Exp Brain Res (1993) 93:165–172

Experimental
Brain Research

Common processing constraints for visuomotor and visual mental rotations

Giuseppe Pellizzer[1,2], **Apostolos P. Georgopoulos**[1,2]

[1] Department of Physiology, University of Minnesota Medical School, Minneapolis, MN 55455, USA
[2] American Legion and University of Minnesota Brain Chair, Brain Sciences Center, Veterans Affairs Medical Center, 1 Veterans Drive, Minneapolis, MN 55417, USA

Received: 16 July 1992 / Accepted: 30 October 1992

Abstract. Naive human subjects were tested in three different tasks: (1) a visuomotor mental rotation task, in which the subjects were instructed to move a cursor at a given angle from a stimulus direction; (2) a visual mental rotation task, in which the subjects had to decide whether a displayed letter was normal or mirror image regardless of its orientation in the plane of presentation; and (3) a visuomotor memory scanning task, in which a list of two to five stimuli directions were presented sequentially and then one of the stimuli (test stimulus), except the last one, was presented again. Subjects were instructed to move a cursor in the direction of the stimulus that followed the test stimulus in the previous sequence. The processing rate of each subject in each task was estimated using the linear relation between the response time and the angle (mental rotation tasks) or the list length (memory scanning task). We found that the processing rates in the mental rotation tasks were significantly correlated but that neither correlated significantly with the processing rate in the memory scanning task. These results suggest that visuomotor and visual mental rotations share common processing constraints that cannot be ascribed to general mental processing performances.

Key words: Cognitive processes – Movement direction – Mental rotation – Memory scanning – Human

Introduction

The question of how the brain manages mental images has markedly progressed in the last decades (Hebb 1968; Kosslyn 1988). Studies in cognitive psychology and neuroscience have provided a sufficient framework to allow for interactions between them. Notably, evidence has been provided that mental imagery is composed of different processing components, which are mediated by different neural systems (Farah 1984; Kosslyn 1988). For example, studies of normal and brain damaged human subjects have suggested that the *generation* and the *transformation* of mental images are distinct processes that involve differently posterior left and right cerebral hemispheric structures (see Farah 1989 for a review). In this paper we will focus on mental transformations and more specifically on mental rotations.

In a pioneer work, Shepard and Metzler (1971) have shown that the time required to determine whether two perspective drawings of a three dimensional object represent the same object or two mirror-image objects increases with the angular difference between their portrayed orientation. Several subsequent studies using two dimensional shapes and alphanumeric characters have confirmed these results (Shepard and Cooper 1982). This suggests that the subjects mentally rotate the image of the object from one orientation to another (e.g., rotation toward the standard upright position for alphanumeric characters) in order to check for its identity; therefore the larger the angular difference, the longer the time of rotation and the longer the response time (RT). Shepard and colleagues advanced the hypothesis that the process of mental rotation has analog properties in which the ongoing mental transformation has a one to one correspondence with the external rotation of an object. However, it was argued that mental transformations might be accounted for by propositional processing (Pylyshyn 1981). Although there are arguments in favor of the existence of nonpropositional cognition (Weiskrantz 1988), it was suggested that there might be no definitive answer to this question without neurophysiological data (Anderson 1978). As indicated below, recent neural studies argue for the existence of analog transformations.

Mental rotation is typically studied using visual stimuli (a few studies have also used tactile stimuli, e.g., Marmor and Zaback 1976) and therefore is exclusively considered as a perceptual-like process either implicitly or explicitly. This point of view is strengthened by evidence showing similar functional properties (Finke 1976; Podgorny and Shepard 1978) and brain areas involved

---

Correspondence to: A.P. Georgopoulos, Brain Sciences Center

(Kosslyn 1988; Farah 1989) for mental imagery and visual perception. However, the mental rotation is likely to be of more general application. Indeed, recent studies have supported the hypothesis of a mental rotation process when a movement has to be made at an angle from a visually defined direction (i.e., visuomotor mental rotation; Georgopoulos and Massey 1987; Georgopoulos et al. 1989; Lurito et al. 1991). When human subjects are asked to move the hand at an angle from a stimulus direction, the RT increases with the angle, which suggests that subjects do a mental rotation of an intended movement direction from the direction of the stimulus to the direction of the movement (Georgopoulos and Massey 1987). This hypothesis have been then verified with neural studies (Georgopoulos et al. 1989; Lurito et al. 1991). Monkeys were trained to execute an arm movement either in the direction of a visual stimulus (i.e., direct task) or at 90° counterclockwise from it (i.e., transformation task), depending on the brightness of the stimulus. The activity of cells in the motor cortex was recorded while monkeys performed the task. The data were analyzed using the neuronal population vector, which shows the intended movement direction coded by an ensemble of neurons (Georgopoulos et al. 1983, 1984, 1986). In direct reaching movements, the time-varying neuronal population vector points, during RT, in the direction of the upcoming movement (Georgopoulos et al. 1984, 1988; Lurito et al. 1991). In the transformation condition, the neuronal population vector rotated gradually from the direction of the stimulus toward the direction of the movement (Georgopoulos et al. 1989; Lurito et al. 1991). These results provide direct evidence for a rotation of a neuronal population signal and support the claim for the existence of an analog transformation.

