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RESEARCH ARTICLE

Claudio de'Sperati

Saccades to mentally rotated targets

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Abstract In order to investigate the role of mental rotation in the directional control of eye movements, we instructed subjects to make saccades in directions different from that of a visual stimulus (rotated saccades). Saccadic latency increased linearly with the amount of directional transformation imposed between the stimulus and the response. This supports the hypothesis that reorienting a saccade is accomplished through a mental rotation process. No differences were found in amplitude, duration, velocity, and curvature between rotated and visually guided saccades. Analogous to mental rotation tasks involving reaching arm movements, it is surmised that frontal/prefrontal cortical structures participate in rotated saccades by reorienting the intended saccadic direction. A linear increase in response time with the imposed directional transformation was also found in an analogous mental task not requiring a directed motor response, namely, mentally localizing a point in space at a certain angle from a stimulus direction. However, the speed of mental rotation was systematically lower than in the rotated saccade task. These findings indicate that mental rotation is a rather general mechanism through which directional transformations are achieved.

Key words Mental rotation · Saccades · Anti-saccades · Direction coding · Visuo-motor transformation

Introduction

Several commonly employed experimental paradigms developed to study visuo-motor transformations require simple movements to be performed towards a visual stimulus. This is the case, for example, in pointing or reaching arm movements or in visually guided saccades. It may be, however, that the visual stimulus is a cue, but not the target of the movement; that is, the movement is performed towards a location different from that of the stimulus. Our knowledge of how the brain transforms visual information into the proper motor command may benefit by experiments in which a dissociation between the direction of the stimulus and the direction of the upcoming movement is deliberately introduced. By asking subjects to make an arm movement at a certain angle with a stimulus direction, i.e., by imposing an angular transformation between the stimulus and the response, one has the opportunity to observe how direction coding changes along the stages of sensorimotor transformations (Georgopoulos and Massey 1987; Georgopoulos et al. 1989; Alexander and Crutcher 1990b).

One basic finding derived from studies on manual reaching involving different stimulus and response directions (visuomotor mental rotation task) is that these angular transformations are gradual, time-consuming processes, so that a linear relationship exists between the latency of the movement and the amount of angular transformation required. This phenomenon is reminiscent of what happens in classic mental rotation tasks, in which the time to recognize the sameness of two objects presented at different orientations increases proportionally with the angle between the two orientations, as if an analogue of the object is internally rotated (see Shepard and Cooper 1986). These apparently very different tasks share some common constraints, to the extent that the visuo-motor mental rotation task is regarded as a motor variant of the classic mental rotation paradigm (Tagaris et al. 1997). In fact, subjects who are faster in a mental rotation task are also faster in a visuo-motor mental rotation task (Pellizzer and Georgopoulos 1993). Moreover, it has recently been shown that, in both tasks, the angular transformation operations are associated with the activation of the motor cortex (Georgopoulos et al. 1989; Tagaris et al. 1997). At the neurophysiological level, during the stimulus-response time lapse, a gradual reorientation of the neural population vector, which codes for the intended movement direction, has been observed in the primary motor cortex of a monkey performing a

C. de'Sperati
Laboratory of Action, Perception, Cognition,
Università S. Raffaele, via Olgettina 58, I-20132 Milano, Italy
e-mail: desperati.claudio@hsr.it
Tel.: 39-2-2643 4859, Fax: +39-2-2643 4892

visuo-motor mental rotation task (Georgopoulos et al. 1989).

If indeed mental rotation is a widespread process acting in various perceptual and motor systems, it is to be expected that it also applies to oculomotor behavior. In the present research, we asked whether, in making a saccadic eye movement at a certain angle with the direction of a stimulus, the response time increases as a function of the amount of the angular transformation. To evaluate to what extent these angular transformation processes intrude into the saccadic "low-level" motor properties, a parametric analysis was performed to compare the dynamic characteristics of visually guided saccades with those of saccades resulting from stimulus-response directional transformations. In addition, we compared the behavior in this oculomotor task with the behavior in a visuo-spatial task designed to retain the visual aspects of the oculomotor task, but that did not require any directed motor response. To this end, we assessed whether an increase in response time in parallel with the amount of an imposed angular transformation is present in mentally localizing a point in space at a certain angle from a stimulus direction.

Materials and methods

Subjects

Ten subjects (three males and seven females, aged 18–35 years) volunteered for the experiments without being paid for their services; informed consent was given before the beginning of the experiments. Subjects had normal or corrected-to-normal vision. Of the ten subjects, eight performed in the rotated saccade task and nine in the mental task (see below); seven subjects (three males and four females) performed in both tasks.

Experimental procedure

The experiments took place in a dark room. Subjects were seated inside the eye movement recording device, in front of a computer screen at a distance of 114 cm. The head was fixated with the help of a forehead abutment and a bite-board individually moulded with condensation silicone. The dominant eye was selected for viewing, while the other eye was patched. The task consisted of four steps (Fig. 1). A circle (whose radius subtended a visual angle of 3°) appeared at the center of the screen, together with two radii which formed the so-called instruction angle (Fig. 1A). One radius always appeared at 3 o'clock (defined as 0°), while the other radius appeared in a clockwise direction, forming one of the following instruction angles: 0.0°, 25.7°, 51.4°, 77.1°, 102.9°, 128.6°, 154.3° (positive values refer to clockwise direction). After 4 s, the two radii disappeared and the subjects had to bring the gaze to the center of the circle, signaled by a small spot (Fig. 1B). After 3 s, a second spot appeared on the circle, thus identifying a stimulus direction that was either 0.0°, 51.4°, 102.9°, 154.3°, 205.7°, 257.1°, or 308.6° (Fig. 1C). In one experimental session, subjects had to mentally identify, as soon as possible, the location on the circle corresponding to the stimulus direction augmented, in the clockwise direction, by the instruction angle previously showed, and press a button (mental task, Fig. 1E). The gaze had to remain at the center of the circle. In another experimental session, subjects instead had to bring, as soon as possible, the gaze to that point with a single saccadic eye movement (rotated saccade task, Fig. 1D). The reason of the small amplitude of the target circle is that we attempted to minimize the occurrence of spurious saccades that subjects could have used to inspect the target circle appearing in peripheral vision before giving the "true" response. It should be recalled, however, that almost 50% of the saccades occurring during natural scene viewing have an amplitude of less than 7° (Bahill et al. 1975). Since the central fixation dot remained on at the appearance of the second spot, the saccadic task belongs to the "overlap paradigm" type (Saslow 1967).

In each of the two experimental sessions, the seven instruction angles and the seven stimulus directions were administered in a completely randomized order, for a total of 49 trials per subject per task. Although no repetitions were planned, given that the stimulus direction has no effect upon response times (see the second paragraph of the Results section), the seven stimulus directions became in fact seven repetitions for each instruction angle. Each session lasted about 10 min. Among the seven subjects that

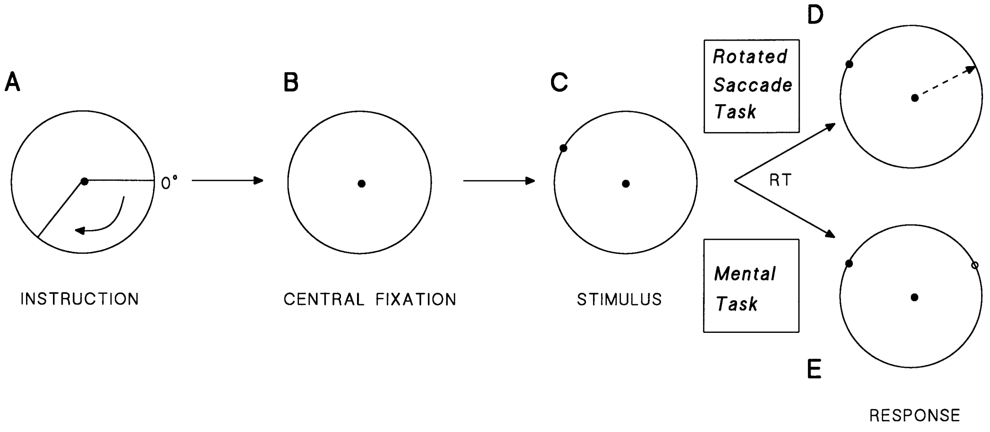

Fig. 1A–E The experimental task. **A** The instruction angle was presented on the computer screen as two radii (one radius always at 3 o'clock) together with an *arrow* indicating that the angular transformation was to be performed in the clockwise direction. **B** After 4 s, the instruction angle disappeared and the gaze was to be brought to the center of the circle. **C** After a further 3 s, a small spot (*stimulus*) appeared somewhere on the circle. At this time, recording of eye movements started for a fixed period of 5 s. In the rotated saccade task (**D**), subjects made a saccade (represented as a *dashed arrow*) to the point on the circle corresponding to the stimulus direction augmented, in the clockwise direction, by the instruction angle. In the mental task (**E**), subjects pressed a button upon mental localization of that same point on the circle (here represented as an *open circle*, but in fact absent in the display). The response time was computed as the time lapse between the stimulus presentation and either the beginning of the primary saccade (rotated saccade task) or the button press (mental task). The radius of the target circle subtended a visual angle of 3°

participated in both experiments, three performed first in the mental task, while the other four first performed in the rotated saccade task, on different days. Eye movements were recorded only during the rotated saccade task. To check that, in the mental task, subjects indeed succeeded in keeping the gaze still in the central fixation position, an additional control experiment was run in three subjects who had already participated in both the rotated saccade and the mental task. Eye movements were recorded while subjects performed in the mental task.

