a cortical motor program is set that disinhibits, via caudate and SNr, the SC neurons of intermediate and deep layers related to the expected space position. The increase in firing of these neurons facilitates the collicular superficial neurons (Wurtz and Mohler 1976). As a consequence, the superficial neurons allow a better detection of the stimuli, while the deeper (premotor) collicular neurons provide an increase in the readiness to respond when the expected stimulus occurs (for a more extensive discussion of these mechanisms see Rizzolatti et al. 1994).

Finally, it is important to stress that the experimental condition and the results of experiment 3 indicate that the customary distinction between exogenous and endogenous orienting is not complete. In experiment 3 attention was moved endogenously, but, since the imperative stimulus was already displayed, there was no stimulus expectancy. The results were more similar to those of experiment 1 (no expectancy, exogenous orienting) than to those of experiment 2 (expectancy, endogenous orienting). It appears, therefore, that to use endogenous orienting of attention as synonymous with expectancy is incorrect. Our data suggest that in terms of mechanisms, a distinction between conditions in which there is expectancy and those in which there is not is as fundamental as that based on how attention movements are generated.

Relationships between SRT and saccadic deviation

Although saccadic reaction time and saccadic deviation are both related to attentional mechanisms, the factors controlling them are not identical. Saccadic deviation depends essentially on the intensity of attention engagement. Clear evidence in favor of the dependence of saccadic deviation on attention strength was provided by our previous experiments (Sheliga et al. 1994). In those experiments, we found that deviation was larger when the subjects had to perform a difficult detection task (experiments 2 and 3) than when they had to perform an easy one (experiment 1). Furthermore, when the subject expected and received the stimulus in the same hemifield, the deviation was stronger than when he expected the stimulus in one hemifield but received it in the opposite one (Sheliga et al. 1994; experiment 1). These findings were confirmed by the present experiments showing that the greater attentional demands related to the presence of a discriminative task resulted in saccade deviations larger than those observed in the previous experiments.

Unlike saccade deviation, reaction time depends on several factors. Among them, besides attention engagement, particularly important are the location of attention at the moment of stimulus presentation, and the time employed by attention to reach the imperative stimulus. Accordingly, in the present study the reaction times were faster in experiment 2, in which attention was already on the target at the moment of the imperative stimulus presentation. They were intermediate in experiment 1, where the imperative stimulus exogenously triggered attention shift, and were the slowest in experiment 3, where a central cue determined the movement of attention. The differential time course of orienting in response to peripheral (exogenous) and central cues is in agreement with previous data (e.g., Yantis and Jonides 1984; Muller and Findlay 1988; Muller and Rabbitt 1989).

Given these premises, let us examine which relations between reaction time and saccadic deviation one may predict for the three experiments of the present study. For experiment 1, there is no obvious reason to find an interdependence between the SRTs and saccade deviation. Whereas SRTs strongly depend on the time necessary to shift attention from the fixation point to the imperative stimulus, this factor does not play any role in determining the magnitude of saccadic deviation. In contrast, in experiment 2, in which attention is already on the imperative stimulus location, the strength of attention engagement should influence both factors, increasing the saccadic deviation and shortening the SRTs. The results basically confirmed these predictions. No relation was found between SRTs and saccadic deviation in experiment 1, whereas there was a trend for a (negative) correlation between the two factors in experiment 2.

The prediction for experiment 3 is similar to that for experiment 1. Since the saccade deviation depends on attention engagement, while the SRTs depend on the time in which attention arrives at (or near to) the imperative stimulus, no correlation between the two phenomena should be observed. The results did not confirm this prediction. Surprisingly enough, they showed that SRTs positively correlated with saccadic deviation, being long when the saccadic deviation was large and short when the saccadic deviation was small. From these data, it appears that another factor played a role in determining the relationship between these two factors.

A possibility is that the discrimination of the imperative stimulus was achieved not when attention was on the imperative stimulus, but when it was still at a certain distance from it. If this is accepted, the data could be easily accommodated by the remapping hypothesis. If the saccade was programmed when attention was somewhere between the fixation point and the stimulus, this should have caused a short reaction time, because only a small part of the trajectory towards the imperative stimulus was made, as well as a smaller deviation, because the remapped fovea moved a smaller distance toward the imperative stimulus.

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