However, the rotation of the neuronal population vector, when a movement has to be made at an angle from a stimulus direction, does not prove that the same neural mechanism holds for the mental rotation of visual images, nor does it indicate where the rotation comes from. These considerations raise the question of whether visuomotor and visual mental rotations share common aspects in the way the transformation is realized, or whether they are entirely different processes. We devised the following experiment to answer to this question, taking advantage of the fact that mental rotation rates may vary considerably among subjects (Shepard and Cooper 1982). The working hypothesis was that if visuomotor and visual mental rotations share common processing constraints, then a correlation should be observed between the processing rates of subjects performing in both tasks. However, it is also conceivable that a correlation between processing rates may result from general processing rate differences among subjects, that is, some subjects may perform generally faster, or slower, than others. Thus, a control is needed with a different kind of task where a processing rate can also be estimated independently of the mental rotation. We chose a visuomotor memory scanning task (Georgopoulos and Lurito 1991) which conforms to these requirements. This task allows us to estimate the rate of retrieval of visuomotor information.

In this task, RT increased with the list length (i.e., number of stimuli directions to memorize) and did not correlate significantly with the angle between the stimulus and the direction of movement, nor with the total angle covered by the list of stimuli (Georgopoulos and Lurito, unpublished results). Consequently, the subjects performed in three different tasks: (1) a visuomotor mental rotation task (Georgopoulos and Massey 1987), in which they were instructed to move a cursor at a given angle from a visual stimulus direction; (2) a visual mental rotation task inspired by the Cooper and Shepard letter rotation task (Shepard and Cooper 1982), in which subjects decided whether the letter displayed was normal or mirror image regardless of its orientation in the plane of presentation; and (3) a visuomotor context-recall memory scanning task (Georgopoulos and Lurito 1991), in which a list of two to five stimuli directions were presented sequentially. Then, one of the stimuli, except the last one, was displayed again (test stimulus). The subjects were instructed to move a cursor in the direction of the stimulus that followed the test stimulus in the previous sequence.

Materials and methods

Subjects

Twenty-six healthy human volunteers (11 women and 15 men) participated in the three tasks composing this experiment. The subjects were unpracticed in the tasks and naive concerning the purpose of the experiment.

Apparatus

The tasks were set up on a Silicon Graphics workstation (IRIS 4D/210GTX). Subjects were seated about 50 cm in front of the color monitor on which stimuli were displayed. They responded using the computer mouse, either by displacing it (visuomotor mental rotation and memory scanning tasks) or by pressing on one of the buttons (visual mental rotation task). The clock resolution was set at 1200 Hz. The mouse and the mouse pad were placed horizontally underneath the level of the monitor in the subject's midsagittal plane.

Behavioral tasks

The order of presentation of the following three tasks was randomized across subjects. A schematic diagram of the tasks is presented in Fig. 1.

Visuomotor mental rotation task. Five blocks of 12 trials corresponding to five instruction angles were presented randomly to the subjects. At the beginning of each block, two lines forming an angle were displayed to indicate the instruction angle. One line was always horizontal, whereas the other one formed an angle that could be from 0 to 140°, every 35° in the counterclockwise direction. Two more blocks of trials with different instruction angles were used for practice before the experimental trials. The subjects were instructed to make a movement that deviated from a stimulus direction by an angle that corresponded to the instruction angle. At the beginning of each trial, the subjects had to place the mouse cursor in the center of the screen, where a black dot (0.25 cm radius) was displayed. After a random variable delay from 1 to 1.5 s, the central dot