Measurement of response times and eye movement recording

The response time was measured as the time between the appearance of the stimulus and the response, which was either the button press (mental task) or the beginning of the saccade (rotated saccade task). In the former case, the button press was recorded with a temporal resolution of 2 ms. The beginning of the saccades was measured as the time at which the tangential velocity of the eye exceeded the threshold value of 30°/s. An ANOVA for repeated measures was used for statistical analyses.

Horizontal and vertical components of eye position were recorded by means of the scleral search-coil technique (EPM520, Skalar Medical B.V.). Within the normal oculomotor range, the recording device has a nominal accuracy of <1 min. Position signals were low-pass filtered (cut-off frequency: 300 Hz), sampled (resolution: 16-bit; sampling frequency: 500 Hz per channel), calibrated, and stored for subsequent processing. Eye movements were recorded for 5 s after stimulus presentation. In order to avoid tears, the non-dominant eye was fitted with the lens and patched (de'Sperati and Viviani 1997). Before fitting the lens, the sclera was lightly anesthetized with a local application of oxibuprocaine chlorydrate (Novesine 0.4%), and a small amount of adhesive solution (Idroxy-Propil-Metil-Cellulosa) was applied to the lens. A 2–3 min adaptation period was allowed after fitting the lens. If the subject reported any discomfort during this period, or anytime thereafter, the experiment was immediately terminated. At the end of the experimental session, the lens was removed and the eye was washed with collyrium.

Before starting the recording session, a calibration procedure was performed: the subject had to fixate sequentially 25 targets arranged as a 5×5 rectangular matrix (size: 21.0 × 15.5 cm). Calibration targets were white circles (radius=0.1°) centered on an orthogonal cross (size=0.4°). Individual fixations, or the entire calibration, were repeated, if necessary. These eye-position data served to evaluate the parameters of two 3rd degree polynomials X=f(x,y) and Y=f(x,y) that best mapped (in the least-square sense) the recorded calibration grid into the theoretical one. The obtained parameters were used to calibrate the raw eye position data. Horizontal and vertical eye velocity were computed by means of a 3-points digital filter.

Results

Rotated saccade task

Response times

Our subjects were instructed to make a single saccadic eye movement and then to keep the gaze still during the 5-s recording window that started with the presentation of the stimulus dot. In spite of this, in roughly one-third of the cases, we observed a corrective saccade occurring within 200 ms after the offset of the primary saccade, as well as a number of other saccades, variously distributed within the 5-s recording window. Data in this section refer to primary saccades. For instruction angles greater than 0°, we excluded a few trials in which the response time was less than 150 ms or in which the achieved angle was less than half of the instruction angle (meaning that the saccade direction was closer to the stimulus direction). These cases were considered as departure errors. When the single responses were pooled, we used the mean as the measure of central tendency of response time. Similar results were obtained by using the median.

Examples of saccades for three different instruction angles in both the spatial and the time domain are reported in Fig. 2. The saccadic response times (SRT) from an individual subject are reported in Fig. 3 as a function of both the stimulus direction (A) and the instruction angle (B). We first checked whether SRT was dependent on the stimulus direction. However, in none of the subjects did the SRTs show any systematic relation with the stimulus direction. The individual regression lines of SRT versus stimulus direction were flat, and the accounted variances ranged between 0.2% and 3.8%. By considering all subjects, no statistically significant effect of the stimulus direction was found [F(6,42)=0.399; P=0.876].

Instead, we found a systematic dependence of SRT from the instruction angle in seven of eight subjects, with the SRT increasing in an almost linear fashion with the instruction angle. The individual slopes computed over these subjects' data were rather variable, similar to what had been previously reported in a visuo-motor mental rotation task involving arm responses (Georgopoulos and Massey 1987), and ranged between 0.23 and 3.19 ms/deg. Except for one subject, the accounted variances ranged between 62% and 89%. In one subject (P.T.), the SRT remained constant (mean SRT: 384 ms) for all instruction angles (slope=–0.007 ms/deg; intercept=388 ms, r=0.289). Since, in terms of direction of saccades and of relation to the saccadic task response

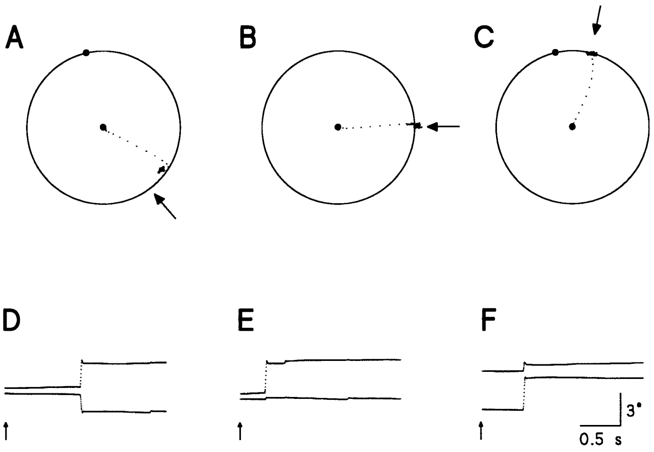

Fig. 2A–F Three examples of saccades, both in the spatial (**A–C**) and time (**D–F**) domain. **A–C** The *dot* on the circle represents the stimulus position, while the *arrow* indicates the expected saccade direction [instruction angle in **A**: 154.3°; in **B**: 0° (control saccade); in **C**: 25.7°]. **D–F** Horizontal (*upper traces*) and vertical (*lower traces*) eye position recordings, starting at the time of appearance of the stimulus dot (*arrow*). For graphical purposes, the vertical alignment of the traces is arbitrary. The plot is limited to the initial 2 s of the recordings

