Mental object rotation and the planning of hand movements

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Recently, we showed that the simultaneous execution of rotational hand movements interferes with mental object rotation, provided that the axes of rotation coincide in space. We hypothesized that mental object rotation and the programming of rotational hand movements share a common process presumably involved in action planning. Two experiments are reported here that show that the mere planning of a rotational hand movement is sufficient to cause interference with mental object rotation. Subjects had to plan different spatially directed hand movements that they were asked to execute only after they had solved a mental object rotation task. Experiment 1 showed that mental object rotation was slower if hand movements were planned in a direction opposite to the presumed mental rotation direction, but only if the axes of hand rotation and mental object rotation were parallel in space. Experiment 2 showed that this interference occurred independent of the preparatory hand movements observed in Experiment 1. Thus, it is the planning of hand movements and not their preparation or execution that interferes with mental object rotation. This finding underlines the idea that mental object rotation is an imagined (covert) action, rather than a pure visual-spatial imagery task, and that the interference between mental object rotation and rotational hand movements is an interference between goals of actions.

The time it takes to compare two similar shapes of different orientation is known to increase linearly with the angular disparity between the two shapes (Förster, Gebhardt, Lindlar, Siemann, & Delius, 1996). This so-called mental rotation effect occurs most reliably if mirror images are used as odd comparison stimuli (M. C. Corballis & McLaren, 1984; for a review, see M. C. Corballis, 1988; Shepard & Cooper, 1982). Mental rotation is considered to be an analogue process that rotates an image of one of the shapes in the mind (see M. C. Corballis, 1986; Metzler & Shepard, 1974). Recently, the analogue nature of mental rotation (impressively demonstrated by Cooper, 1976) found a neural correlate in the monkey's motor cortex (Georgopoulos, Lurito, Petrides, Schwartz, & Massey, 1989). The neuronal population vector—calculated from a cell assembly's activity pattern—was found to rotate prior to the onset of a movement pointing 90° to the left of a target light. Although this task was the mental rotation of a movement direction, the analogue process of mental object rotation² might be based on similar continuous changes of neuronal activity. The brain area most likely involved in mental object rotation—namely, the pos-

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terior parietal cortex (area 7a)—shows strong reciprocal connections to area 6. Area 6 consists of the supplementary motor area, known to be involved in movement planning (Roland, Larsen, Lassen, & Skinhøj, 1980), and the premotor area—an area that plays a role in coding space (Graziano, Yap, & Gross, 1994), in extracting the intrinsic properties of objects (Jeannerod, Arbib, Rizzolatti, & Sakata, 1995; Rizzolatti et al., 1988), and in recognizing and generating object-oriented hand actions (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). A similar parietal-to-premotor cortical circuit might exist for the mental rotation of objects, suggesting that mental object rotation is also related to the processing of object-oriented actions.

In the beginning, cognitive psychologists considered mental object rotation a visual-spatial imagery process (Shepard & Metzler, 1971) that is related to apparent motion perception (M. C. Corballis & McLaren, 1982; Shepard & Judd, 1976; see also M. C. Corballis, 1986; Heil, Bajric, Rösler, & Hennighausen, 1997) and that is void of any motor, premotor, or action-planning component. Meanwhile, however, there is cumulating evidence that mental object rotation is more than that. Just and Carpenter (1976) pointed out that mental object rotation is fairly strategic, as compared with the largely automatic processing of apparent motion (see also Carpenter & Just, 1978), Jolicœur and Cavanagh (1992) could show that it is object motion, and not low-level motion perception, that interacts with mental object rotation, and recently, P. M. Corballis and M. C. Corballis (1993) concluded that "the act of mental rotation itself clearly seems to be distinct from that of apparent motion" (p. 465). Note that the quotation labels mental rotation an act, and indeed mental rotation shares some characteristics with voluntary actions: It can be started and stopped voluntarily (Cooper & Podgorny, 1976), and its speed is a matter of free choice (Cooper & Shepard, 1973).