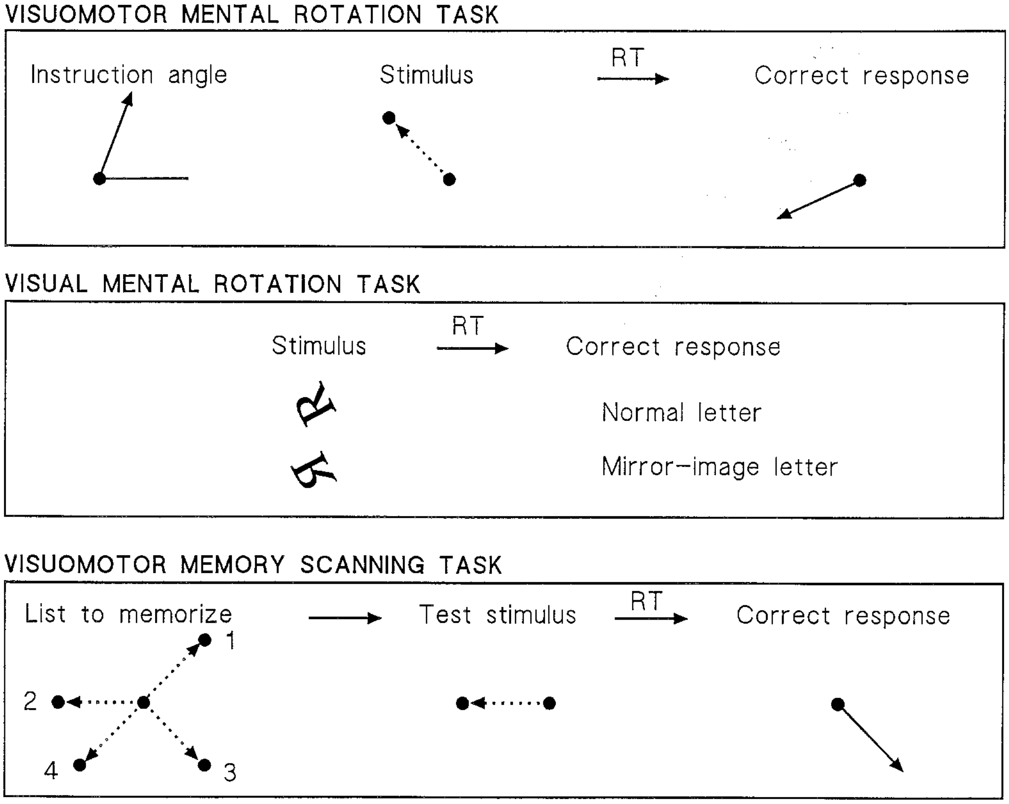

Fig. 1. Schematic diagram of the three tasks used. See text for details. *RT*, response time

disappeared and a peripheral dot was displayed in one of 12 directions, every 30° on a circle of 4.5 cm radius. A beep was simultaneously presented with the peripheral dot. The subjects were asked to respond quickly and accurately when the peripheral target appeared. The RT was measured from the presentation of the peripheral dot until when the cursor exited the central dot of 0.25 cm radius. The direction of the movement was calculated relative to the center when the cursor exited a circle of 1.75 cm radius. The calibration between the displacement of the mouse and the displacement of the cursor was 1: 2. Trials in which the direction of the response deviated by more than 22° from the ideal direction, or the RT was less than 100 ms were presented again randomly in the sequence of trials.

Visual mental rotation task. An upper case letter R (Times roman typeface, 200 points) and its mirror image were used as stimuli. The stimuli were presented at various angles, every 60° between 0 and 300° from the standard upright position. Ten repetitions of each combination of stimulus and orientation were randomly presented to the subjects. Twenty trials with a letter L and its mirror image as stimuli were presented at the beginning for practice. The subjects were asked to discriminate quickly and accurately whether the stimulus was the normal letter or its mirror image regardless of the orientation in the plane of presentation. The left mouse button was assigned for the normal letter and the right one for the mirror-image letter. Subjects responded by pressing on the appropriate button of the mouse. The RT was measured from the presentation of the stimulus to when one button was pressed. The trials with wrong responses, or with RT less than 100 ms, were presented again randomly.

Visuomotor memory scanning task. At the beginning of each trial, the subjects had to place the mouse cursor in the center of the screen, where a black dot (0.25 cm radius) was displayed. Pseudorandom lists of two to five stimuli directions were presented to the subjects. The stimuli were black dots that appeared successively at random locations on a circle of 4.5 cm radius. Each stimulus lasted 800 ms, and an interval of 150 ms separated the end of one stimulus presentation and the beginning of the next one; during this time subjects did not move, unlike in a previous study (Georgopoulos and Lurito 1991). After 1 s from the end of the sequence, one of the stimuli presented during the sequence, except the last one, was chosen randomly and presented again (test stimulus) with a beep. The subjects were instructed to give a quick and accurate response by moving in the direction of the stimulus that followed the test stimulus in the list. Twelve repetitions for each list length were presented randomly. Although the number of repetitions was the same for each list length, the number of repetitions for the serial positions was variable across list lengths and across subjects because of the random assignment of the stimuli. A series of 12 more trials was presented at the beginning for practice. The RT was measured from the presentation of the test stimulus until the cursor exited a circle of 0.25 cm radius. The calibration of the mouse and the measure of the direction of the movement were done as in the visuomotor mental rotation task above. Trials where the direction of the response deviated by more than 22° from the ideal direction, or the RT was less than 100 ms, were presented again randomly with the same list length, but composed of other stimuli.

Data analysis

Directional analyses. The spatial performance in the visuomotor tasks (viz., the mental rotation and memory scanning tasks) was assessed using circular statistics (Mardia 1972) including all the movements, whether or not they met the criterion of correct response. *Constant directional error* for each subject and condition was calculated as the mean direction of the movement. The overall mean direction and its circular standard deviation (CSD) across subjects was then computed. The signed difference between this direction and the ideal direction was the constant directional error (counterclockwise errors were positive; clockwise errors were negative). *Directional variability* for each subject and condition was calculated as the CSD of the movement direction. The mean CSD across subjects and its standard deviation (SD) was then computed.

