RESEARCH ARTICLE

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Effects of spatial attention on directional manual and ocular responses

Abstract The aim of the present study was to investigate how spatial attention influences directional manual and saccadic reaction times. Two experiments were carried out. In experiment 1 subjects were instructed to perform pointing responses toward targets that were located either in the same or the opposite hemifield with respect to the hemifield in which an imperative stimulus was presented. In experiment 2, they were instructed to make saccadic or pointing responses. The direction of the responses was indicated by the shape of the imperative stimulus. Reaction time (RT), movement time, and, in experiment 2, saccadic trajectory were measured. The imperative stimulus location was either cued (endogenous attention) or uncued. In the latter case the imperative stimulus presentation attracted attention (exogenous attention). The main results of the experiments were the following: First, exogenous attention markedly decreased the RTs when the required movement was directed toward the imperative stimulus location. This directional effect was much stronger for pointing than for ocular responses. Second, endogenously allocated attention did not influence differentially RTs of pointing responses directed toward or away the attended hemifield. In contrast, endogenous attention markedly favored the saccadic responses when made away from the cued hemifield. Third, regardless of cueing, the direction of movement affected both pointing and saccadic reaction times. Saccadic reaction times were faster when the required movement was directed upward, while manual reaction times were faster when the movement was directed downward. Fourth, lateralized spatial attention deviated the trajectory of the saccades contralateral to the attention location. This pattern of results supports the notion that spatial attention depends on the activation of the same sensorimotor circuits that program actions in space.

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Introduction

Traditionally, attention is conceived as a unitary, supramodal mechanism subserved by anatomical circuits separated from those involved in data processing (Klein 1980; Posner 1980; LaBerge and Brown 1989; Rafal et al. 1989; Posner and Petersen 1990; Klein et al. 1992). A modern version of this theory postulates the existence of two attentional systems: a posterior system subserving spatial attention and an anterior one involved in the attentional recruitment and control of brain areas in order to perform complex cognitive tasks (Posner and Dehaene 1994).

The necessity, however, of neural systems specifically devoted to attention is under dispute. An alternative possibility is that attention derives from an activation of those same circuits that process sensory and motor data. Thus, selective attention for spatial locations would result from the activity of circuits that program oculomotion, arm reaching movements, walking, and other motor activities that require spatial computation (Rizzolatti 1983; Rizzolatti and Camarda 1987; Rizzolatti et al. 1987, 1994; Umiltà et al. 1991, 1994; Tipper et al. 1992; see also Berthoz 1996), while selective attention for object recognition would derive from the activation of cortical areas responsible for object property processing (see Desimone and Duncan 1995; Duncan 1996).

While the mechanism proposed for object attention seems to be related to those for object analysis (Moran and Desimone 1985; Chelazzi et al. 1993), the mechanism for spatial attention appears to be related to processes responsible for the organization of movements in space (premotor theory of attention). According to this view, the difference between selective spatial attention and actions directed toward a target is that in the first case the motor plan to act upon the target is set but not executed, in the second case it is set and executed.

Evidence in favor of the premotor theory of attention derives from neurophysiological studies of cortical areas coding space (single-neuron recordings, ablation experiments) and from psychological studies on attention orienting. The outcome of the neurophysiological studies most relevant here is the discovery that some parietal and frontal cortical areas contain a representational system that relates spatial representation, action control, and attention (Colby et al. 1993; Rizzolatti et al. 1994; Graziano and Gross 1996; Graziano and Gross, in press). Ablation of these areas produces inattention (neglect) to a particular space sector. Inattention is accompanied by motor deficits concerning the effectors represented in the ablated area and movements directed toward the space represented in it (Rizzolatti et al. 1983). The cortical areas programming spatially specific movements are controlled by other cortical areas (e.g., pre-supplementary-motor area, pre-SMA) and by subcortical centers (e.g. basal ganglia). When the control exerted by these centers is released, movement occurs. Without such a release, the portion of spatial map activated by the intended movement gains advantage on all other space locations. This motor determined spatial activation in what is, at another level of description, referred to as spatial attention (see Rizzolatti et al. 1994).

Psychological evidence in favor of the premotor theory comes from reaction time (RT) studies on attention reorienting. From these studies it appears that, when human 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; Gawryszewski et al. 1992; Reuter-Lorenz and Fendrich 1992) is difficult to explain if attention is not related to motor programming, while it becomes an expected event if one accepts that oculomotor programming underlies attention orienting.

Further evidence in favor of premotor theory of spatial attention is provided by experiments in which subjects were instructed to make vertical saccades toward a predetermined target while their attention was allocated to different positions in space (Sheliga et al. 1994, 1995a). The results showed a deviation of saccades contralateral to the hemifield to which attention was allocated. Similar results were recently obtained also for horizontal saccades (Sheliga et al. 1995b).

Another important finding of those experiments was that saccadic RTs depended on where attention was allocated at the time of imperative stimulus presentation (Sheliga et al. 1995a). When it was located in the same hemifield toward which the saccade was directed, the RTs were longer than when it was located in the opposite hemifield.

These results were interpreted as follows. Subjects in order to pay attention to the imperative stimulus location must set a motor program for covertly directing the eyes toward it. This "attentional" motor program interferes with the subsequent motor program necessary for saccade generation. The interference between the two motor programs causes modifications both in saccade trajectories and RTs. The literature shows that two motor tasks, when executed simultaneously or in a rapid serial order, interfere one with another (Welford 1952; Kahneman 1973; Keele 1973; Pashler and Johnston 1989; McCann and Johnston 1992; Pashler 1992) and that the degree of this interference is greater when the similarity is greater between motor tasks (Fitts and Seeger 1953; Fitts and Deininger 1954; Kornblum 1965; Rizzolatti et al. 1982; Kinsbourne and Hiscock 1983; Lempert and Kinsbourne 1985). Accordingly, the longer reaction times when the changes in motor program were within one visual hemifield were accounted for by the greater similarity between concomitant oculomotor programs in "same hemifield" than in the "opposite hemifield" conditions.

In the present experiment we compared the effect of spatial attention on manual (pointing) and ocular (saccadic) responses in an experimental condition that required a visual discrimination of a peripheral stimulus. According to the classic theories of attention, since attention is a supraordinate function, it should influence the two motor responses in the same way. In contrast, according to the premotor theory of attention, since attention derives from planning of different motor activities, its properties would depend on the type of motor activity that is planned. The task of the present experiment, if freely executed, would have produced foveation. Attention, therefore, according to premotor theory, should be mediated in this case by the oculomotor system. Attention mechanisms related to arm movements (Tipper et al. 1992; Chieffi et al. 1993; Jackson et al. 1995) should play only a marginal role, if any. The results showed a differential effect of attention on saccadic and pointing RTs. The predictions of the premotor theory were therefore confirmed.

Experiment 1

Materials and methods

Subjects

Six subjects (five men and one woman) participated in the experiment. They were all right-handed according to the Edinburgh Inventory (Oldfield 1971), had normal or corrected-to-normal vision, and except for two (authors of this study) were not aware of the purpose of the experiment. All subjects had previously participated in experiments involving attention orienting and eye movements.