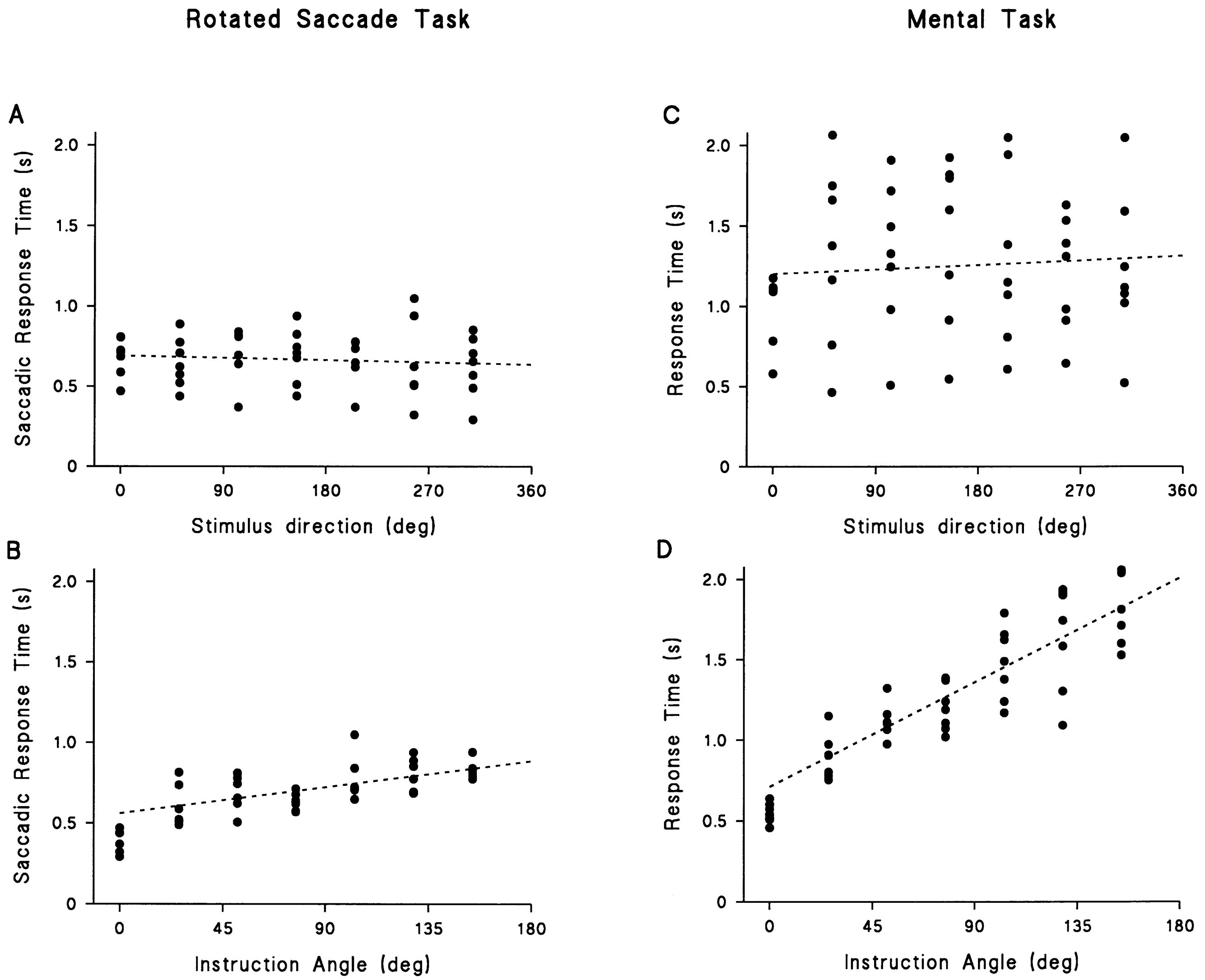

Fig. 3A–D The relation between saccadic response time and stimulus direction (**A**) and instruction angle (**B**), together with the regression lines, in a representative subject. The individual data points represent the saccadic latency at each value of the independent variables. Reaction times from the same subject in the mental task as a function of the stimulus direction (**C**) and instruction angle (**D**)

times (see below), the performance of this subject was equivalent to that of the other subjects, the data were included in the subsequent analyses. However, similar results were obtained by excluding this subject from the sample.

In Fig. 4A, the mean SRTs are plotted as a function of the instruction angle, together with the 95% confidence intervals and the interpolating linear curve fit. Fig. 4B reports the SRT distribution for each instruction angle. The instruction angle was found to affect the response times significantly [*F*(6,42)=6.317; *P*=0.0001]. The regression line performed on the averaged data has a slope of 1.87 ms/deg and an intercept of 524 ms (*r*=0.910). By excluding subject P.T. from the sample, the slope, intercept, and correlation coefficient are 2.12 ms/deg, 569 ms, and 0.958, respectively. In order to dissociate the internal operations related to stimulus-response from those that are related to angular transformation processes, but independent of the amount of transformation, in calculating the regression line, we omitted the value corresponding to the 0° instruction angle. In fact, for this instruction angle, subjects were faster than predicted on the basis of the data extrapolated from the regression line [*t*(53)=3.421; *P*=0.0012]. This step increase in response time passing from the 0° to the 25.7° instruction angle indicates the presence of an additional component involved in transforming the stimulus direction into the movement direction, which is independent of the amount of the required transformation. This phenomenon is also present in the mental task (see below), and it had also been reported in a visuo-motor mental rotation task (Georgopoulos and Massey 1987). In summary, we could estimate three different components in the rotated saccade task: visual elaboration of the stimulus together with the oculomotor response, which were responsible for 417 ms of the total response time (the mean SRT at 0° of instruction angle); a fixed extra-time of 107 ms, resulting from the difference between the actual SRT and

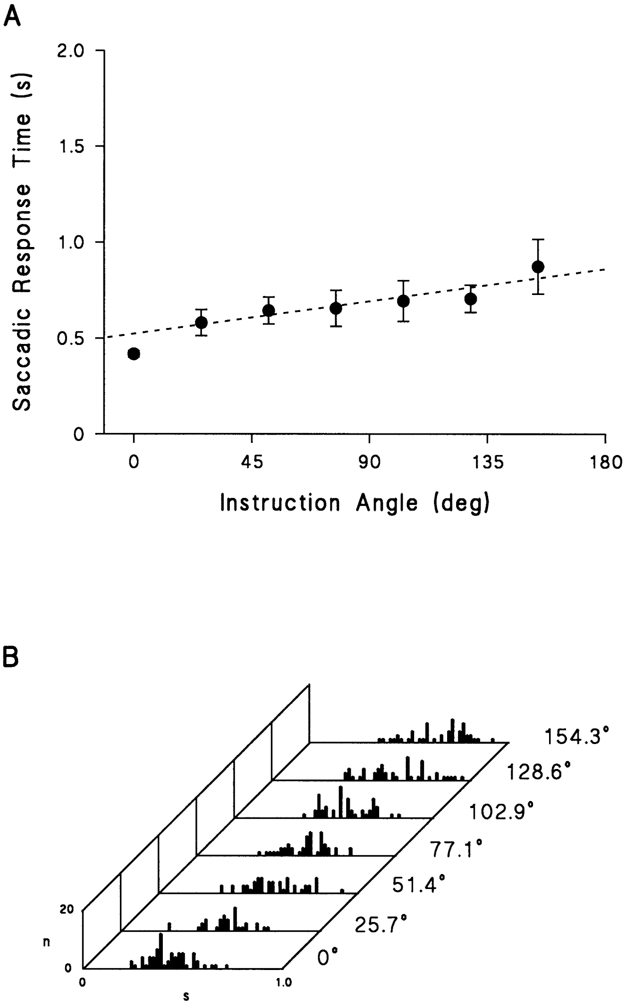

Fig. 4 **A** Rotated saccade task: mean saccadic response time (SRT) across subjects together with the 95% confidence interval as a function of the instruction angle, together with the regression line. In calculating the regression line, the SRT value for the 0° instruction angle was omitted (see text). **B** Distributions of SRTs for each instruction angle. Data for all subjects were pooled together. SRT range: 0.00–1.00 s. Bin width: 20 ms

the intercept of the regression line at the 0° instruction angle, possibly related to operations such as the recall of the instruction angle (Georgopoulos and Massey 1987) or the suppression of reflexive saccades towards the stimulus dot (Remington et al. 1992; Biscaldi et al. 1996); and a further 1.87 ms/deg (slope of the regression line), in charge of angular transformation processes, whose inverse gives the speed of rotation (535°/s). As for the particularly high saccadic latency at the 0° instruction angle, compared to the values usually reported for visually guided saccades (around 200 ms, see Becker 1991), this might have been partly due to the use of the overlap paradigm, which is known to increase saccadic latency up to almost 300 ms (Saslow 1967), associated with the rather low luminance level employed in the present study (Doma and Hallett 1988). It is unlikely that it was due to the uncertainty of the amount of rotation, because the saccade was released at least 7 s after the presentation of the instruction angle (see Methods).

In addition to studying the relationship between SRT and the instruction angle, which allowed us to estimate the performance as a function of the task requirement, we also examined the relation between SRTs and the effective angle defined by the saccadic direction, that is, the performance as a function of the actual motor response, which could not be identical to the expected one. In fact, directional undershoots occurred in rotated saccades (see “Accuracy and precision of saccades” in the Results section), especially for large instruction angles, meaning that, on average, the covered angles were smaller than the instruction angles. Thus, the regression line of SRT versus instruction angle was recalculated by using, as the independent variable, the average covered angle, i.e., the instruction angle corrected by the average directional error of the saccades (see “Accuracy and precision of saccades” in the Results section). Due to the presence of directional undershoots for large instruction angles, the slope of the regression line of SRT versus the covered angle was somewhat higher (2.29 ms/deg, corresponding to a speed or rotation of 437°/s; r=0.924) than when the instruction angle was used, but the difference was not statistically significant [$t(7)$=0.718, P=0.496]. Although the correlation coefficient computed for the actual performance was slightly higher than that computed for the expected performance, the difference was not statistically significant, as assessed by a paired Student’s t test on the z-transformed r values [$t(7)$=0.790, P=0.455], meaning that, in spite of the directional errors, the instruction angle and the covered angle are almost equivalent predictors of the response time. The step increase of RTs by passing from the 0° to the 25.7° instruction angle was still present [71 ms; $t(53)$=2.481, P=0.016] when using the covered angle as the independent variable, though more moderate than when computed on the basis of the instruction angle.