Analyses of RT. For the two visuomotor tasks, only the trials that met the criterion of correct response (i.e., movement direction within ± 22° from the ideal direction) were used for the analyses of RT. Similarly, in the visual mental rotation task only the correct responses were used in the analyses of RT. As the incorrect trials were repeated during the experiment, the same number of trials was considered in each condition for the analyses of RT. For each subject and each task we computed a Pearson correlation coefficient r and a least squares linear regression (Snedecor and Cochran 1980) between the median RT of the correct responses and the appropriate independent variable, that is, (1) the instruction angle for the visuomotor rotation task, (2) the letter orientation angle from the upright position for the visual rotation task, and (3) the list length for the visuomotor memory scanning task. The inverse of the slope obtained by linear regression is an estimate of the individual rate of processing in each task. For the two rotation tasks, we considered the smaller of the two possible angles (i.e., angle $\leq 180°$). For the visuomotor rotation task, we have also computed for each subject the linear regression of RT on achieved angle (i.e., angle between the direction of the stimulus and the direction of the movement) using the raw data. This latter method provides another way to estimate the rate of rotation in the visuomotor rotation task, which cannot, however, be used for the visual rotation task, for there is no achieved angle that can be measured in this task.

The correlation between the *processing rates* in the different tasks was tested using the Spearman rank correlation coefficient r_s, which is equivalent to the rank correlation between the slopes. The correlation between the *slopes* was also assessed using the Pearson correlation coefficient r. Effects were tested using standard statistical techniques (Snedecor and Cochran 1980).

We used the median as a nonparametric measure of the middle of the RT distributions because of the positive skewness of these distributions and for its resistance to outliers. However, very similar results were obtained using the maximum normed residual criterion to exclude outliers (Snedecor and Cochran 1980) and computing arithmetic or geometric means, the last to correct for the distribution asymmetry. A preliminary account of the results has been published (Pellizzer et al. 1991).

Results

Visuomotor mental rotation task

Spatial performance. In the direct trials (i.e., instruction angle = 0°) the constant directional error was small (constant directional error ± CSD: 1.8 ± 3.6°). In the transformation trials the movement direction tended to overshoot the smaller instruction angles of 35, 70, and 105° (constant directional error ± CSD: 19.4 ± 4.6°; 2.3 ± 5.9°; and 13.2 ± 9.2°, respectively) and undershoot the largest instruction angle of 140° (–21.5 ± 6.5°). The variability of the movement direction increased with the instruction angle (mean CSD ± SD: 8.7 ± 7.4°; 15.7 ± 7.3°; 18.9 ± 7.8°; 21.8 ± 3.8°; and 21.7 ± 6.5°, respectively). Thirty percent of all the trials did not meet the spatial criterion for correct response (see Materials and methods).

Response time. For all the subjects the median RT of the correct responses increased with the instruction angle. The correlation r ranged from 0.620 to 0.998, and its mean across subjects was 0.945 (the mean of r was computed using the z Fisher transformation; Snedecor and Cochran 1980). The average linear relation between RT (in milliseconds) and instruction angle (θ in degrees) over all the subjects was:

$$\mathrm{RT} = 447 + 4.08\,\theta \qquad (1)$$

which indicates an average processing rate of 245°/s. However, the slopes for the different subjects varied considerably and ranged from 0.58 to 12.26 ms/degree, which correspond to processing rates of 1728 and 82°/s, respectively. Examples of data from three subjects (S_1, S_2, and S_3) in the visuomotor mental rotation task are presented in Fig. 2. In these plots median RT is plotted as a function of the instruction angle, and the error bars show the interquartile range (i.e., range between the 25th and the 75th percentiles). It can be observed that RT increased with the angle and that the processing rates differed greatly among these subjects.

Using the raw data, the average linear relation between RT (in milliseconds) and achieved angle (θ in degrees) over all the subjects was:

$$\mathrm{RT} = 445 + 4.39\,\theta \qquad (2)$$

which corresponds to an average processing rate of 228°/s. The slopes computed with the first and second methods were obviously highly correlated ($r = 0.951$).

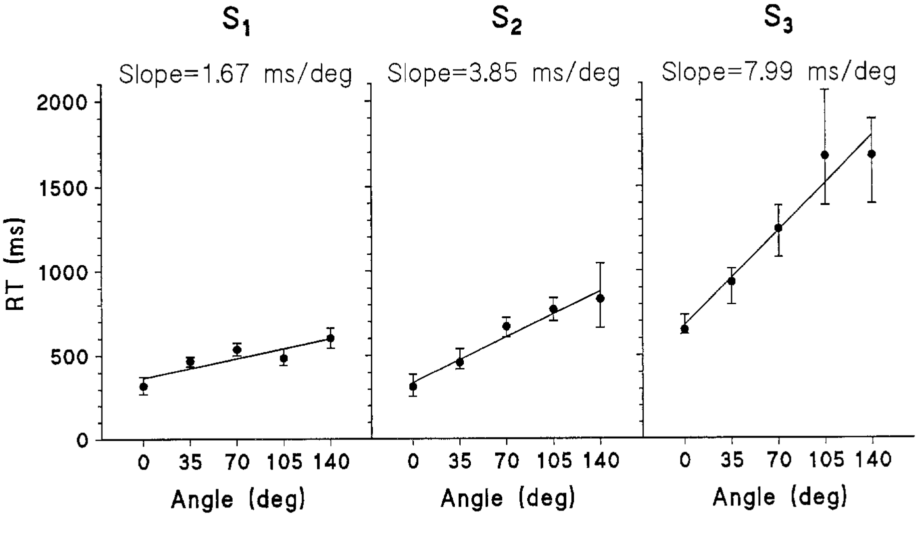

Fig. 2. Examples of data from three subjects (*left*, S_1; *center*, S_2 ; and *right*, S_3) in the visuomotor mental rotation task. The median response time (RT) is plotted as a function of the instruction angle. The *error bars* indicate the interquartile range. The slope obtained for each subject is shown inside each plot. The corresponding estimated processing rates were 600°/s, 260°/s, and 125°/s for S_1, S_2, and S_3, respectively

Visual mental rotation task

Errors. The error rate was low and corresponded to 3.8% of the trials. The mean number of errors increased with the angle of the letter from the standard upright position (mean number of errors ± SD: 0.35 ± 0.89; 0.46 ± 0.76; 1.58 ± 2.19; 2.50 ± 3.09 for the angles of 0, 60, 120, and 180°, respectively).