Procedure

The experiments took place in a sound-attenuated room, dimly illuminated by an 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 38 cm.
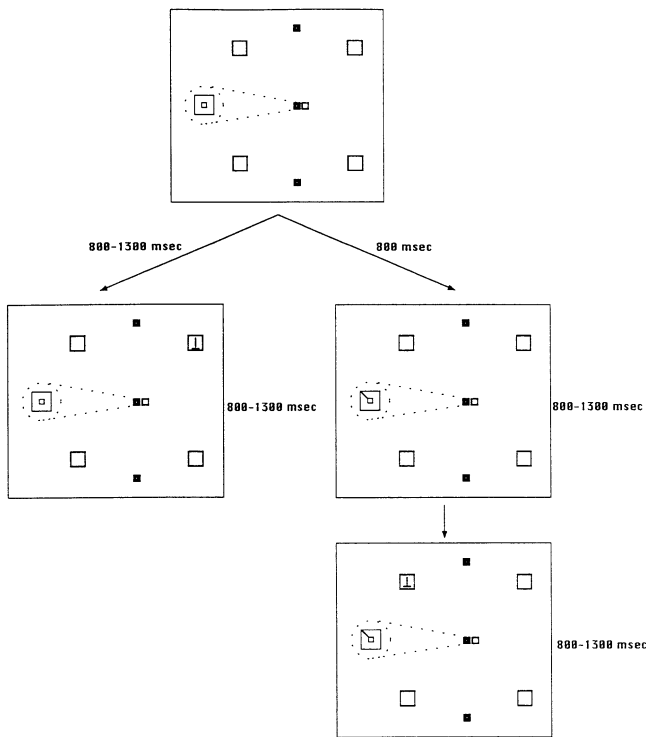
Fig. 1 Visual display and time sequence of events in experiments 1 and 2. The uncued condition is shown on the *left*, the cued condition is shown on the *right*. *Numbers* indicate the duration of the presentation of the various displays. The central, "fixation", box of each panel is represented enlarged (*the dashed lines and surrounding circles* show the enlarged representation) in order to provide a clear view of events occurring inside that box. For further explanations see text

All trials started with the presentation of the visual stimulus display (Fig. 1). The display contained four small boxes (0.9°×0.9°) and four large boxes (2.25°×2.25°). One small box, "fixation" box, was located at the geometric center of the screen. Another two small boxes, "target" boxes, were positioned 12° (center to center) below and above the fixation box. They served as targets for manual responses. The fourth small box, "start" box, was positioned immediately to the right of the fixation box (1.13°, center to center). The large boxes, "stimulus" boxes, were located at the angles of an imaginary square having the fixation box as its center. The horizontal and vertical eccentricity of the stimulus boxes from the fixation box was 9°. The stimulus boxes indicated the possible positions in which the imperative stimulus could appear. The imperative stimulus was the letter "T" (horizontal line 1.2°; vertical line 1.5°), which was presented either normally oriented or inverted. Normally oriented and inverted Ts required responses to the lower or upper target box, respectively.

Following visual display presentation, the subjects, when ready, placed their right index finger on the start box, initiating in this way the trial sequence. On their index finger was attached a microswitch. The contact between the microswitch and the screen started the trial. The microswitch was connected to the computer by means of wires arranged in such a way as to not disturb arm movements. There were two experimental conditions:

A. Uncued imperative stimulus location. The subjects were instructed to fixate the central box of the visual display (Fig. 1) and to remain still, keeping their index finger on the start box, until the appearance of the imperative stimulus. After a variable interval (800–1300 ms) the imperative stimulus (a normal or inverted T) was presented inside one of the four stimulus boxes (Fig. 1, left). At the presentation of the imperative stimulus, the subject had to

point, as fast as possible, to the upper or lower target box, according to the imperative stimulus orientation, while maintaining fixation on the central fixation box.

B. Cued imperative stimulus location. The basic instructions were as in the uncued condition. Eight hundred milliseconds after the beginning of the trial, a directional cue was shown inside the fixation box (Fig. 1, right). The cue was an oblique, thin line (0.3°×0.06°). 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. 1, right). The subject was instructed to fixate the fixation box, to direct attention to the cued stimulus box without breaking fixation, and, at the imperative stimulus occurrence, to point to the upper or lower target box, according to the imperative stimulus orientation, while maintaining fixation on the central fixation box.

In both conditions, successive trials were separated by a pause of approximately 2–3 s. At the end of each 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.

Eye stability during the trial was controlled by recording eye movements with an infrared oculometer (Bach et al. 1983; for technical details see experiment 2). In the case of eye movements the trial was aborted and subsequently rerun.

Half of the subjects was tested in the uncued condition during the first session and in the cued condition during the second session. The other half of the subjects were tested in the two conditions in reversed order. Each session consisted of 20–25 initial practice trials, a series of eye movement calibration trials, and 160 correctly performed experimental trials. Thus, any stimulus-response combination: location of the imperative stimulus (four possible locations)×direction of manual response (up or down) was tested 20 times in each condition. The presentation order of the various stimulus-response combinations was randomized. Each session was subdivided into four blocks of 40 correctly performed trials, with some rest between the blocks.

Data collection and analysis

Manual reaction time and movement time

Both RT and movement time (MT) were measured. RT was considered the time between the imperative stimulus presentation and the onset of the arm movement (release of the microswitch). MT was considered the time between the onset of the movement and its end (contact of the microswitch with the screen following the arm movement).

Error handling

All types of errors except the one concerning the accuracy of manual responses were controlled on line by the computer. Three types of errors arose from inappropriate manual responding. They were: anticipations, retardations, and "opposite direction" errors. Anticipations were considered RTs shorter than 150 ms. Retardations were considered RTs longer than 600 ms. Opposite direction errors were responses directed opposite to the direction indicated by the imperative stimulus. The accuracy of movements was controlled visually by an experimenter, located behind the subject. All trials in which the direction of the responses differed from that indicated by the imperative stimulus were eliminated.

Another type of error ("eye movement" error) was that in which the subjects did not maintain fixation on the central box. All trials with errors, regardless of their type, were repeated.

Statistical evaluation of data

Manual response parameters (RT and MT) were subjected to two univariate analyses of variance (ANOVAs). ANOVAs were performed using median values. A logarithmic transformation was

performed upon RT data before subjecting them to the statistical analysis. Both ANOVAs had three within-subjects factors: (a) Condition (cued or uncued), (b) Direction (upward or downward), and (c) Field (response to the same or opposite field with respect to the field where the imperative stimulus was presented). Post hoc comparisons were made using Newman-Keuls test. The significance level was always set at 0.05.

Results

Table 1 shows the RTs recorded in the various experimental conditions. The statistical analysis performed upon the RTs showed that the main effect of Condition ($F_{1,5}=10.74$, $P<0.05$) and the two-way interaction Condition×Field ($F_{1,5}=33.7$, $P<0.005$) were significant. Condition was significant because RTs were faster in the uncued (384 ms) than in the cued condition (394 ms).

Figure 2 explains the significance of the Condition×Field interaction. In the uncued condition, RTs were faster ($P<0.005$) when the response was directed toward the hemifield in which the imperative stimulus occurred (same hemifield condition, 377 ms) than when it was directed toward the opposite hemifield (opposite hemifield condition, 391 ms). In the cued condition, RTs were the same in both the hemifields (same hemifield condition, 396 ms, opposite hemifield condition, 392 ms).

Concerning MT the only significant factor was Direction ($F_{1,5}=19.4$, $P<0.01$). Downward movements were faster (175 ms) than upward movements (210 ms).

Error analysis

Anticipations and retardations were rare (less than 1%). Eye movement errors were encountered in 6.1% of cases in the uncued condition and in 8.7% of cases in the cued condition. Opposite direction errors were present in 4.7% and 2.5% of cases in the uncued and cued condition, respectively.

Opposite direction and eye movement errors were subjected to two separate ANOVAs. In the case of opposite direction errors, Direction ($F_{1,5}=8.59$, $P<0.05$) and Field ($F_{1,5}=13.79$, $P<0.05$) reached significance. Wrong downward responses following presentation of an imperative stimulus indicating an upward movement were observed more frequently than wrong upward responses following presentation of an imperative stimulus indicating a downward movement. Opposite-direction errors
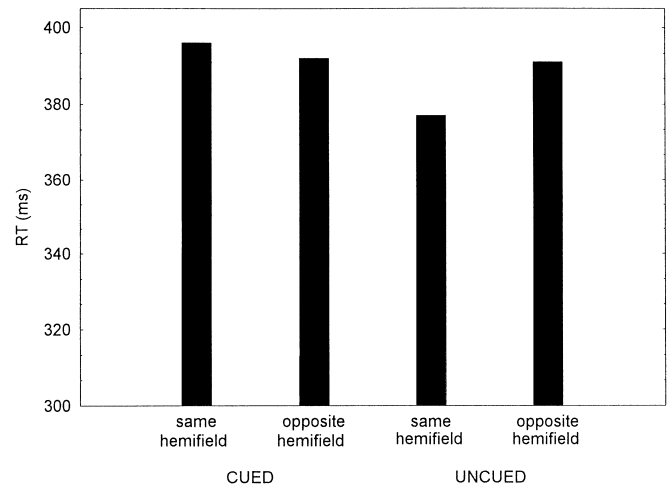

Fig. 2 Manual reaction times (*RT*) of experiment 1 as a function of Field (same hemifield vs opposite hemifield) and Condition (cued vs uncued). In the uncued condition the manual reaction times were faster in the same hemifield then in the opposite hemifield. In the cued condition there were no significant differences between the fields

were more frequent when the subject had to perform a movement to the target located in the hemifield opposite to that where the imperative stimulus was located than in the reverse case. No factor or interaction was significant for eye-movement errors.