Amplitude, velocity and duration of saccades

The endpoints of primary saccades were distributed throughout the entire distance to be covered with the eye, especially for instruction angles greater than 0°, for which the mean saccadic amplitude was 2.14°±0.04 (SE). No relation was found between saccadic amplitude and either SRT or the instruction angle. For the 0° instruction angle, however, saccades of short amplitude (less than 1.0°) disappeared almost completely, suggesting that this phenomenon, albeit marginal (6% of the total saccades), was peculiar to S-R direction transformation operations when the saccadic end-point had to be calculated anew and the tendency to make a short temptive eye movement might have overcome the request to shift the gaze by means of a single saccadic eye movement. Apart from their small amplitude, however, these saccades were not different from the other rotated saccades in terms of latency-instruction angle relationship, directional accuracy, or precision. As for the 0° instruction angle, the mean saccadic amplitude (2.51±0.02°), although greater than when a rotation was to be performed [$t(387)=3.863$, $P<0.0001$], was less than the expected one, indicating a general tendency to undershoot the target.

The average duration of rotated saccades was 28.1±0.27 ms. The amplitude-duration relationship was fitted by means of a linear model and the slope was 5.1 ms/deg, except for the short-amplitude saccades, which, though few, were well fitted by a linear function with a slope of 17.8 ms/deg. Control saccades (those with a 0° instruction angle) and rotated saccades had almost identical slopes. An asymmetry index was computed as the ratio between the duration of the decelerating phase and the duration of the accelerating phase of the saccade; the mean value was 1.39±0.02. Again, control and rotated saccades were not significantly different in these respects. It should be noted, however, that, given the short duration of these saccades, the asymmetry index has a rather poor resolution.

In the narrow amplitude range of our saccades, the relationship amplitude to maximum tangential velocity was well represented by the linear function $Y=48.35*X+13.31$, with a correlation coefficient of 0.895. On average, the tangential velocity had a maximum of 119.4±1.93°/s and peaked at 10.8 ms from the beginning of the saccade.

Accuracy and precision of saccades

Standard techniques for treating directional data (Mardia 1972) were used to evaluate the directional accuracy (mean directional error) and precision (circular standard deviation: s_0) of saccades. How well did subjects perform in terms of direction of eye movements? To address this point, we calculated the post-saccadic gaze direction, i.e., the average gaze direction computed in an interval of 30 ms starting 60 ms after the saccade offset (which was defined as the moment in which the tangential velocity of the eye returned to below 30°/s); by this time, the eye was well stabilized on the new fixation point. However, care was taken to terminate the averaging of eye position data points if a corrective saccade occurred within 90 ms of the end of primary saccade. We defined the directional error as the difference between the post-saccadic gaze direction and the expected direction, i.e., the one required by the task. Positive values indicate clockwise direction. As can be appreciated from Table 1 and in Fig. 5, when the instruction angle was 0°, saccades were directed towards the target with high accuracy. When the saccades had to be directed at an angle to the stimulus direction, however, larger directional errors occurred for higher instruction angles and the precision decreased. The behavior of subject P.T. closely replicated that of the other subjects.

Table 1 Mean directional error of saccades and circular standard deviation (s_0) for each instruction angle. Negative values represent angular undershoots (saccades directed counterclockwise relative to the expected direction)

Instruction angle (deg)	Mean directional error (deg)	s_0 (deg)
0.0	0.27	6.04
25.7	1.33	8.69
51.4	–1.92	12.21
77.1	–11.57	16.79
102.9	–17.30	16.43
128.6	–17.16	29.35
154.3	–19.57	24.53

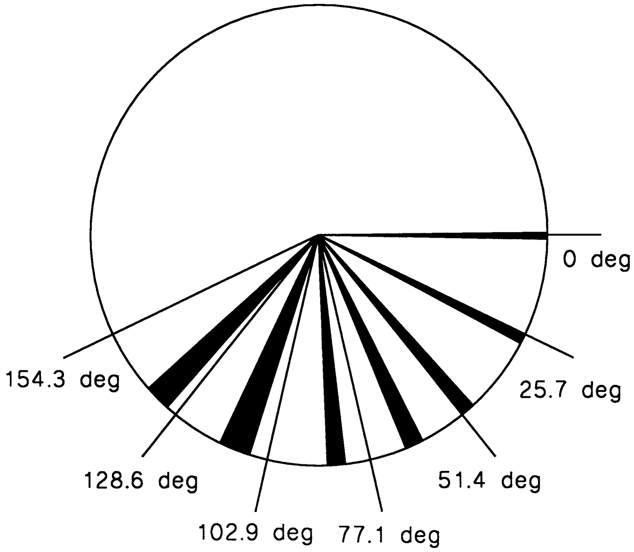

Fig. 5 Polar plot of mean saccade accuracy and precision. The center of the directional cones (*filled-in cones*) represents the mean direction for each instruction angle (indicated by the *lines* extending outside the circle), whereas the aperture of the cones represents the ±standard error [s_0/SQR(N), where N = no. of saccades for each instruction angle]. For clarity of the graphical presentation, the direction of saccades was recomputed by subtracting the value of stimulus direction, i.e., as if the stimulus always appeared at 0°

Saccadic curvature

Most saccades were curved. We checked whether any difference could be detected between control and rotated saccades. To evaluate the curvature, we computed the difference between the initial direction of the saccade (from onset to peak tangential velocity) and the direction of the subsequent part (from peak tangential velocity to offset). No significant difference emerged between control and rotated saccades [1.29°±0.93 SE and 2.76°±0.54, respectively; $t(387)=1.051$, $P=0.294$].

We also asked whether such curvature depended on the presence of some corrective mechanisms tending to improve saccadic accuracy in the mid-flight. To this aim, we defined: (1) the initial directional error as the difference between the initial direction of the saccade and the expected direction, and (2) the directional correction as

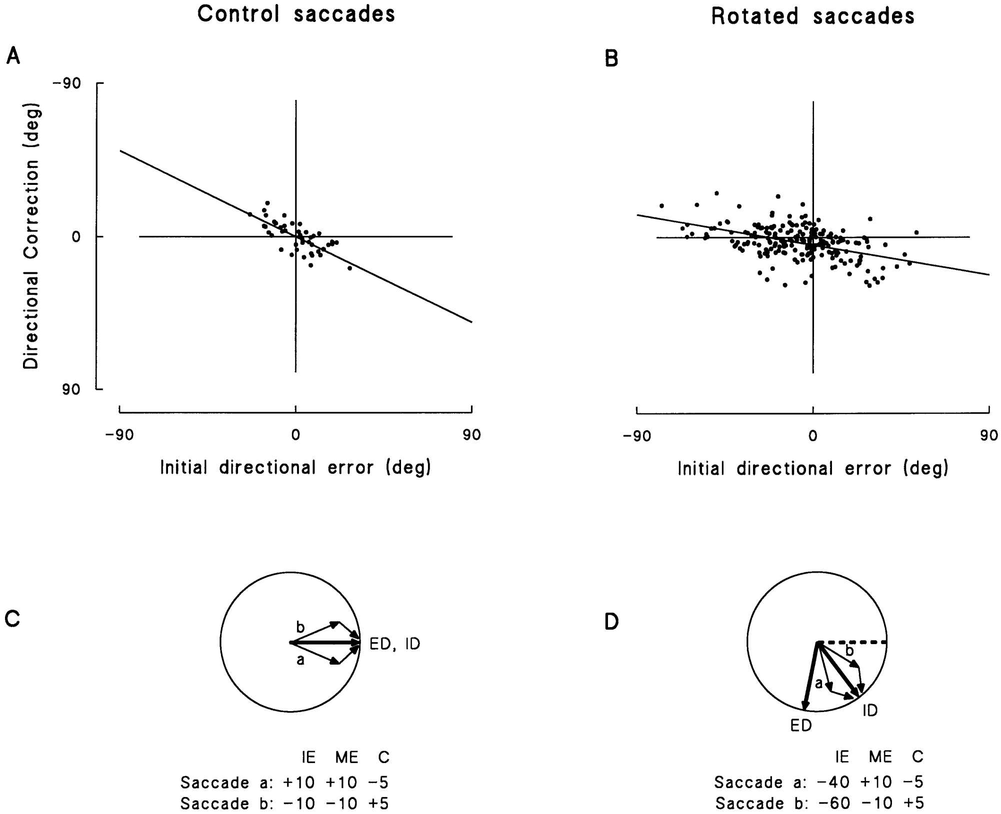

Fig. 6A–D Relationship between the directional correction and the initial directional error, together with the regression lines, for both control (**A**) and rotated (**B**) saccades. Data from all subjects were pooled together. **C, D** Hypothetical schema of two couples of control (**C**) and rotated (**D**) saccades. Saccades (*a* and *b*) are represented by the *thinner arrows*, each saccade being subdivided into two components: the *first arrow* represents the initial saccadic direction, and the *second arrow* represents the directional correction operated in the second part of the saccade. For control saccades, the expected direction (*ED*, the direction required by the task: *thicker arrow*) was assumed to be equivalent to the intended direction (*ID*, the internally coded saccadic desired direction). In rotated saccades, ED may differ from ID. *IE* Initial directional error, *ME* directional motor error, *C* correction. The values for IE, ME, and C shown in **C** and **D** are arbitrary

the difference between the final saccadic direction (i.e., the direction of the gaze precisely at the moment of saccadic offset) and the initial direction of the saccade. For control saccades (Fig. 6A), the directional correction was linearly correlated with the initial error, with a slope of 0.56 (r=0.691), which means that, for each degree of initial error in whichever direction, there was an average correction in the opposite direction of 0.56° (gain=0.56). This result is in line with the values of 0.66 and 0.72 reported in a previous study (Becker and Jurgens 1990). For rotated saccades (Fig. 6B), we found a similar relation, but with a lower average slope (0.18) and a lower correlation coefficient (0.440). Both the slopes and the correlation coefficients were significantly different from zero. A more detailed analysis showed that the slope decreased as the instruction angle increased; the slope decrease was accompanied by a joint decrease in the correlation coefficient.