Response time. For all the subjects, the median RT increased with the angular departure of the stimulus (normal or mirror-image letter) from the standard upright position. When the stimulus was the normal letter, the average relation between RT (in milliseconds) and the angle (θ in degrees) was:

$$RT = 531 + 2.54\,\theta \qquad (3)$$

with a mean correlation r of 0.932 (range from 0.751 to 0.995). When the stimulus was the mirror-image letter the average relation was:

$$RT = 622 + 2.54\,\theta \qquad (4)$$

with a mean correlation r of 0.927 (range from 0.763 to 0.992). The intercepts were significantly smaller with the normal letter than with the mirror-image letter [paired $t(25) = 4.62$; $P < 0.001$], whereas the slopes did not differ [paired $t(25) = 0.0008$; $P > 0.99$]. As we were interested in the slopes, we computed the median RT, putting together the responses to the normal and mirror-image letters. The average relation between RT and the angle from the upright position was then:

$$RT = 573 + 2.50\,\theta \qquad (5)$$

with a mean correlation r of 0.944 (range from 0.773 to 0.999). This relation indicates an average processing rate of 400°/s. However, as in the previous task, the individual slopes varied appreciably among subjects and ranged from 0.53 to 5.23 ms/degree corresponding to processing rates of 1878 and 191°/s, respectively. Examples of data from the same three subjects chosen for Fig. 2 are presented in Fig. 3, where median RT is plotted as a function of the letter orientation angle from the upright position and the error bars show the interquartile range. Similar to the visuomotor mental rotation task, the RT increased with the angle, and the estimated processing rates of each subject were markedly different.

Visuomotor memory scanning task

Spatial performance. The constant directional error did not vary systematically with the list length (constant directional error ± CSD: 2.1 ± 3.6°; 1.1 ± 4.4°; 3.1 ± 5.8°; and 2.1 ± 8.9° for the list lengths of 2, 3, 4, and 5 stimuli, respectively). In contrast, the CSD increased with the list length (mean CSD ± SD: 8.8 ± 2.0°; 11.8 ± 7.1°; 22.4 ± 12.1°; and 43.0 ± 11.9° for the lists of 2, 3, 4, and 5 stimuli, respectively). Eighteen percent of all the trials did not meet the spatial criterion for correct response (see Materials and methods).

Response time. We performed a multiple linear regression analysis over all the RTs of the correct responses with the list length and the serial position of the stimulus test in the list as independent variables. All the trials were included in this analysis because the number of repetitions for each combination of list length and serial position was variable (see Materials and methods). The result showed that RT was significantly correlated with list length [$t(1245) = 13.22$; $P < 0.001$], but not with serial position [$t(1245) = 0.10$; $P = 0.92$]. The average relation between RT (in milliseconds) and the list length (s, number of items) was:

$$RT = 130 + 163.1\,s \qquad (6)$$

with a mean correlation r of 0.977 (range from 0.637 to 0.998). This relation indicates an average processing rate of 6.1 items per second. The individual slopes ranged from 86.6 ms/item to 387.0 ms/item, which correspond to processing rates of 11.6 items per second and 2.6 items per second, respectively. In Fig. 4 we present the data of the same subjects used for the two previous figures, where median RT is plotted as a function of list length and the error bars show the interquartile range. It can be ob-