Experiment 2

The pattern of results obtained in the first experiment was markedly different from that we had previously obtained with saccadic ocular responses in a rather similar paradigm (Sheliga et al. 1995a). In that experiment, ocular responses were faster with cueing than without it. Furthermore, in the cued condition saccades were slower in the same-hemifield condition than in the opposite-hemifield condition. Finally, in the uncued condition there was no difference between the same- and opposite-hemifield responses.

These results suggest that spatial attention influences ocular and manual responses in a different way. The aim of experiment 2 was to compare directly the effects of spatial attention on manual and ocular responses. To this purpose subjects were instructed to execute manual, ocular, and combined manual and ocular responses.

Table 1 Mean and standard error of manual reaction time for each of the eight conditions

| | Cued condition | | | | Uncued condition | | | |
| | Same hemifield | | Opposite hemifield | | Same hemifield | | Opposite hemifield | |
	Up	Down	Up	Down	Up	Down	Up	Down
Mean	410	382	398	387	381	373	396	386
SE	12.1	17.9	8.0	12.9	12.1	17.1	9.0	10.7

Materials and methods

Subjects

Eighteen subjects (15 men and 3 women) participated in the experiment. They were all right-handed according to the Edinburgh Inventory (Oldfield 1971), had normal or corrected-to-normal vision, and, except one, were not aware of the purpose of the experiment. Six subjects had previously participated in experiments involving attention orienting and eye movements. The other 12 were inexperienced subjects.

Procedure

The experimental setup and visual display were those of experiment 1. There were two experimental conditions: the uncued condition and the cued condition. The time sequence of events in the two conditions were the same as in experiment 1.

The experiment consisted of three blocks of trials, which differed according to the type of required response: (1) manual response (MR). This situation was a replica of the response situation of experiment 1; (2) saccadic response (SR), saccadic eye movement to the target box. The hand was positioned at the start box and remained still on it; (3) double response (MR+SR), movement of the hand and eyes to the target box. All three response situations were included in a single experimental session. They were run in blocks with the order of blocks randomized among subjects.

Subjects without previous experimental experience attended four sessions, two for practice and two for data collection, while the experienced subjects participated in only the two experimental sessions. The practice sessions were used to familiarize subjects with the experimental setup and to provide some training with the task. Half of the subjects ran first the uncued condition and then the cued one, while the other half ran the two conditions in reverse order. Each experimental session consisted of a series of eye movement calibration trials and of 288 experimental trials, correctly performed – 96 trials×three response types. Thus, any combination, location of the imperative stimulus (four possible locations)×direction of response (up or down), was tested 12 times in each response situation. For any given response situation, the presentation order of the various combinations was randomized.

Movements of the subjects' left eye were recorded continuously starting 500 ms after the moment of the stimulus display presentation (uncued condition) or at the moment of cue presentation (cued condition). The sampling rate was 1000 Hz. Eye stability during the time interval preceding the imperative stimulus presentation was controlled by a "spatial window" centered at the fixation box. Additionally, a control of possible horizontal drifts preceding saccadic responses was performed. To this purpose the position of the eyes 20 ms before the onset of the saccade was assessed and this position compared with that of the eyes at the moment when the continuous registration of eye movements began. No meaningful relation was found between the horizontal presaccadic drift and the saccadic deviation.

Data collection and analysis

Manual reaction time and movement time

Manual reaction time (MRT) and MT were measured as in experiment 1.

Saccadic reaction time and saccadic kinematic parameters

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

Saccadic 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 presentation gave the saccadic reaction time (SRT).

Horizontal saccadic 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

In addition to manual response errors (see experiment 1), three types of errors were related to inappropriate ocular responding. They were: anticipations, retardations, and opposite direction errors. Anticipations were considered SRTs shorter than 80 ms (see Werban-Smith and Findlay 1991). Retardations were considered SRTs longer than 600 ms. Finally, opposite direction errors were saccades directed opposite to the direction indicated by the imperative stimulus. All these types of errors were controlled on-line by the computer. The accuracy of the saccades was checked in an off-line analysis. Saccades with amplitudes lower than 6° or larger then 18° were rejected. Saccades directed toward visual imperative stimuli were also eliminated.

Statistical evaluation of data

MRT, manual MT, SRT, saccadic horizontal deviation, and saccadic y-component velocity were subjected to univariate ANOVAs. ANOVAs were performed using median values. A logarithmic transformation was performed upon RT data before subjecting them to ANOVA. Post hoc comparisons were made using Newman-Keuls test. The significance level was always set at 0.05.

Results

Reaction times

Tables 2 and 3 show the RTs of experiment 2. SRT and MRT data were submitted to two separate ANOVAs with four within-subject factors: (a) Condition (uncued or cued); (b) Mode (single-manual or saccadic only or double-manual and saccadic); (c) Field (response to the same or opposite field where the imperative stimulus had been presented); (d) Direction (upward or downward direction of the response).

Saccadic reaction times. The main effect of Direction ($F_{1,17}=17.1$, $P<0.001$) and two two-way interactions – Condition×Field ($F_{1,17}=16.84$, $P<0.001$) and Field×Direction ($F_{1,17}=13.73$, $P<0.01$) – were significant. Direction was significant because upward SRTs were faster (309 ms) than downward SRTs (325 ms).

Figure 3 shows the interaction Condition×Field. In the cued condition, same-hemifield condition SRTs (316 ms) were slower ($P<0.005$) than opposite-hemifield condition SRTs (308 ms). On the contrary, in the uncued condition, same-hemifield condition SRTs (318 ms) were

Table 2 Mean and standard error of saccadic reaction time (*SRT*) for each of the eight conditions and in both single and double conditions of response

SRT (ms)	Cued condition				Uncued condition			
	Same hemifield		Opposite hemifield		Same hemifield		Opposite hemifield	
	Up	Down	Up	Down	Up	Down	Up	Down
Eyes only								
Mean	311	313	295	320	314	324	317	336
SE	11.7	10.8	10.6	13.3	9.5	12.8	10.9	11.9
Eyes and hand								
Mean	316	325	294	324	313	323	311	336
SE	10.6	10.0	7.7	11.6	6.0	7.8	6.8	8.4

Table 3 Mean and standard error of manual reaction time (*MRT*) for each of the eight conditions and in both single and double conditions of response

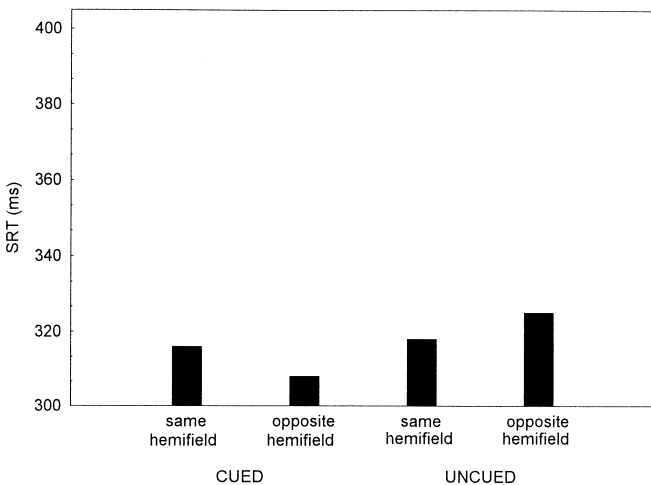| MRT (ms)	Cued condition				Uncued condition			
	Same hemifield		Opposite hemifield		Same hemifield		Opposite hemifield	
	Up	Down	Up	Down	Up	Down	Up	Down
Hand only								
Mean	398	379	392	396	386	368	393	397
SE	9.3	10.0	8.5	9.3	9.0	10.0	9.0	9.0
Hand and eyes								
Mean	407	387	402	399	391	379	404	406
SE	10.8	9.9	8.6	10.0	7.6	8.4	7.6	8.1