It is unlikely that both the reduced slope and correlation coefficient found for rotated saccades can be accounted for by differences in the dynamic characteristics of rotated and control saccades. Consider two hypothetical control saccades (*a* and *b*), as depicted in Fig. 6C. Here, the expected saccadic direction (ED) is assumed to be coincident with the intended saccadic direction (ID, thick arrow). A 10° directional motor error (ME) is corrected (C) by 5° in the opposite direction (values are arbitrary): the resulting gain is 0.5. Consider now two hypothetical rotated saccades (*a* and *b*, Fig. 6D), with the same ME and directional correction relative to the ID, which is now different from the ED because of the presence of a directional underestimation. Given an initial directional error of 50° counterclockwise, it turns out that measuring the directional correction versus the initial directional error results in an apparent gain of only 0.083 (5°/60°) for saccade *b* and even 0.125 (5°/40°) in the anticompensatory direction for saccade *a*. Thus, a reduced slope, such as that of Fig. 6B, as compared with that of Fig. 6A, may result just from a misjudgement of the instruction angle. Moreover, the fact that the two apparent gains of saccades *a* and *b* of Fig. 6D have very different values means that the plot of directional correction versus initial directional error, built over a large number of saccades, is more scattered for rotated than for control saccades, resulting in a lower correlation coefficient of the regression line. Indeed, both a reduced slope and a lower correlation coefficient characterize the plot of Fig. 6B, as compared with that of Fig. 6A. In addition, it can be noticed that a large proportion of the data points falls within the bottom left quadrant of Fig. 6B, meaning that, in spite of the fact that the angle achieved by these saccades is less than the instruction angle, the directional corrective mechanism, in the attempt to recover the motor error, brought the gaze even closer to the stimulus direction, with the effect of increasing the error of the final saccadic direction. This corresponds to the saccade *a* in Fig. 6D. Notice that a direct comparison of the gains of the corrective mechanisms in control and rotated saccades was not possible because of the lack in the latter case of a reliable estimate of the intended saccadic direction for each given saccade, which cannot be derived from either the individual or the average final direction of the saccades.

We also asked how much of the direction compensation was achieved in the post-saccadic period. Therefore, we compared the data obtained by considering the direction of the eye measured at the end of the saccade with those obtained by considering eye position in the interval 60–90 ms after saccadic offset. The post-saccadic drift boosts the directional correction, in both control (slope= 0.64, r=0.754) and rotated (slope=0.23, r=0.497) saccades. The effect is statistically significant in both cases [control saccades: $t(104)=5.791$; $P<0.0001$; rotated saccades: $t(668)=25.821$, $P<0.0001$]. This finding lead us to ask whether corrective saccades also contribute to decreasing the initial error. To this end, gaze direction was measured at the end of corrective saccades, when they were present, or in the interval 60–90 ms after saccade offset, when they were lacking. As a result of corrective saccades, gaze direction further approached the expected direction, bringing the average compensatory capability to 0.73 and 0.33, respectively, for control and rotated saccades. As compared with the data reported in Fig. 6A and B, the effect was statistically significant in both cases [control saccades: $t(104)=5.790$; $P<0.0001$; rotated saccades: $t(668)=42.487$, $P<0.0001$].

Mental task

As also documented for the rotated saccade task, here too the response times depended in a linear fashion on the instruction angle and were not influenced by the stimulus direction. An individual example is reported in Fig. 3C and D. As shown in Fig. 7A and B, both the average slope (3.65 ms/deg) and intercept (1077 ms) were significantly higher than in the case of the rotated saccade task [slope: $t(6)=3.400$, $P=0.014$; intercept: $t(6)=11.005$, $P<0.0001$].

Given that we have no access to the "real" angular distance mentally covered before emitting the response, in order to compare the data of the mental task with that of the rotated saccade task, we must forcefully rely on the instruction angles as estimates of the angular distance. However, the slope difference persists, though less marked, even by considering, in the rotated saccade task, the SRT slope corrected for the effectively covered angle [$t(6)=2.527$, $P=0.044$]. That the slope difference was only apparent and the larger RTs in the mental task were simply the result of larger mentally covered angles can be excluded also by the following consideration. Two processes, starting at the same time with the same angular velocity of 1.87 ms/deg (the slope obtained in the rotated saccade task), would cover an angle of 154.3° in 289 ms. In the following 274 ms (i.e., the time difference between the moments in which a process rotating at 1.87 ms/deg and another rotating at 3.65 ms/deg, which is the slope obtained in the mental task, cover an angle of 154.3°), the covered angle would reach 301°, and this is untenable. Even if we consider the effective angles covered by saccades, we should admit that, for the same instruction angle of 154.3°, a saccade was directed at 134.7° and the point in space was mentally localized at 214.4°, which would mean that the mentally estimated angle should be 60% larger than that estimated in the rotated saccade task with the same visual input. Therefore, the different slopes cannot be fully explained by a process rotating at constant velocity covering different angles in the two tasks.

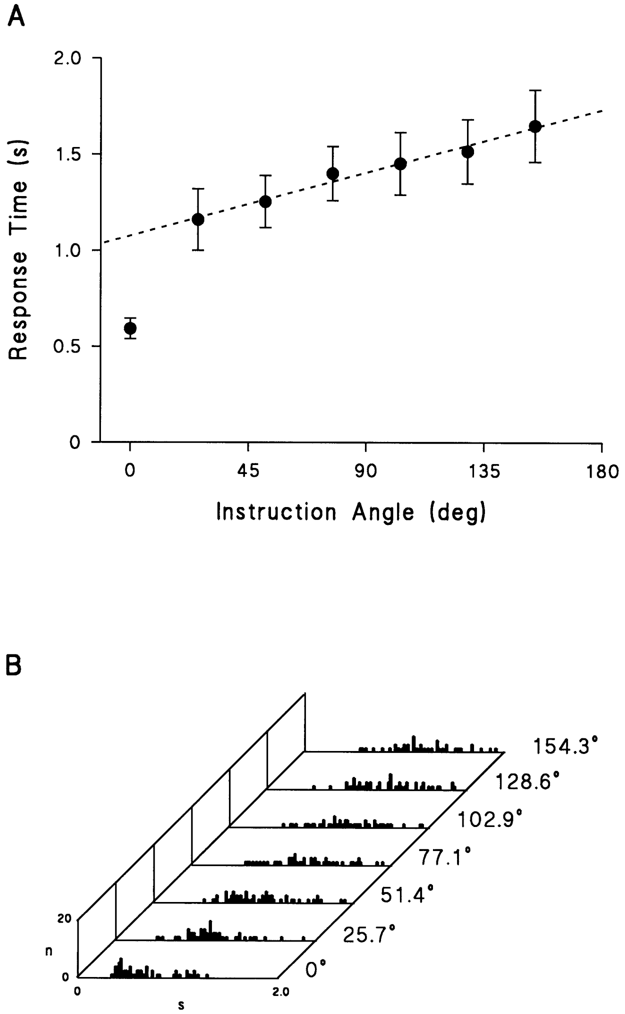

Fig. 7 **A** Mental task: mean response times across subjects, together with the 95% confidence interval, as a function of the instruction angle, together with the regression line. As in Fig. 4, in the regression analysis the response time value for the 0° instruction angle was omitted. **B** Distributions of response times for each instruction angle. Data for all subjects were pooled together. Response time range: 0.00–2.00 s. Bin width: 40 ms

In addition to a higher slope, the response time at the 0° instruction angle was also higher, as compared to the rotated saccade task, meaning that more time was required to press the button than to make a saccade. Moreover, similar to what was observed for SRT data, the response time for the 0° instruction angle was lower than that predicted on the basis of the extrapolated regression line calculated across the other six instruction angles. The difference amounted to 484 ms.