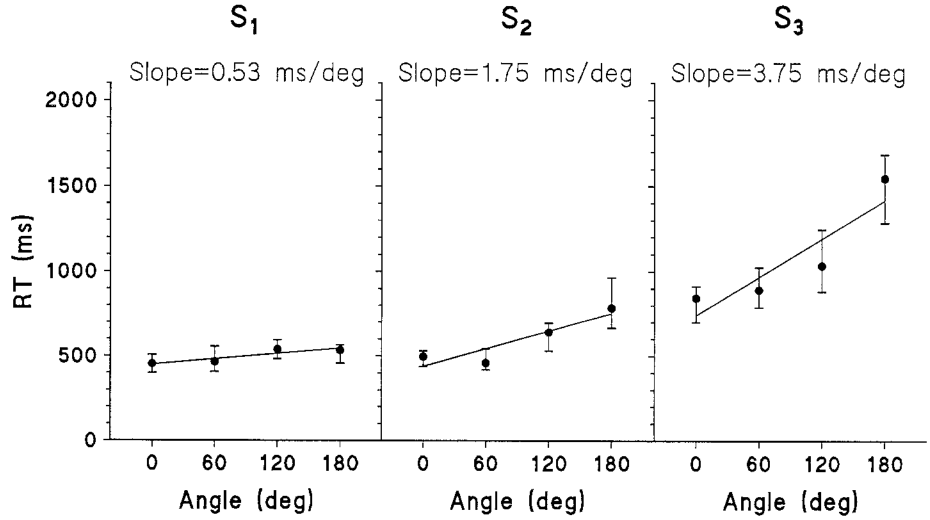

Fig. 3. Examples of data from three subjects (*left*, S_1; *center*, S_2; and *right*, S_3) in the visual mental rotation task. The subjects are the same as those chosen for Fig. 2. The median response time (RT) is plotted as a function of the letter orientation angle from the upright position. The *error bars* indicate the interquartile range. The slope obtained for each subject is shown inside each plot. The corresponding estimated processing rates were 1878°/s, 573°/s, and 267°/s for S_1, S_2, and S_3, respectively

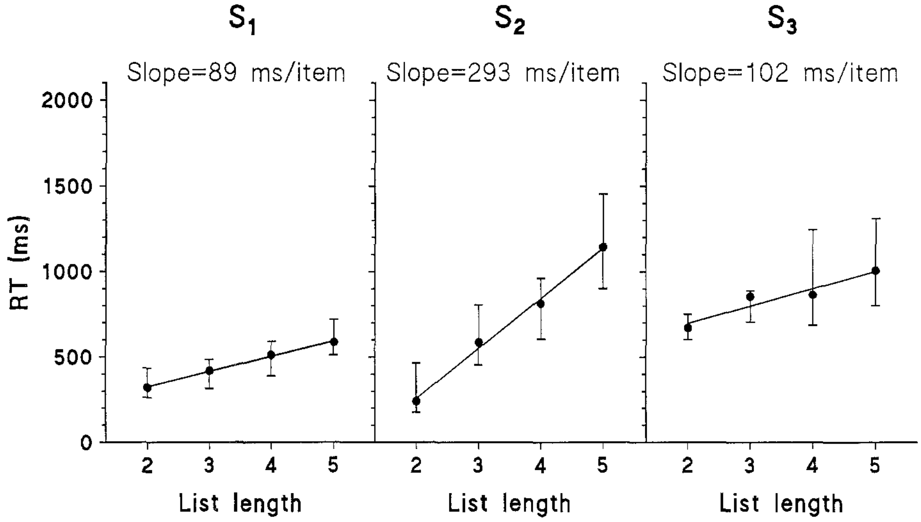

Fig. 4. Examples of data from three subjects (*left*, S_1; *center*, S_2; and *right*, S_3) in the visuomotor memory scanning task. The subjects are the same as those chosen for Figs. 2 and 3. The median response time (RT) is plotted as a function of the list length (i.e., number of stimuli directions to memorize). The *error bars* indicate the interquartile range. The slope obtained for each subject is shown inside each plot. The corresponding estimated processing rates were 11.2 items per second, 3.4 items per second, and 9.8 items per second for S_1, S_2, and S_3, respectively

Table 1. Spearman rank correlation r_s between estimated processing rates of each subject ($n = 26$) in each task

	Visual mental rotation	Visuomotor memory scanning
Visuomotor mental rotation	0.653*	0.253
Visual mental rotation		0.279

* $P < 0.001$

served that RT increased with list length and that the individual processing rates were very different.

Association between processing rates

The notable variability of the individual slopes and processing rates in each task legitimates the computation of a correlation. The rank correlations r_s between the individual estimated processing rates in the different tasks (which is equivalent to the rank correlation between the individual slopes) are presented in Table 1. For this table we used for the visuomotor rotation task the processing rate estimated from the linear regression of median RT on instruction angle. This method is the most similar to the one used for the other tasks (see Materials and methods). The only significant correlation was between the processing rates in the visuomotor and visual mental rotation tasks ($r_s = 0.653$; $P < 0.001$). No significant correlation (at least $P > 0.16$ in both cases) was obtained between processing rates in both mental rotation tasks and processing rates in the visuomotor memory scanning task. Moreover, no significant correlation resulted between the intercepts of the individual linear regressions in each task. The same effects occurred when the processing rate in the visuomotor rotation task was estimated from the linear regression of RT on achieved angle. In this case, the rank correlation between the processing rates in the two rotation tasks was $r_s = 0.586$ ($P < 0.001$). The data presented in Figs. 2–4 illustrate these results. Indeed, comparing the performances of the three subjects in each task reveals that in the two mental rotation tasks the slopes are in ascending order from subject S_1 to S_3 (that is, the processing rates are in descending order), whereas they are in a different order for the visuomotor memory scanning task.