Fig. 3 Saccadic reaction times (*SRT*) of experiment 2 as a function of Field (same hemifield vs opposite hemifield) and Condition (cued vs uncued). SRTs in the cued condition were markedly slower in the same hemifield than in the opposite hemifield. In the uncued condition they were faster in the same than in the opposite hemifield
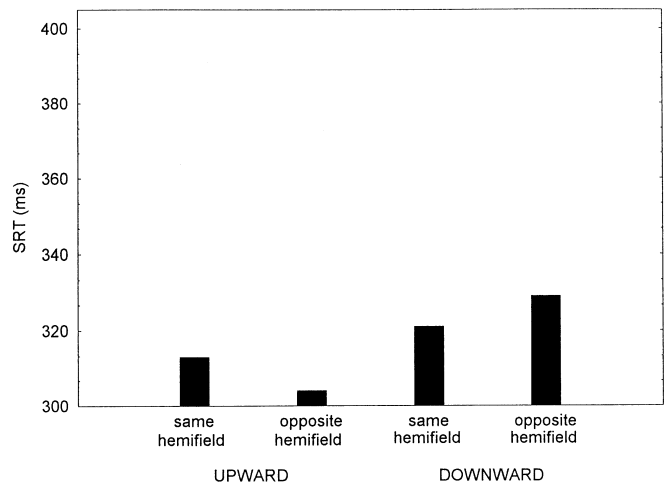
Fig. 4 SRTs of experiment 2 as a function of Field (same hemifield vs opposite hemifield) and Direction (up vs down). Upward SRTs were slower in the same hemifield than in the opposite hemifield. Downward SRTs were faster in the same hemifield than in the opposite

faster (*P*<0.05) than opposite-hemifield condition SRTs (325 ms).

The interaction Field×Direction is shown in Fig. 4. This interaction was significant because upward SRTs were slower (*P*<0.01) in the same-hemifield condition (313 ms) than in the opposite-hemifield condition (304 ms), whereas downward SRTs were faster (*P*<0.05) in the same-hemifield condition (321 ms) than in the opposite-hemifield condition (329 ms).

Manual reaction times. The main effects of Mode ($F_{1,17}$=5.96, *P*<0.05), Field ($F_{1,17}$=10.37, *P*<0.01) and Direction ($F_{1,17}$=4.83, *P*<0.05) and two two-way interactions – Condition×Field ($F_{1,17}$=10.5, *P*<0.01) and Field×Direction ($F_{1,17}$=42.59, *P*<0.001) – were significant.

Mode was significant because MRTs were faster in the single-response condition (388 ms) than in the double-response condition (397 ms). Note, however, that Mode did not interact with any of the other factors. Field
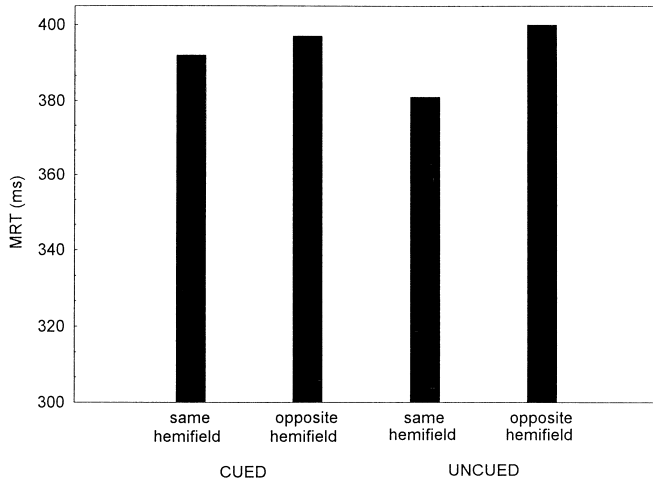
Fig. 5 Manual reaction times (*MRT*) of experiment 2 as a function of Field (same hemifield vs opposite hemifield) and Condition (cued vs uncued). MRTs in the uncued condition were faster in the same hemifield than in the opposite hemifield, while they were of approximately of the same value in the cued condition
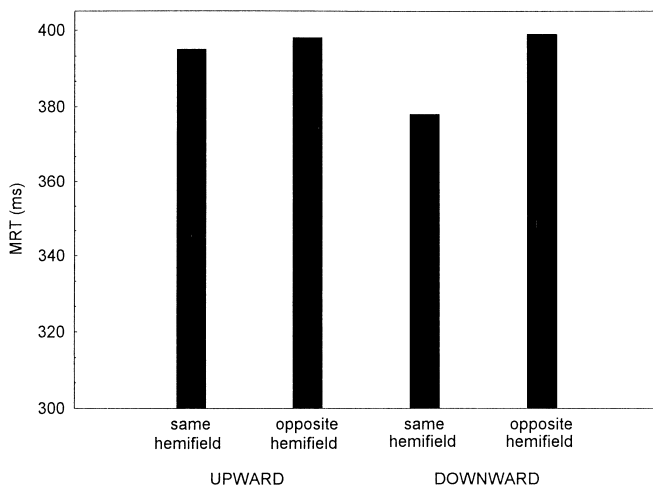

Fig. 6 MRTs of experiment 2 as a function of Field (same hemifield vs opposite hemifield) and Direction (up vs down). Downward MRTs were faster in the same hemifield than in the opposite hemifield. On the contrary, the difference between the same- and opposite-hemifield conditions was not significant in the case of upward MRTs

was significant because MRTs were faster in the same-hemifield condition (387 ms) than in the opposite-hemifield condition (399 ms). Direction was significant because downward MRTs were faster (389 ms) than upward MRTs (397 ms).

Figure 5 shows the interaction Condition×Field. In the uncued condition MRTs were faster ($P<0.001$) in the same-hemifield condition (381 ms) than in the opposite-hemifield condition (400 ms). On the contrary, in the cued condition, same-hemifield condition and opposite-hemifield condition MRTs did not differ (392 ms vs 397 ms).

The interaction Field×Direction is shown in Fig. 6. The interaction was significant because downward MRTs

were faster ($P<0.001$) in the same-hemifield condition (378 ms) than in the opposite-hemifield condition (399 ms). On the contrary, the difference between the same- and opposite-hemifield conditions was not significant in the case of upward MRTs (395 ms vs 398 ms).

Manual movement time

Manual MTs were submitted to an ANOVA with four within-subject factors: (a) Condition (uncued or cued); (b) Mode (MR or MR+SR); (c) Direction (upward or downward direction of the response); (d) Field (response to the same field as the imperative stimulus location or to the opposite one).

Field, Direction, and the two-way interaction Mode×Direction were significant ($F_{1,17}=11.2$, $P<0.01$; $F_{1,17}=28.09$, $P<0.001$; and $F_{1,17}=9.09$, $P<0.01$, respectively). The responses to the same-hemifield condition (229 ms) were faster than those to the opposite hemifield (231 ms); downward movements were faster (219 ms) than upward movements (241 ms); finally, downward movements accompanied by a saccadic response were longer (223 ms; $P<0.05$) than those without a concomitant saccade (215 ms), whereas upward movements were the same in both modes (MR, 240 ms; MR+SR, 241 ms).

Saccadic horizontal deviation

Saccadic horizontal deviations were analyzed using AD. Data were submitted to an ANOVA having five within-subject factors: (a) Side (left or right field location of the imperative stimulus); (b) Condition (uncued or cued); (c) Mode (SR or MR+SR); (d) Direction (upward or downward); (e) Field (response to same hemifield as the imperative stimulus location or to the opposite one).