By considering only the subset of the seven subjects that participated in both tasks, we more directly compared the performance in the two conditions by a within-subjects analysis of variance on the response times, which revealed a significant effect of the task [*F*(1,6)= 68.247, *P*<0.0001] and a significant interaction between the instruction angle and the task [*F*(6,36)=17.776, *P*<0.0001], thus confirming that the effect of the instruction angle on the response times was different in the two tasks. This can be better seen by pairing, for each individual trial, the response time in the rotated saccade task with the response time in the mental task (Fig. 8A). Given that, a priori, there is no way of establishing which is the dependent and which is the independent variable, the slopes of the scatterplots were determined by the major axes of the confidence ellipses. A precise relation emerged both at the level of single subjects (dashed lines) and in the pooled data (solid line). The obtained average relationship between SRT and the response times in the mental task (MRT), together with the so-called normal coefficient of correlation (r), was:

$$SRT=0.28*MRT-1.15,\ r=0.783 \qquad (1)$$

The individual slope values were very consistent across the two tasks. In spite of the rather large between-subjects variability, it can be seen that a systematic increase of the slope emerged passing from the rotated saccade task to the mental task (Fig. 8B), regardless of the actual temporal order in which the two sessions were run. Remarkably, the performances in the two tasks were not independent. For each subject, we paired the slopes of the response time versus instruction angle obtained in the two tasks (Fig. 8C). The slopes were highly correlated. The relationship was:

$$SR=0.44*SM-0.31,\ r=0.850 \qquad (2)$$

where SR = slope in the rotated saccade task and SM = slope in the mental task.

Subjects were very reliable in suppressing saccades and maintaining a stable central fixation while performing in the mental task: in those subjects in which eye movements were recorded during the mental task, only in 2% of the trials was a saccade with an amplitude greater than 0.2° detected. The intercept and the slope of response times versus instruction angle obtained in this control experiment were almost indistinguishable from those obtained during the previous mental task sessions.

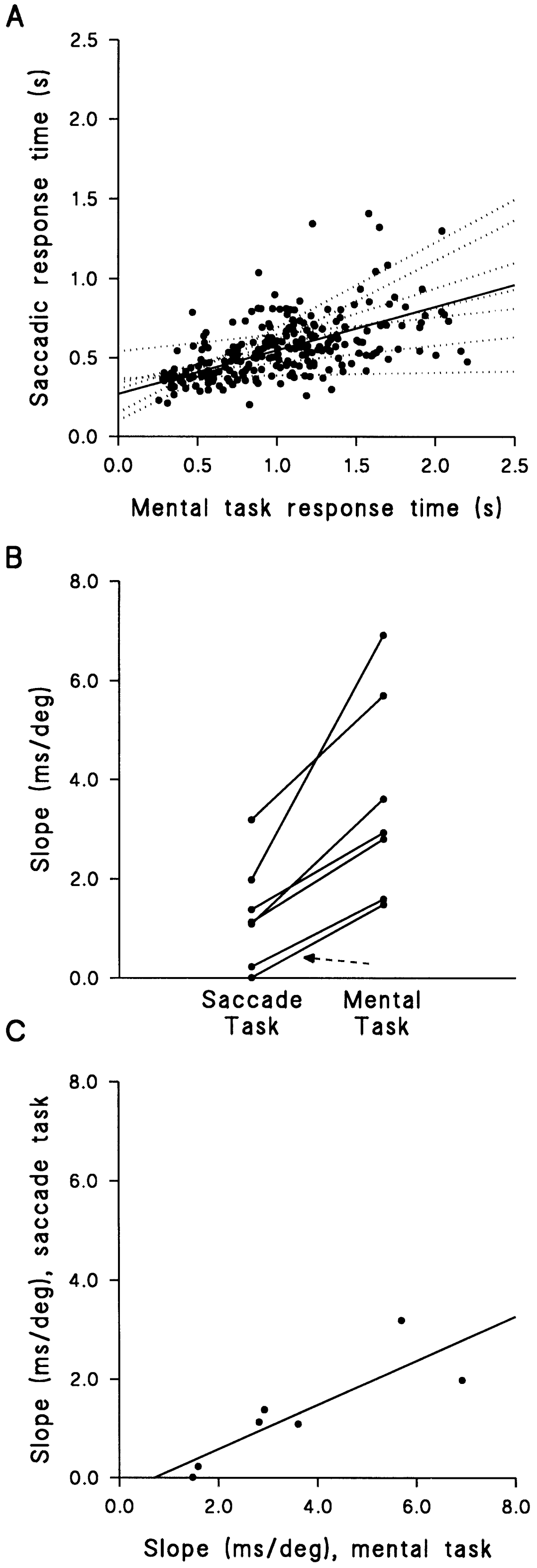

Fig. 8 **A** Relationship between the response times in the rotated saccade task and in the mental task. The coordinates of each data point represent the response times in the two tasks for each subject for the same stimulus direction and instruction angle. The *lines* are the major axes of the confidence ellipses (normal regression) calculated for each subject's data (*dashed lines*) and for all data points (*continuous line*). **B** Increase of individual slopes passing from the rotated saccade task to the mental task. Notice the consistency of the behavior, regardless the actual order of task administration (not shown) and in spite of the between-subject variability of the absolute slope values. The *arrow* indicates subject P.T. **C** Relationship between the individual slopes of response time versus instruction angle in the rotated saccade task and in the mental task, together with the regression line

Discussion

A first finding of this research is that the SRT is independent of the stimulus direction (e.g., Fig. 3A). This observation rules out a response strategy based upon the mental rotation of the entire virtual triangle representing the instruction angle (i.e., the one formed by the two radii as sides, one side being always at 0°, Fig. 1A) from its reference orientation up to the direction specified by the stimulus spot ("template model" strategy, Georgopoulos and Massey 1987). In fact, were this the case, it would be expected that the amount of mental rotation is determined by the angle that the stimulus direction forms with the reference orientation (3 o'clock): the larger this angle, the larger the SRT. However, this was not the case.

On the other hand, the SRT increased linearly with the instruction angle (Fig. 4). In general, longer response times associated with larger angular deviations have been claimed to depend on mental rotation processes in visuo-motor and perceptual-like tasks (Shepard and Cooper 1986; Georgopoulos and Massey 1987; see, however, Perrett et al. 1998). Clear evidence in favor of the mental rotation hypothesis came with the discovery, in the primary motor cortex of the monkey, of a reorientation of the direction coded by the neural population vector, which, in the course of 100 ms prior to movement onset, passed gradually through values intermediate between stimulus direction and movement direction (Georgopoulos et al. 1989; Lurito et al. 1991). Therefore, on the basis of the increasing saccadic latency for larger angular deviations and in virtue of the similarity of our task design with that of the visuo-motor mental rotation task, for which robust neurophysiological evidence is available, it can be proposed that rotated saccades involve a mental rotation process, which gradually transforms the stimulus direction into a saccade direction.

Mental rotation as a perceptual-like process

Mental rotation has been traditionally considered to be a perceptual-like process, in which visual mechanisms play a key role. This probably stems from the fact that the tasks usually employed for testing mental rotation involve visual stimuli that had to be variously rotated with the "mind's eye" in order for some evaluation to be made. This is the case, for example, of deciding whether two letters or geometrical shapes presented at different orientations are identical or mirror images (see Shepard and Cooper 1986). Thus, mental rotation has been depicted as that analog process through which we imagine rotating a visual object along a continuous trajectory (Shepard 1984). The functional equivalence advocated between visual perception and visual imagery (Finke 1989) further contributed to regarding mental rotation as a perceptual-like process (see Kosslyn 1994).

Within this theoretical framework, the tasks employed in the present study may be conceptualized as involving a visuo-spatial process that would rotate the stimulus direction into a given, desired direction and that would then feed the motor circuitry, whose only role would be to produce the required response, namely a saccade to the new target direction or a button press. Although a comprehensive picture establishing a precise anatomical localization for visuo-spatial abilities is not easy to draw (Kosslyn 1994, pp. 372–376), parieto-occipital regions would appear to be good candidates for performing visuo-spatial directional transformations. In fact, these areas have been shown to be implicated in several visuo-spatial operations (e.g., Corbetta et al. 1993), including visual imagery (Farah 1989) and classical visual mental rotation (Deutsch et al. 1988; Ditunno and Mann 1990; Cohen et al. 1996; Alivisatos and Petrides 1997).

Motor aspects of mental rotation

Despite purely visuo-spatial processes may be at the core of mental rotation, there are reasons for considering motor processes to be crucially involved as well. Much evidence has accumulated favoring the general view that the motor system cannot be merely regarded as an output system, but also participates as a causal link in some "mental" operations (Schereer 1984; Viviani and Stucchi 1992; Rizzolatti et al. 1994; Gallese et al. 1996; Viviani et al. 1997), suggesting that there might be a more strict interplay, yet poorly understood, than previously believed between motor and visual processes in mental rotation as well. Indeed, a clear distinction between what is "visual" and what is "motor" may be difficult to draw (Goodale 1998).