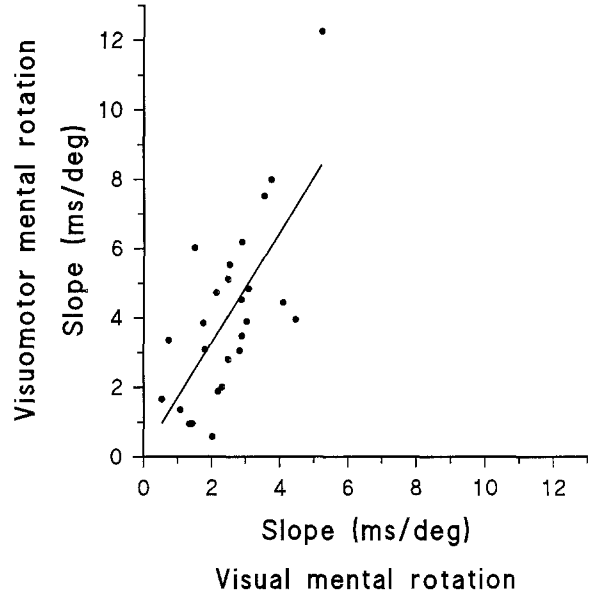

Fig. 5. The individual slopes obtained from the linear regression of median response time on angle for the visuomotor mental rotation task and for the visual mental rotation task are plotted against each other

The correlation between slopes was also analyzed using the Pearson correlation coefficient r. As with the previous analyses, the only significant correlation was between the slopes obtained in the two mental rotation tasks, using for the visuomotor rotation task either the slope resulting from the linear regression of median RT on instruction angle ($r = 0.694$: $P < 0.001$), or the linear regression of RT on achieved angle ($r = 0.660$; $P < 0.001$). In Fig. 5 are plotted the individual slopes obtained for the visuomotor mental rotation task by linear regression of median RT on instruction angle against the slopes obtained for the visual mental rotation task by linear regression of median RT on angle from upright position. The linear regression between the slopes in both tasks is plotted as a continuous line and was equal to:

$$Slope_{\text{Visuomotor mental rotation}} = 0.12 + 1.59\ Slope_{\text{Visual mental rotation}} \tag{7}$$

The intercept of (7) was not significantly different from zero [$t(24) = 0.13$; $P = 0.90$].

The slopes in the visuomotor mental rotation task were significantly higher than in the visual mental rotation task [paired $t(25) = 4.10$; $P < 0.001$], whereas the intercepts were significantly lower [paired $t(25) = -4.64$; $P < 0.001$]. No significant differences were obtained between men and women in the comparisons between intercepts and between slopes in the three tasks (all t-tests with at least $P > 0.14$).

Discussion

We were interested to assess whether visuomotor and visual mental rotations share common processing constraints, or whether they are independent processes. For this purpose, we compared the performances of human subjects in a visuomotor mental rotation task and a visual mental rotation task. More specifically we tested whether the estimated individual processing rates in both tasks were correlated. Moreover, to control for the possible effect of a more general processing speed factor (i.e., subjects might be generally fast or slow for mental processing), we also compared performance in the mental rotation tasks with those in a visuomotor memory scanning task. We found that the processing rates in the two mental rotation tasks were correlated, but neither correlated significantly with the processing rate in the visuomotor memory scanning task. These results suggest that visuomotor and visual mental rotations are not completely independent and that, instead, they possess some common processing constraints that cannot be ascribed to general processing rate performances. Moreover, we found that the slopes of RT versus angle obtained in the visuomotor mental rotation task were 59% higher than those obtained in the visual mental rotation task. This suggests that mentally rotating an intended movement direction is more time-consuming than for two-dimensional visual images such as letters. Instead, the difference obtained between intercepts is related to the time spent for all other processes that are not the mental rotation itself. It can be related to the encoding of the stimulus, the preparation and execution of the response, and to the method to determine the RT, which was different for the visuomotor and the visual mental rotation tasks.

Studies concerning the neural bases of mental imagery in humans subjects have documented activation in the occipital, parietal, and temporal cortex; these same regions are also activated during visual tasks (for a review see Kosslyn 1988; Farah 1989). As far as mental rotation is concerned, studies on human brain-damaged subjects showed that performance in a visual mental rotation task was more impaired after a right posterior lesion than a left posterior lesion (Ratcliff 1979). A result compatible with the latter one was obtained in a study with a patient who had undergone commissurotomy performed close to normal mental rotations only when stimuli were presented to the left visual field (i.e., to the right cerebral hemisphere; Corballis and Sergent 1988). Moreover, the measures of evoked potentials and regional cerebral blood flow in normal human subjects performing in a mental rotation task showed a greater activation in the right parietal region (Papanicolaou et al. 1987). These results show that visual mental rotations in human subjects involve structures in the parietal region and primarily in the right cerebral hemisphere. On the other hand, studies on monkeys have shown changes of neuronal activity in the motor cortex in relation to visuomotor mental rotation (Georgopoulos et al. 1989; Lurito et al. 1991).

There are two major hypotheses that can account for the results obtained in this study. One idea is that mental rotation, be it perceptual or visuomotor, involves a certain brain area which is jointly accessed by both the perceptual and the motor systems, and therefore the similar processing constraints observed would be due to processing features of that particular brain area. Although this hypothesis is possible, data for or against it are lacking.