The main effects of Side ($F_{1,17}=90.95$, $P<0.001$) and Direction ($F_{1,17}=7.79$, $P<0.05$), six two-way interactions – Side×Condition ($F_{1,17}=26.4$, $P<0.001$), Side×Mode ($F_{1,17}=5.83$, $P<0.05$), Side×Field ($F_{1,17}=52.53$, $P<0.001$), Side×Direction ($F_{1,17}=47.29$, $P<0.001$), Mode×Direction ($F_{1,17}=10.83$, $P<0.005$), and Field×Direction ($F_{1,17}=5.79$, $P<0.05$), – and two three-way interactions – Side×Mode×Field ($F_{1,17}=8.37$, $P<0.05$) and Side×Condition×Direction ($F_{1,17}=4.96$, $P<0.05$) – were significant.

The effect of Side was due to the fact that saccades deviated to the left (0.106°) when the imperative stimulus was located in the right visual hemifield and to the right (0.021°) when the imperative stimulus was located in the left hemifield (see, for similar results, Sheliga et al. 1994, 1995a,b).

The effect of Direction is explained by the interaction Side×Direction. This interaction resulted from larger contralateral deviations of saccades directed upward with respect to those directed downward.

The interaction Side×Condition was significant because the deviation contralateral to the imperative stimulus was larger in the cued condition than in the uncued condition.

The interaction Side×Mode was significant because, following the imperative stimulus presentation to the left visual hemifield, contralateral deviation of saccadic trajectories was smaller in MR+SR trials than in SR trials (0.015° vs 0.028°, respectively), while the presentation of the imperative stimulus to the right visual hemifield resulted in a virtually identical contralateral deviation in both types of trials (0.105° and 0.107°, respectively).

The interaction Side×Field was due to the fact that the deviation contralateral to the imperative stimulus was greater in the same-hemifield than in the 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 upward, the contralateral deviation was larger when the imperative stimulus was located in the upper hemifield (see, for similar results, Sheliga et al. 1995a,b).

Saccadic y-component

An ANOVA with the same factors as those for saccadic deviation data was performed upon the *y*-component peak velocity. The main effect of Direction ($F_{1,17}$=18.94, $P<0.001$) and the interaction Condition×Field ($F_{1,17}$= 18.99, $P<0.001$) were significant. Downward saccades were faster (318°/s) than upward saccades (255°/s).

The Condition×Field interaction was significant because in the uncued condition saccades were faster in the same-hemifield condition (293°/s) than in the opposite-hemifield condition (284°/s); whereas similar values (284°/s and 285°/s) resulted in the cued condition for responses directed toward the same and the opposite hemifield with respect to the imperative stimulus location.

Error analysis

Saccade anticipations, retardations, and accuracy errors occurred in 0.6%, 0.6%, and 1.9% of the cases, respectively, in the uncued condition, and in 1.6%, 0.9%, and 1.9% of the cases, respectively, in the cued condition. The rate of saccades wrongly directed toward the imperative stimulus was 0.1% in the uncued condition and 0.2% in the cued condition. A large number of errors were found during MR trials, that is in the condition in which the subjects have to move the hand, but not the eyes. These errors consisted in eye movements preceding or accompanying the hand movement. They were observed in 8.3% of cases in the uncued condition and in 12.2% of cases in the cued condition. An ANOVA showed that the difference in the rate of errors in the two conditions was significant.

Manual response anticipations and retardations occurred in 0% and 1.8% of cases, respectively, in the uncued condition, and in 0.2% and 1.7% of cases, respectively, in the cued condition. Hand movements toward the imperative stimulus were never observed. During SR trials, hand movements were erroneously executed in 2.4% of cases in the uncued condition and in 3% of cases in the cued condition.

Saccadic plus manual opposite-direction errors were present in 5.6% and 3.4% of cases in the uncued and cued conditions, respectively. A series of ANOVAs revealed that they were more frequently observed in the uncued condition than in the cued condition, that they occurred more often in the opposite-hemifield than in the same-hemifield condition, and that they were less numerous during MR trials than during the other types of trials.

Discussion

The assumption on the basis of the experimental paradigms usually employed in the studies of spatial attention is that the recorded motor responses (key pressing or releasing) are independent of the attentional processes under investigation. They are attentionally neutral and simply reflect how stimuli are processed.

Recent neurophysiological discoveries on the organization of the cerebral cortex and, in particular, on the strict link that exists in many parietal and frontal areas among spatial representation, attention, and action control (see Introduction) renders such an assumption rather dubious. It is certainly true that the relation between the examined attention phenomenon and the examined motor response may be in some cases very tenuous, or even absent. This, however, does not justify the claim that attention is not related to motor programming (see Klein 1980; Rafal et al. 1989; Klein et al. 1992; Klein and Pontefract 1994). If the neurophysiological data are correct, a link between spatial attention and motor programming should appear once attention is investigated, not in an abstract way using arbitrary responses as probes for attentional processes (i.e., key pressing), but using behaviorally relevant goal-directed actions. Under such conditions, attention should appear linked to motor responses and not any more "disembodied" from basic sensorimotor processes.

In the present experiments we studied spatial attention by asking subjects to make spatially directed motor responses. According to the imperative stimulus orientation, the response was directed toward or away from the imperative stimulus spatial location. Manual and ocular responses were investigated.

It is well known that, when responses are spatially directed, the speed of their onset depends crucially on whether there is correspondence between the spatial positions of the effectors and the targets (stimulus-response spatial compatibility; Fitts 1951; Fitts and Seeger 1953; Wallace 1971; Brebner 1973; Simon 1968, 1969; Nicoletti et al. 1982; Umiltà and Nicoletti 1985; Umiltà and Liotti 1987; Nicoletti and Umiltà 1989; Kornblum et al. 1990; Stoffer 1991; Stoffer and Yakin 1994; Hietanen and Räma 1995). Two main types of spatial compatibility are

usually distinguished: spatial compatibility proper and the Simon effect. In the case of spatial compatibility proper, the spatial position of the stimulus determines the direction of the subsequent response. In the case of the Simon effect, a nonspatial attribute of the stimulus indicates its direction. The spatial location of the stimulus, however, although irrelevant for responding, is processed and influences the response speed. In our experiments the stimulus orientation indicated the direction of the impending movement, while its spatial location varied. Our paradigm was therefore a paradigm analogous to those that produce a Simon effect.

In the first two sections of the following discussion, we will discuss our findings in relation to attention theories. We will try also to show that, by accepting the premotor theory of attention, it is possible to give a unitary, coherent interpretation of data that are traditionally discussed under the heading of spatial attention and of data dealt with in terms of spatial compatibility effect (Simon effect in particular). The two last sections will be devoted to the discussion of some specific motor aspects of our data.

Effect of passive (exogenous) and active (endogenous) attention on manual responses

As far as MRs are concerned, there are two main points that require discussion. The first is why exogenous attention strongly favored the responses congruent with attention focus. The second is why this effect was absent in the case of endogenous attention.

It is a classic finding that the abrupt occurrence of a stimulus evokes an orienting reaction accompanied by arousal and vegetative reactions (Pavlov 1927; Sokolov 1960). In our case, verbal instructions prevented movements. The imperative stimulus presentation determined, therefore, only a covert allocation of attention toward the stimulus. The fact that opposite-direction errors (responses in the direction of the imperative stimulus location but opposite to that required by its orientation) occurred significantly more frequently in the uncued than in the cued condition clearly indicates that attention (passive or *exogenous attention*) was attracted by the imperative stimulus.

The important finding was, however, not that attention was attracted by the imperative stimulus, but that the speed of RT was differently influenced according to whether the response was directionally congruent or not with the imperative stimulus location: RTs followed by a movement directed toward the stimulated hemifield were much faster than RTs followed by a movement in the opposite direction.