In classical mental rotation tasks involving the comparison of planar geometrical shapes presented at different orientations, a concomitant hand rotation selectively interferes with the response times (Wexler et al. 1998; see also Wohlschlager and Wohlschlager 1998): mental rotation is faster when the hand rotation is in the same direction. This allows the hypothesis that covert hand movements may guide the reorientation of the visual stimulus: we may take advantage of mentally "getting a grasp" on the visual object to mentally rotate it (Kosslyn 1994, p. 349). Moreover, it appears that we depend on a motor simulation strategy in distinguishing between a visually presented right- or left-hand or other body parts (Sekiyama 1982; Parsons 1987, 1994), motor neural structures being critically implicated (Parsons et al. 1995; Kawamichi et al. 1998). The motor hypothesis has been recently extended to the case of event recognition when the observed scene involves the motion of a manipulable object (de'Sperati and Stucchi 1997). In all these cases, covert motor processes have been claimed to underlie these various manifestations of mental rotation.

Compelling evidence for the notion that motor processes are involved in mental rotation is provided by the above-mentioned data showing a rotation of the intended movement direction in the monkey's primary motor cortex (Georgopoulos et al. 1989; Lurito et al. 1991). Truly, it might be argued that the participation of this motor area could be secondary to the fact that, in the visuo-motor mental rotation task, the response consists of a directed arm movement. The motor cortex may not be involved when the task does not require a directed motor response. In addition, the participation of motor structures could merely reflect the changes of the internally coded direction occurring upstream in the pathway mediating the reorientation of the stimulus direction into a movement direction, perhaps in parietal areas (Snyder et al. 1997), as suggested by previous studies on cortical activation during mental rotation. However, first, besides posterior/parietal regions, frontal premotor areas are also activated in classical mental rotation tasks, as revealed by brain-imaging techniques (Deutsch et al. 1988; Cohen et al. 1996). Second, in their fMRI study on classical mental rotation, Tagaris et al. (1997) were able to demonstrate, by means of a hierarchical tree modeling technique, that posterior parietal cortex activation is related to subsidiary aspects of mental rotation, while the key parameter characterizing mental rotation, namely, the speed of rotation, is associated with the amount of activation of the primary motor cortex (and, possibly, of part of adjacent premotor cortex), even in the case of this perceptual-like task. The involvement of the primary motor cortex in both a perceptual-like and a visuo-motor mental rotation task has been recently confirmed (Tagaris et al. 1998).

These findings fit with recent attributions of “higher” functions to the primary motor cortex, which may not play simply an executive role in arm movements (Georgopoulos et al. 1989; Alexander and Crutcher 1990a, 1990b; Georgopoulos 1991; Lang et al. 1996; Kawamichi et al. 1998). Therefore, it appears that the gradual reorientation of the neural population vector coding for the intended movement direction at the level of the primary motor cortex cannot be only regarded as a marginal aspect of mental rotation.

Mental rotation and the oculomotor system

From a general perspective, a growing body of evidence points to the existence of parallel pathways for arm/hand and oculomotor systems, even at the higher computing stages (Alexander et al. 1986; Rizzolatti et al. 1994; Passingham 1995; Snyder et al. 1997). It is doubtful that, in the context of visuo-motor transformations, a single neural structure dedicated to spatial processing per se even exists. Rather, spatial information would be separately processed within each specific sensorimotor domain (Rizzolatti et al. 1994). Parieto-frontal circuits appear to be segregated in this respect, area LIP–area 8 circuit being mostly concerned with visuo-oculomotor domain, and areas 7b–F4 and AIP–F5 circuits being primarily dedicated to sensorimotor transformations for reaching and grasping.

A crucial property of the neurons in the primary motor cortex of the monkey, as well as in several other motor and premotor structures (Kalaska et al. 1983; Fortier et al. 1989; Caminiti et al. 1991), is that the direction of a reaching arm movement is coded at the population level; that is, the movement direction can be predicted, even in advance of the actual movement, by considering the individual contribution of a large number of neurons, each discharging more strongly for a particular direction of movement (preferred direction). In particular, the discharge rate of each neuron can be described by a cosine function of the difference between the movement direction and the cell’s preferred direction (Georgopoulos et al. 1982). The closer the movement direction with the cell’s preferred direction, the higher the firing rate of that neuron. This implies that a pure frequency code is ambiguous, the same neuron discharging at the same rate for any two directions oriented symmetrically around the preferred one. In contrast, an ensemble of neurons unambiguously codes for a given direction. It is precisely this directional information coded at the population level that has been observed to change in a visuo-motor mental rotation task (Georgopoulos et al. 1989; Lurito et al. 1991).

A number of neural structures controlling saccadic eye movements are endowed with a somewhat similar direction-coding mechanism. Although differences exist, in lateral intraparietal area (Gnadt and Andersen 1988), frontal eye field (Bruce and Goldberg 1985), supplementary eye field (Russo and Bruce 1996), internal medullary lamina complex of the thalamus (Schlag-Rey and Schlag 1984), and superior colliculus (Sparks and Mays 1980), neurons whose discharge is broadly tuned for a particular saccade direction have been found. In the frontal eye field (FEF) and the supplementary eye field (SEF) of the monkey, the discharge rate of each neuron is best described by a Gaussian function (Bruce and Goldberg 1985; Russo and Bruce 1996), which is not so dissimilar from the cosine function found for primary motor cortex neurons. In addition, from microstimulation studies, it is known that the coded saccadic direction is mapped anatomically and not by a frequency code (Robinson 1972; Bruce et al. 1985; Anderson et al. 1998).

Thus, it appears that these neurons obey some computational principles similar to those governing the specification of direction for arm movements and, thus, posses the characteristics for mediating mental rotation in a similar manner; that is, through a rotation of the coded direction at the population level (Georgopoulos 1990). Yet, we do not know whether mental rotation for rotated saccades is indeed accomplished as in arm movements, nor which crucial structures are implicated in this process. We can simply propose, by analogy, that, in the rotated saccade task, in some of the structures of the oculomotor neural pathway it should be possible to observe a gradual reorientation of the coded saccadic direction, similar to what is observed in the primary motor cortex of monkeys engaged in visuo-motor mental rotation tasks.

Given the proposed parallelism of the arm/hand and the eye-motor systems at the cortical level, it can be expected that, in rotated saccades, cortical frontal motor/premotor structures controlling eye movements are involved in reorienting the stimulus direction into the saccade direction. The FEF, in particular, has been somewhat considered as an analog of the primary motor cortex (see Fisher and Bloch 1991; Passingham 1995); it not only establishes anatomical connections with brainstem oculomotor structures (Stanton et al. 1988), but it has been known for a long time that electrical stimulation evokes contralaterally directed saccades (Robinson and Fuchs 1969; Bruce et al. 1985). In addition, as we have seen, the saccade direction is coded here in a way not dissimilar from the way a reaching arm-movement direction is coded within the primary motor cortex (Bruce and Goldberg 1985). If we endorse the view that "Motor cortex governs movements of the limb and face, and the FEF the movements of the eye" (Passingham 1995, p. 122), then this latter structure can be regarded as a site where the rotation of the intended saccadic direction might be found.

Another piece of evidence also points to the participation of FEF in rotated saccades. In fact, FEF has been shown to be crucially involved in another variety of saccades whose target is internally-computed as well, namely, anti-saccades (Hallett 1978; Hallet and Adams 1980). These are saccades made in a direction opposite to that of the visual stimulus and are thought to involve a multistep process, including the inhibition of the "visual grasp reflex", i.e., the tendency to reflexively glimpse towards the visual stimulus, and the inversion of the directional vector (Guitton et al. 1985; Biscaldi et al. 1996). It is well established that anti-saccades, as opposed to visually guided saccades, require frontal and prefrontal brain structures (Guitton et al. 1985; O'Driscoll et al. 1995; Sweeney et al. 1996; Doricchi et al. 1997). The precise mechanism that inverts the intended direction of eye movement, however, is still poorly understood (Schlag-Rey et al. 1997). Mental rotation might be that mechanism, and anti-saccades might be considered as a 180° rotated saccade.