The other hypothesis is that mental rotation involves different systems, perceptual or motor, depending on the task, and that similar processing constraints reflect limitations due to the process of rotation itself, irrespective of whether it is implemented in perceptual or motor systems. There is evidence in support of this idea. First, as discussed above, different structures seem to be involved in visual and visuomotor mental rotations, namely parietal and frontal areas, respectively. Second, the processing of motor directional information in frontal cortex and visual directional information in parietal cortex follows the same rules, both at the single cell and neuronal population levels. That is, in both frontal (Georgopoulos et al. 1983, 1984, 1986, 1988; Caminiti et al. 1991) and parietal (Steinmetz et al. 1987) areas directional information is coded in broadly tuned cell activity and, unambiguously, in the neuronal ensemble (population vector). This similarity in directional processing may underlie the similarity in the characteristics of the perceptual and visuomotor mental rotation, and thus be the neural substrate for the common constraints observed at the behavioral level.

Acknowledgements. This research was supported by United States Public Health Service grant NS17413, Office of Naval Research contract N00014-88-K-0751, and a grant from the Human Frontier Science program. G. Pellizzer was supported by a fellowship of the Swiss National Science Foundation. Part of this work was done at the Department of Neuroscience, The Johns Hopkins University School of Medicine, Baltimore Md., USA.

References

Anderson JR (1978) Arguments concerning representations for mental imagery. Psychol Rev 85:249–277

Caminiti R, Johnson PB, Galli C, Ferraina S, Burnod Y, Urbano A (1991) Making arm movements within different parts of space:

the premotor and motor cortical representation of a coordinate system for reaching at visual targets. J Neurosci 11:1182–1197

Corballis MC, Sergent J (1988) Imagery in a commissurotomized patient. Neuropsychologia 26:13–26

Farah MJ (1984) The neurological basis of mental imagery: a componential analysis. Cognition 18:245–272

Farah MJ (1989) The neural basis of mental imagery. Trends Neurosci 12:395–399

Finke RA (1976) Levels of equivalence in imagery and perception. Psychol Rev 87:113–132

Georgopoulos AP, Lurito JT (1991) Cognitive spatial-motor processes. 6. Visuomotor memory scanning. Exp Brain Res 83:453–458

Georgopoulos AP, Massey JT (1987) Cognitive spatial-motor processes. 1. The making of movements at various angles from a stimulus direction. Exp Brain Res 65:361–370

Georgopoulos AP, Caminiti R, Kalaska JF, Massey JT (1983) Spatial coding of movement: a hypothesis concerning the coding of movement direction by motor cortical populations. Exp Brain Res [Suppl] 7:327–336

Georgopoulos AP, Kalaska JF, Crutcher MD, Caminiti R, Massey JT (1984) The representation of movement direction in the motor cortex: single cell and population studies. In: Edelman GM, Gall WE, Cowan WM (eds) Dynamic aspects of neocortical function. Wiley, New York, pp. 501–524

Georgopoulos AP, Schwartz AB, Kettner RE (1986) Neuronal population coding of movement direction. Science 233:1416–1419

Georgopoulos AP, Kettner RE, Schwartz AB (1988) Primate motor cortex and free arm movements to visual targets in three-dimensional space. II. Coding of the direction of movement by a neuronal population. J Neurosci 8:2928–2937

Georgopoulos AP, Lurito JT, Petrides M, Schwartz AB, Massey JT (1989) Mental rotation of the neuronal population vector. Science 243:234–236

Hebb DO (1968) Concerning imagery. Psychol Rev 75:466–477

Kosslyn SM (1988) Aspects of a cognitive neuroscience of mental imagery. Science 240:1621–1626

Lurito JT, Georgakopoulos T, Georgopoulos AP (1991) Cognitive spatial-motor processes. 7. The making of movements at an angle from a stimulus direction: studies of motor cortical activity at the single cell and population levels. Exp Brain Res 87:562–580

Mardia KV (1972) Statistics of directional data. Academic, New York London

Marmor GS, Zaback LA (1976) Mental rotation by the blind: does mental rotation depend on visual imagery? J Exp Psychol [Hum Percept] 2:515–521

Papanicolaou AC, Deutsch G., Bourbon WT, Will KW, Loring DW, Eisenberg HM (1987) Convergent evoked potential and cerebral blood flow evidence of task-specific hemispheric differences. Electroencephalogr Clin Neurophysiol 66:515–520

Pellizzer G, Massey JT, Bains H, Georgopoulos AP (1991) Are there common processing constraints for visuomotor and perceptual mental rotations? Soc Neurosci Abstr 17:1226

Podgorny P, Shepard RN (1978) Functional representations common to visual perception and imagination. J Exp Psychol [Hum Percept] 4:21–35

Pylyshyn ZW (1981) The imagery debate: analogue media versus tacit knowledge. Psychol Rev 88:16–45

Ratcliff G (1979) Spatial thought, mental rotation and the right cerebral hemisphere. Neuropsychologia 17:49–54

Shepard RN, Cooper LA (1982) Mental images and their transformations. MIT, Cambridge, Mass.

Shepard RN, Metzler J (1971) Mental rotation of three-dimensional objects. Science 171:701–703

Snedecor GW, Cochran WG (1980) Statistical methods, 7th edn. Iowa State University Press, Ames, Iowa

Steinmetz MA, Motter BC, Duffy CJ, Mountcastle VB (1987) Functional properties of parietal visual neurons: radial organization of directionalities within the visual field. J Neurosci 7:177–191

Weiskrantz L (ed) (1988) Thought without language. Oxford University Press, Oxford