This finding is not easy to explain if one considers attention as something supramodal, disembodied from basic sensorimotor circuits. The logical sequence of events triggered by the imperative stimulus should be the following: (a) "disembodied" attention is attracted by the stimulus, (b) the stimulus is discriminated, (c) according to the stimulus orientation the appropriate response is emitted. There is no obvious reason why the disembodied attention should favor responses to one direction with respect to the opposite one. The disembodied attention should only "reach" the imperative stimulus and help in discriminating it. The fact that the movement that follows discrimination is congruent or not with the imperative stimulus location should not influence the RTs. In contrast, if one conceives passive attention as a consequence of the activation of a series of sensorimotor circuits (for reaching, eye movements, head movements, etc.) the facilitation of same-hemifield responses is the predicted event, because the primary function of these circuits is movement and movement implies direction. RTs congruent with the coded direction ought to be facilitated.

Disembodied attention, however, can be saved by adding some assumptions. One can postulate, for example, that, when attention is attracted passively, two processes start simultaneously: an attentional shift toward the stimulus location and an activation of sensorimotor circuits. The faster RTs toward the stimulated field are the consequence of the second process. Only the first, however, is attentional, the second is not. It belongs to the organization of movements. In our particular case it was due to stimulus-response compatibility and to the Simon effect specifically.

It is interesting that in the original paper describing the effect named after him, Simon suggested (1969) that the origin of the effect he observed was attentional. It reflects the natural tendency to orient toward the stimuli. Subsequently, Simon (1970; Simon et al. 1973) discarded his original proposal, because of some differences in habituation time between the Simon effect and the classic orienting reaction. The point of view, however, that the Simon effect is basically a reflexive shift of attention toward the stimulus location was maintained by Kahnemann (1973) and by Bauer and Miller (1982).

A series of recent studies provided strong support for an attentional interpretation of the Simon effect. Firstly, Nicoletti and Umiltà (1989) have shown that, when subjects are instructed to segment a series of six boxes in different groups by allocating attention to points between them, their RTs are faster whenever the imperative stimulus is on the same side as the position of the responding hand in relation to attentional focus. The Simon effect depends, therefore, on the position of the attentional focus. Secondly, the same authors (Nicoletti and Umiltà 1994) showed also that when attention, at the moment of the stimulus presentation, is anchored to a point close to the fixation point, the Simon effect disappears. Thirdly, Stoffer (1991) has demonstrated that the Simon effect is present when attention is summoned by two spatially separated, small boxes, in which, subsequently, stimuli are presented. However, when attention is summoned by a large box, in which identical stimuli to those of the previous condition are presented, the Simon effect disappears. The difference between the two conditions consists in the fact that with two boxes attention separates

the display into a left and right part, with one large box there is a single space, not subdivided into two sectors. Fourthly, and most importantly, Stoffer and Yakin (1994) have shown that a directional MR that depends on the shape of the presented stimulus shows the Simon effect when the subject cannot predict where the stimulus will be presented (neutral trials), whereas the advantage of the spatially congruent stimuli vanishes when a cue (valid trials) indicates where the stimulus will appear.

Taken together, these data indicate that a distinction between a "real" attentional mechanism that allocates the attentional focus on the imperative stimulus and a nonattentional sensorimotor mechanism responsible for the Simon effect is artificial. The evidence shows that the Simon effect is an attentional effect. The presentation of an unexpected stimulus in a certain spatial location determines an automatic activation of several sensorimotor circuits controlling eye movements as well as arm movements. The activation of these circuits manifest itself as attention if movements are prohibited, as movements if they are allowed.

It is outside the scope of the present article to discuss other spatial attention effects that are not directly connected with those reported here such as, for example, the so-called inhibition of return (Posner and Cohen 1984; Maylor 1985; Possamaï 1986; Tassinari et al. 1987, 1989). It will suffice to note here that for this effect the current interpretation (see Tassinari 1987, 1989; Possamaï 1991) is that the instruction to refrain from making a movement in response to a stimulus (the first of a pair) biases the "entire motor system against reacting to stimuli in that direction" (Tassinari et al. 1987). This interpretation fits well with the notion that passive attention and activation of sensorimotor circuits are different descriptions of the same phenomenon.

The second important aspect of manual response experiments was that, unlike exogenous attention, *endogenous attention* did not improve the speed of responses directed toward the attended hemifield with respect to those directed to the opposite one. Results in line with this finding were found also by Possamaï (1991) in an experiment in which cued stimuli were presented to the right or left of the fixation point and the responses (key pressing) were emitted either with the right or the left hand. The results showed that the combination "stimulus location-responding hand" was the predominant factor in determining the speed of RTs. The fastest RTs were those made with the hand ipsilateral to the stimulated field. Cued RTs to a stimulus located contralateral to the responding hand were slower than uncued RTs made with the hand spatially congruent with the target.

The lack in efficacy of endogenous attention in facilitating MRs toward the target is well accounted for by the experiments on the Simon effect presented above and their theoretical explanations. Briefly, when attention is already on the locus of the imperative stimulus presentation, the stimulus presentation has only negligible effects in determining the activation of circuits controlling actions in space. This is because the reference center for actions is determined by the focus of attention. Thus, in the cued condition the imperative stimulus occurs in the center of the movement reference system and not above or below it as in the uncued condition. Hence the lack of directional effects observed in the case of active attention.

Effect of passive (exogenous) and active (endogenous) attention on ocular responses

SRTs were affected by *exogenous attention* in a way qualitatively similar to that of MRTs. Like the latter, they were faster when the imperative stimulus occurred in the hemifield toward which the subsequent saccade was made. The only difference was the entity of the effect. Spatially congruent MRTs were faster than the incongruent ones by 19 ms, while spatially congruent SRTs led the incongruent ones by only 7 ms. It is possible that this difference was due to the fact that while the MRs were unambiguously directed toward the target, the ocular responses have to be directed (covertly) toward the location of the imperative stimulus for its discrimination and then overtly to the target. This complex behavior might have decreased the exogenous facilitation for ocular responses because of interference between the motor program directed to the imperative stimulus and that for the saccade.

In the case of active attention (*endogenous attention*), the result was apparently paradoxical. The RTs of the saccades directed toward the hemifield *opposite* to the attended one were faster than the RTs of the saccades directed toward the latter. This finding is in accordance with a previous observation we made in a similar experimental condition (Sheliga et al. 1995a).

A difference in RT between ocular saccades toward or away the imperative stimulus location is hard to account for by any theory that considers attention independent of motor programming. There is no obvious reason, if such theories are accepted, why the speed of RT should be faster when the subsequent movement is away from the locus of imperative stimulus presentation than when is made toward it.

The situation is quite different if one admits that active attention is the result of motor programming. In our experimental condition, the locus of imperative stimulus presentation and the locus of response were spatially separated. When the cue appeared, the subjects, in order to process optimally the imperative stimulus, have to direct their attention to the locus of its presentation. In terms of premotor theory of attention, endogenous attention for stimulus discrimination means preparation of an oculomotor program. As a consequence, when subjects had discriminated the stimulus and were ready to emit the appropriate saccade, they had to change motor program. The similarity between oculomotor programs toward the same hemifield (responses toward adjacent locations in space) explains the apparently paradoxical finding that RTs were faster away from the stimulus rather that toward it, as one should expect if some effects of exogenous attention due to imperative stimulus presenta-

tion were still present (for literature on interference, see Introduction).

In conclusion, the differential effects of endogenous and exogenous attention on manual and ocular RTs fit well the assumptions of the premotor theory of attention. In contrast, they appear to be difficult to explain by using the theory of disembodied attention. We are aware that we have not achieved here the "final" demonstration of the validity of the premotor theory of attention and that, by adding some post hoc assumptions, one can probably find an explanation for the present data without discarding the time-honored theory of disembodied attention. We have, however, provided new data and theoretical considerations that indicate the deep involvement of sensorimotor circuits in attention.

Directional biases of eye and hand responses

A variable that concurred with the attentional factors in determining the speed of RT was the direction of the impending movement. SRTs were faster when the subsequent movement was directed upward, whereas MRTs were faster when the hand moved downward.

Previous experiments showed that, in the case of simple MRT (key release or key pressing), stimuli presented in the lower hemifield are responded to faster than stimuli presented in the upper hemifield (Payne 1967; Gawryszewski et al. 1987; Rizzolatti et al. 1987). This finding is usually interpreted in terms of retinal sensitivity. The upper hemiretina is richer in receptors (Österberg 1935; Van Buren 1963; Perry et al. 1984) and its sensitivity to visual stimuli is higher than that of upper visual field (Skrandies 1987). Retinal factors, however, cannot account for our findings, since RTs followed by a movement directed downward were faster than RTs followed by an upward movement regardless of where in the visual field the imperative stimulus was presented.