Yet, although the relevant differences between anti-saccades and rotated saccades might turn out to be related to the use of some "smart" strategy in executing anti-saccades (thus allowing the possibility that a mental rotation strategy might in fact also be employed in the anti-saccade task), it is unlikely that the same mechanism is at play in anti- and rotated saccades. In fact, first, anti-saccades show a number of peculiarities, notably, a longer duration, a lower peak velocity, and a more asymmetric velocity profile, compared with visually guided saccades (Smit et al. 1987). No comparable features emerged in our data for rotated saccades. Second, the longer latency of anti-saccades [+15 ms on average, compared with visually guided saccades under the overlap paradigm, Fisher and Weber (1992)], is considerably less than what can be derived by extrapolating our SRT data for an instruction angle of 180° (+444 ms, compared with control saccades, Fig. 4). However, given the differences in the experimental conditions, and especially the small amplitude of our saccades, a direct comparison is needed before firmly accepting this conclusion. At any rate, whether or not anti-saccades and rotated saccades make use of the same, yet unknown mechanism, both require an internal recomputation of the target direction, which sharply contrasts them with reflex-like visually guided saccades. In commenting the impairments exhibited by patients with frontal lesions in an anti-saccade task, Guitton et al. (1985, p. 470) observe that "... these structures appear crucial to the more complex task whereby a visual stimulus itself is not the target but defines a new target on the basis of prior instructions".

As in the case of anti-saccades, it is likely that a successful performance of rotated saccades may also depend on frontal/prefrontal structures other than FEF, such as the SEF (Schlag and Schlag-Rey 1987; Bon and Lucchetti 1992) and the dorsolateral prefrontal cortex (Funahashi et al. 1993). In particular, the firing properties and the anatomical connectivity of SEF neurons are not so dissimilar from those of FEF neurons (Russo and Bruce 1996). Interestingly, the saccadic directional tuning that many SEF neurons exhibit, far from being a fixed characteristic of the cells, may change as a result of a learning procedure (Chen and Wise 1996).

Rotated saccades may thus recruit a complex cortical network comprising prestriate, parietal, and frontal/prefrontal cortices, which mediate the generation of various kinds of purposive saccades (Fisher and Bloch 1991; Muri et al. 1996; Gaymard et al. 1998; Terao et al. 1998), as well as a subcortical loop involved in the preparation of the oculomotor command, in turn comprising the caudate nucleus, the substantia nigra (pars reticulata), and the thalamus (Gaymard et al. 1998). The precise role of these different neural structures in "high-level" oculomotor programming is still under investigation. Rotated saccades may constitute a useful experimental model in that not only the direction of the stimulus and the direction of the saccade are experimentally dissociated, but an on-line gradual transformation appears to be required to produce an eye movement in the appropriate direction. The application of the population-vector analysis (e.g., Lurito et al. 1991; see also Anderson et al. 1998) to various oculomotor structures may represent an helpful research tool for revealing the neural dynamics accompanying such stimulus-response directional transformations.

Common processes for mental rotation?

Given the similarity of behavior observed across very different perceptual and motor tasks, namely, a linear increase of response times for increasing angular differences, the hypothesis can be put forth that the same mental rotation process is shared by different systems. In addressing this point, Pellizzer and Georgopoulos (1993) found that the processing rates in a visuo-motor and a visual mental rotation task were highly correlated: subjects whose mental rotation speed was higher in the former task also had an higher speed in the latter task. It was also shown that such correlation could not be accounted for by some general processing-speed characteristics. To explain this finding, the authors envisaged both the hypothesis that a common neural structure performing the directional transformation is jointly accessed by both the motor and the perceptual systems and the hypothesis that the similarity of performance could be accounted for by similar directional information processing in various cortical areas. The fact that both common and separate neural structures have been shown to be activated in the two tasks (Tagaris et al. 1998) is not of much help in distinguishing between these alternatives.

In the present study, we made a similar comparison between an oculomotor-oriented and a visuo-spatial task. However, as opposed to previous research, the mental task was designed to retain, as much as possible, the visuo-spatial aspects of the rotated saccade task, including an identical visual stimulus. As in the case of rotated saccades, here too the response times increased linearly with the instruction angle (Fig. 7). Both the overall data (Fig. 7) and the subject-by-subject analysis (Fig. 8) indicated that the directional transformations were more time consuming in the mental task than in the rotated saccade task. The slope increase that could be observed by passing from the rotated saccade task to the mental task was very systematic despite the actual order of task presentation and the large between-subjects variability (Fig. 8B). Indeed, even in subject P.T. (Fig. 8B, arrow), the slope increase was almost exactly the same as that observed in the other subjects. In addition, the response times in the two tasks were not independent. Subjects faster in the rotated saccade task were also faster in the mental task (Fig. 8B and C).

These results are similar to what has been shown in the comparison between visuo-motor and classic mental rotation (Pellizzer and Georgopoulos 1993), with the difference that, in our case, subjects were slower in the mental rotation task than in the rotated saccade task, while in Pellizzer and Georgopoulos' study subjects were slower in the visuo-motor mental rotation task than in the classical mental rotation task. However, it should be noted that – besides the fact that, in that study, the two tasks employed different stimuli – in the visuo-motor task, subjects were required to move the arm in the horizontal plane in response to a visual stimulus presented in the vertical plane. Additional operations may be required to perform this kind of transformation.

A first interpretation of the different slopes observed in our tasks may be that mentally rotating a target for a saccade and mentally rotating a point in space, although the two tasks were designed to be as similar as possible, still remain quite distinct processes, each characterized by a given rotation speed. In this view, the correlation between the slopes may be ascribed to similarities in the mechanisms of directional transformation taking place in different neural structures. One hypothesis that we are currently testing is that the mental task is accomplished through an imagined rotation of the dot along the target circle, while, in the rotated saccade task, a "pure" directional transformation takes place, independent of the size of the target circle.

On the other hand, mental rotation may be carried out in a single structure recruited by both tasks. Although this would explain the correlation of RTs in the two tasks, the different slopes call for some additional assumptions. One possibility is that different computational loads are associated with different tasks: the same mechanism would work at a different speed according to the complexity of the object to be mentally rotated (see Cooper and Podgorny 1976). However, mental rotation speed is not a simple function of stimulus complexity: different mental rotation speeds can be observed when mentally rotating planar figures as similar as letters, numbers, or simple geometrical shapes (Shepard and Cooper 1986; Kosslyn 1994), yet stimuli with different complexities can also be processed with a similar mental rotation speed (Cooper and Podgorny 1976). In our case, the visual stimulus was the same in both tasks, so that the different slopes are unlikely to be related to visual aspects of the task. It can also be ruled out that the slope difference can be ascribed to the different response modality, since in this case we would have only expected a constant RT difference between the two tasks, as dictated by the requirements of the different final motor output, that is, the release of a saccade or a button press. Notice that a similar, constant RT difference is to be expected even if one posits that the mental task was purely modeled as a mental saccade task, that is, a motor imagery task. In fact, according to current views of motor imagery (see Jeannerod 1994), mentally imagining a movement is functionally equivalent to preparing it. Thus, neither sensory nor motor processes can account for the slope differences between the two tasks.

However, a slope difference can coexist with the notion of a common process guiding mental rotation, as it can be related to other aspects of the tasks. One possibility is that responding in the mental task takes longer than in the rotated saccade task because of a different response criterion. From some verbal reports of our subjects, it would appear that some additional final "checks" were performed in the mental task, as if there were greater concerns in explicitly localizing the point in the new direction when the task "required not simply moving the eye, but to be sure that the point was really 'there'". This would be consistent with both the larger step increase in passing from the 0° to the 25.7° instruction angle observed in the mental task, compared with the rotated saccade task, and the slope difference: the larger the instruction angle, the more difficult the task; hence, additional checks would be required.

If a common process underlies mental rotation in the two tasks, then, in light of a possible participation of oculomotor structures in reorienting the target direction in the rotated saccade task and given the involvement of the motor cortex in a classical perceptual-like mental rotation task (Tagaris et al. 1997, 1998), it is tempting to speculate that, not only in the rotated saccade task, but also in the mental task, what is actually being rotated is an intended eye movement vector. After a certain time lapse after stimulus presentation, the saccadic program accomplishing the directional transformation comes to completion and either an eye movement is released or, after additional angle-dependent operations, an explicit spatial evaluation is performed. Further investigations are needed to clarify this point.

In conclusion, although neither the available evidence argues for or against a common locus of mental rotation for motor-oriented and perceptual-like tasks nor can it yet be established whether the crucial operations occur in a purely visuo-spatial domain and/or as motor plans, in the light of the complex interplay between perceptual and motor processes, we may surmise that frontal oculomotor structures participate in rotated saccades through a reorientation of the intended saccadic direction. If a unique process can be shown to underlie both the rotated saccade and the mental task, then it still remains to be assessed: (1) whether oculomotor programming is indeed crucial not only in making a saccade to a point at an angle from the stimulus direction, but also in explicitly localizing it; and (2) why the mental task is more time-consuming than the rotated saccade task.

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