Another factor that may determine a difference in MRT is the complexity of the subsequent movements. Typically, complex movements produce RTs longer than simple movements (see Keele 1973). Although upward and downward arm movements could appear similar in complexity, yet upward arm movements require an organization that is more complex than that for downward movements. The effort necessary for their execution is greater and more complex, therefore, than the mechanism for mobilization and coordination of the muscle groups necessary for their execution. An alternative explanation, which does not contradict the former, is based on postural considerations. In humans the natural position of the arms is with hand located in a downward position. It could be, therefore, that deviations from this position need an extra effort to counteract not only gravity but also a natural postural bias. Conversely, movements bringing the hand to a downward position or a position closer to it could be helped by the same bias.

In contrast to MRTs, SRTs were faster when the subsequent eye movement was directed upward than downward. This finding is in accord with previous data showing that both RTs and MTs of upward directed saccades are faster than those in the opposite direction (see references in Heywood and Churcher 1980; Previc 1990). The explanation of this bias for upward movement is not clear. A possibility is related to the fact that, in primates, upward movements are more related to the exploration of environment and detection of enemies, while downwards movements are more related to the search for food, and object inspection and manipulation (see, for a similar proposal, Previc 1990).

Attention and saccadic deviation

In addition to RT, another response variable that we investigated in the present experiment was the trajectory of ocular saccades. Confirming our previous findings (Sheliga et al. 1994, 1995a,b), the results showed that attention allocation modifies the saccadic trajectories. When the subject's attention was focussed on a stimulus in the right hemifield, vertical saccades deviated to the left. In contrast, when the subject's attention was focussed on a stimulus in the left hemifield, vertical saccades deviated to the right. The contralateral deviation was greater when the visual stimulus triggering the saccade was in the same (upper or lower) hemifield as the target for the saccade than when the visual stimulus and target for the saccade were in the opposite hemifields.

Besides confirming previous results, the analysis of saccadic trajectories showed also that the contralateral deviations were significantly larger in cued conditions than in uncued conditions. In previous experiments we observed a similar tendency, but the finding was not statistically significant. The difference is most likely due to the fact that in the present experiment a larger number of subjects was used.

In the context of the premotor theory of attention, the explanation of this finding appears to be straightforward. In the cued condition, the subjects expect the imperative stimulus in a precise space location. This expectancy implies an endogenously generated oculomotor program toward that location, very probably related to an activation of circuits involving the basal ganglia (see Rizzolatti et al. 1994; Sheliga et al. 1994). In contrast, in the uncued condition the spatial allocation of attention is determined passively through a mechanism involving mostly the superior colliculus. If one accepts the notion that the saccadic deviation is a consequence of the necessity to suppress the extant oculomotor programs (Rizzolatti et al. 1994; Sheliga et al. 1994), the difference in the complexity of oculomotor programs in cued and uncued conditions should lead to the observed difference in the strength of saccadic deviation.

References

Bach M, Bouis D, Fischer B (1983) An accurate and linear infrared oculometer. J Neurosci Methods 9: 9–14

Bauer DW, Miller J (1982) Stimulus-response compatibility and the motor system. Q J Exp Psychol [A] 31: 367–380

Berthoz A (1996) Neural basis of decision in perception and in the control of movement. In: Damasio AR, Damasio AR, Damasio H, Christen Y (eds) Neurobiology of decision-making. Springer, Berlin Heidelberg New York, pp 83–100

Brebner J (1973) S-R compatibility and change in RT with practice. Acta Psychol 37: 93–106

Chelazzi L, Miller EK, Duncan J, Desimone R (1993) A neural basis for visual search in inferior temporal cortex. Nature 363: 345–347

Chieffi S, Gentilucci M, Allport A, Sasso E, Rizzolatti G (1993) Study of selective reaching and grasping in a patient with unilateral parietal lesion. Brain 116: 1119–1137

Colby CL, Duhamel J-R, Goldberg ME (1993) Ventral intraparietal area of the macaque: anatomic location and visual response properties. J Neurophysiol 69: 902–914

Downing CJ, Pinker S (1985) The spatial structure of visual attention. In: Posner MI, Marin OSM (eds) Attention and performance XI. Erlbaum, Hillsdale, NJ, pp 171–187

Desimone R, Duncan J (1995) Neural mechanisms of selective visual attention. Annu Rev Neurosci 18: 193–222

Duncan J (1996) Cooperating brain systems in selective perception and action. In: Inni T, McClelland JL (eds) Attention and performance XVI. MIT Press, Cambridge, MA

Fitts PM (1951) Engineering psychology and equipment design. In: Stevens SS (ed) Handbook of experimental psychology. Wiley, New York, pp 1287–1340

Fitts PM, Deininger RL (1954) S-R compatibility: correspondence among paired elements within stimulus and response codes. J Exp Psychol 48: 483–492

Fitts PM, Seeger CM (1953) S-R compatibility: spatial characteristics of stimulus and response codes. J Exp Psychol 46: 199–210

Gawryszewski L, Riggio L, Rizzolatti G, Umiltà C (1987) Movements of attention in the three spatial dimensions and the meaning of "neutral" cues. Neuropsychologia 25: 19–29

Gawryszewski L, Faria RB, Thomaz TG, Pinheiro WM, Rizzolatti G, Umiltà C (1992) Reorienting visual spatial attention: is it based on Cartesian coordinates? In: Lent R (ed) The visual system from genesis to maturity. Birkhauser, Boston, MA

Graziano MSA, Gross CG (1996) Multiple pathways for processing visual space. In: Inui T, McClelland JL (eds) Attention and performance XVI. MIT Press, Cambridge, MA, pp 181–207

Graziano SA, Gross CG (in press) Ventral premotor cortex: III. Cognitive properties (in press)

Heywood S, Churcher J (1980) Structure of the visual array and saccadic latency: Implications for oculomotor control. Q J Exp Psychol 32: 335–341

Hietanen JK, Räma P (1995) Facilitation and interference occur at different stages of processing in the Simon paradigm. Eur J Cogn Psychol 7(2): 183–199

Hughes HC, Zimba LD (1985) Spatial maps of directed visual attention. J Exp Psychol Hum Percept Perform 11: 409–430

Hughes HC, Zimba LD (1987) Natural boundaries for the spatial spread of directed visual attention. Neuropsychologia 25: 5–18

Jackson SR, Jackson GM, Rosicky J (1995) Are non-relevant objects represented in working memory? The effect of non-target objects on reach and grasp kinematics. Exp Brain Res 102: 519–530

Kahneman D (1973) Attention and effort. Prentice-Hall, New York

Keele SW (1973) Attention and human performance. Goodyear, Pacific Palisades, CA

Kinsbourne M, Hiscock M (1983) Asymmetries of dual task performance. In: Hellige J (ed) Cerebral hemisphere asymmetry: methods, theory and application. Academic, New York, pp 255–334

Klein RM (1980) Does oculomotor readiness mediate cognitive control of visual attention? In: Nickerson RS (ed) Attention and performance VIII. Erlbaum, Hillsdale, NJ, pp 259–276

Klein RM, Pontefract A (1994) Does oculomotor readiness mediate cognitive control of visual attention? Revisited! In: Umiltà C, Moscovitch M (eds) Attention and performance XV. MIT Press, Cambridge, MA, pp 333–350

Klein RM, Kingstone A, Pontefract A (1992) Orienting of visual attention. In: Rayner K (ed) Eye movements and visual cognition: scene perception and reading. Springer, Berlin Heidelberg New York, pp 46–65

Kornblum S (1965) Response competition and/or inhibition in two-choice reaction time. Psychon Sci 2: 55–56

Kornblum S, Hasbroucq T, Osmann A (1990) Dimensional overlap: cognitive basis for stimulus-response compatibility – a model and a taxonomy. Psychol Rev 97: 253–270

LaBerge D, Brown V (1989) Theory of attentional operations in shape identification. Psychol Rev 96: 101–124

Lempert H, Kinsbourne M (1985) The effect of visual guidance and hemispace on lateralized vocal-manual interference. Neuropsychologia 23: 691–695

Maylor EA (1985) Facilitatory and inhibitory components of orienting in visual space. In: Posner MI, Marin OSM (eds) Attention and performance XI. Erlbaum, Hillsdale, NJ, pp 189–204

McCann RS, Johnston JC (1992) Locus of the single-channel bottleneck in dual-task interference. J Exp Psychol Hum Percept Perform 18: 471–484

Moran J, Desimone R (1985) Selective attention gates visual processing in the extrastriate cortex. Science 229: 782–784

Nicoletti R, Umiltà C (1989) Splitting visual space with attention. J Exp Psychol Hum Percept Perform 15: 164–169

Nicoletti R, Umiltà C (1994) Attention shifts produce stimulus spatial codes. Psychol Res 56: 144–150

Nicoletti R, Anzola GP, Luppino G, Rizzolatti G, Umiltà C (1982) Spatial compatibility effects on the same side of the body midline. J Exp Psychol Hum Percept Perform 8: 664–673

Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh Inventory. Neuropsychologia 9: 97–113

Österberg G (1935) Topography of the layer of rods and cones in the human retina. Acta Ophthalmol [Suppl] 6: 1–102

Pashler H (1992) Dual-task interference and elementary mental mechanisms. In: Meyer DE, Kornblum S (eds) Attention and performance XIV. MIT Press, Cambridge, MA, pp 245–264

Pashler H, Johnston JC (1989) Chronometric evidence for central postponement in temporally overlapping tasks. Q J Exp Psychol 41A: 19–45

Pavlov IP (1927) Conditional reflexes. Clarendon, Oxford

Payne WH (1967) Visual reaction times on a circle about the fovea. Science 155: 481–482

Perry VH, Oehler R, Cowey A (1984) Retinal cells that project to the dorsal lateral geniculate nucleus in the macaque monkey. Neuroscience 12: 1101–1123

Posner MI (1980) Orienting of attention. Q J Exp Psychol 32: 3–25

Posner MI, Cohen Y (1984) Components of visual orienting. In: Bouma H, Bouwhuis DG (eds) Attention and performance X. Erlbaum, Hillsdale, NJ, pp 531–556

Posner MI, Dehaene S (1994) Attentional networks. Trends Neurosci 17: 75–79

Posner MI, Petersen SE (1990) The attentional system of the human brain. Annu Rev Neurosci 13: 25–42

Possamaï CA (1986) Relationship between inhibition and facilitation following a visual cue. Acta Psychol 61: 243–258

Possamaï CA (1991) A responding hand effect in a simple-RT precueing experiment: evidence for a late locus of facilitation. Acta Psychol 77: 47–63

Previc FH (1990) Functional specialization in the lower and upper visual fields in humans: its ecological origins and neurophysiological implications. Behav Brain Sci 13: 519–575

Rafal RD, Calabresi PA, Brennan CW, Sciolto TK (1989) Saccade preparation inhibits reorienting to recently attended locations. J Exp Psychol Hum Percept Perform 15: 673–685

Reuter-Lorenz PA, Fendrich R (1992) Oculomotor readiness and covert orienting: differences between central and peripheral precues. Percept Psychophys 52: 336–344

Rizzolatti G (1983) Mechanisms of selective attention in mammals. In: Ewert JP, Capranica RR, Ingle DJ (eds) Advances in vertebrate neuroethology. Plenum, London, pp 261–297

Rizzolatti G, Camarda R (1987) Neural circuits for spatial attention and unilateral neglect. In: Jeannerod M (ed) Neurophysiological and neuropsychological aspects of spatial neglect. North-Holland, Amsterdam, pp 289–313

Rizzolatti G, Bertoloni G, De Bastiani PL (1982) Interference of concomitant tasks on simple reaction time: attentional and motor factors. Neuropsychologia 20: 447–455

Rizzolatti G, Matelli M, Pavesi G (1983) Deficits in attention and movement following the removal of postarcuate (area 6) and prearcuate (area 8) cortex in macaque monkeys. Brain 106: 655–673

Rizzolatti G, Riggio L, Dascola I, Umiltà C (1987) Reorienting attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention. Neuropsychologia 25: 31–40

Rizzolatti G, Riggio L, Sheliga BM (1994) Space and selective attention. In: Umiltà C, Moscovitch M (eds) Attention and performance XV. MIT Press, Cambridge, MA, pp 231–265

Sheliga BM, Riggio L, Rizzolatti G (1994) Orienting of attention and eye movements. Exp Brain Res 98: 507–522

Sheliga BM, Riggio L, Rizzolatti G (1995a) Spatial attention and eye movements. Exp Brain Res 105: 261–275

Sheliga BM, Riggio L, Craighero L, Rizzolatti G (1995b) Spatial attention-determined modifications in saccade trajectories. Neuroreport 6: 585–588

Simon JR (1968) Effects of ear stimulated on reaction time and movement time. J Exp Psychol 78: 344–346

Simon JR (1969) Reaction toward the source of stimulation. J Exp Psychol 81: 174–176

Simon JR (1970) Stereotypic reactions in information processing. In: Smith LE (ed) Psychology of motor learning. Athletic Institute, Chicago, IL, pp 27–57

Simon JR, Craft JL, Webster JB (1973) Reaction toward the stimulus source: analysis of correct response and errors over a five-day period. J Exp Psychol 101: 175–178

Skrandies W (1987) The upper and lower visual field of man: electrophysiological and functional differences. In: Autrum H, Autrum H, Ottoson D, Perl ER, Schmidt RF, Shimazu H, Willis WD (eds) Progress in sensory physiology, vol 8. Springer, Berlin Heidelberg New York

Sokolov EN (1960) Neuronal models and the orienting reflex. In: Brazier MA (ed) The central nervous system and behaviour. Macy, New York

Stoffer TH (1991) Attentional focusing and spatial stimulus-response compatibility. Psychol Res 53: 127–135

Stoffer TH, Yakin AR (1994) The functional role of attention for spatial coding in the Simon effect. Psychol Res 56: 151–162

Tassinari G, Aglioti S, Chelazzi L, Marzi CA, Berlucchi G (1987) Distribution in the visual field of the costs of voluntarily allocated attention and of the inhibitory after-effects of covert orienting. Neuropsychologia 25: 55–71

Tassinari G, Biscaldi M, Marzi CA, Berlucchi G (1989) Ipsilateral inhibition and contralateral facilitation of simple reaction time to non-foveal visual targets from non-informative visual cues. Acta Psychol 70: 267–291

Tipper SR, Lortie C, Baylis GC (1992) Selective reaching: evidence for action-centered attention. J Exp Psychol Hum Percept Perform 18: 891–905

Umiltà C, Liotti M (1987) Egocentric and relative spatial codes in S-R compatibility. Psychol Res 49: 81–90

Umiltà C, Nicoletti R (1985) Attention and coding effects in S-R compatibility due to irrelevant spatial cues. In: Posner MI, Marin OSM (eds) Attention and performance XI. Erlbaum, Hillsdale, NJ, pp 457–471

Umiltà C, Riggio L, Dascola I, Rizzolatti G (1991) Differential effects of central and peripheral cues on the reorienting of spatial attention. Eur J Cogn Psychol 3: 247–267

Umiltà C, Mucignat C, Riggio L, Barbieri C, Rizzolatti G (1994) Programming shifts of spatial attention. Eur J Cogn Psychol 6: 23–41

Van Buren JM (1963) The retinal ganglion cell layer. Thomas, Springfield, IL

Wallace RJ (1971) S-R compatibility and the idea of a response code. J Exp Psychol 88: 354–360

Welford AT (1952) The "psychological refractory period" and the timing of high-speed performance: a review and a theory. Br J Psychol 43: 2–19

Werban-Smith MG, Findlay JM (1991) Express-saccades: is there a separate population in humans? Exp Brain Res 87: 218–222