Kosslyn (1994) was among the first to suggest that premotor (not motor) processes are involved in mental object rotation, an idea that received support by research on the mental rotation of images of human body parts. Using that special class of stimuli, Sekiyama (1982, 1983) and Parsons (1987a, 1987b) could show that response time (RT) depends strongly on the awkwardness of a movement of the depicted limb to the particular orientation. If premotor (or action-planning) processes also contribute to mental object rotation, one should find a close correspondence between mental and manual object rotation (some evidence can be found in de'Sperati & Stucchi, 1997). Recently, using Shepard and Metzler (1971) cube figures, we showed that, indeed, mental rotation RT functions were indistinguishable—at least for Cartesian axes3—from the RT functions of a similar task that consisted of turning the objects on the screen by means of a knob (Wohlschläger & Wohlschläger, 1998). In a second experiment, a mutual interference was found between mental object rotation and simultaneously executed hand movements. Given parallel axes, mental object rotation RTs were considerably longer if the hand rotations went in the opposite direction. Neither hand rotations about an orthogonal axis nor linear hand movements influenced mental rotation RT. The same pattern of interference was found in the hand movements. They were slower and less smooth if the mental object rotation direction was in the opposite direction, but only if the axes were parallel. The mutual interference was found for both hands, although it was weaker for the nondominant left hand.4

In consideration of the results from the above interference experiment together with the close correspondence of mental and manual object rotation, we suggest that mental object rotation is rather an imagined (covert) action than a pure visual-spatial imagery task. More cautiously stated, there is at least a common process involved in mental object rotation and the programming of rotational hand movements. This process is specific with respect to the spatial operation, but only weakly, if at all, involves the selection of the hand. Therefore, we think that the process common to mental object rotation and the programming of hand movements is perhaps better termed a process of action planning than a process that programs concrete hand movements. At this point, it is necessary to make clear that we do not treat action and movement as synonyms. Movements are the pure motor part of actions. Actions consist of a movement and a goal that is the perceivable consequence of a movement. We return to that important differentiation in the General Discussion section.

If our action-planning assumption is correct, the simultaneous *execution* of rotational hand movements *should*

not be a necessary condition for an interference with mental object rotation. In contrast, the mere planning of rotational hand movements should be sufficient to interfere with mental object rotation. Furthermore, the findings that led us to the conclusion that the interference effect is due to a common action-planning process—namely, that the interference effect is specific with respect to the spatial operation of the hand—should be replicated when interference between mental object rotation and the planning of hand movements is investigated.⁵

EXPERIMENT 1

Experiment 1 was designed to determine whether planning a rotational hand movement is sufficient to cause interference with mental object rotation or whether its execution is necessary for the interference. It was expected that mental object rotation RT would be considerably longer for discordant trials (hand movements are planned in a direction opposite to the presumed mental rotation direction) than for concordant trials (planned hand movement direction and presumed mental rotation direction are identical). Furthermore, it was expected that the potential interaction between mental object rotation and the planning of hand movements would show the same spatial specificity as the interference between mental object rotation and simultaneously performed hand movements (Wohlschläger & Wohlschläger, 1998). Three out of the five conditions used in the recent interference experiment were chosen.

- 1. The z-rotation condition. This is the experimental condition. Subjects had to plan a rotational hand movement about an axis parallel to the axis used for the generation of the stimuli (the z-axis, pointing to depth). An interference with mental object rotation RT was expected in this and only in this condition.
- 2. The y-rotation condition. Subjects in this condition had to plan a rotational hand movement about the vertical y-axis—that is, an axis perpendicular to the axis of stimulus rotation (the z-axis). This condition controls whether the planning of an arbitrary rotational movement is sufficient to cause interference.
- 3. The translation condition. Rather than planning a rotational movement, subjects had to plan a linear horizontal movement. This condition controls whether the planning of any spatially directed movement is sufficient to cause interference with mental object rotation.

In order to show an interference between the planning of a movement and the mental object rotation task, it must be guaranteed that the movement plan is prepared before the second task is started and that it is held in memory throughout the completion of the second task. An interlocked dual-task procedure was developed to meet these requirements. The stimuli for the hand movement task were presented in the beginning, whereas the response to the stimuli had to be given at the end of each trial. The

mental rotation tasks were performed between the presentation of the stimuli and the release of the response of the hand movement task.

Method

Subjects. The 66 right-handed subjects were students from different fields at the Ludwig-Maximilians-Universität München (LMU). They were paid 12 DM. About two thirds of the students were women. Care was taken to distribute men and women equally over the experimental conditions. The data from 7 subjects were cancelled owing to technical errors. Three subjects were native Spanish speakers, and it turned out only after the experiment that their knowledge of German was poor and that they only pretended that they understood the instructions. Sixteen out of the remaining 56 subjects were suspected to have solved the mental rotation task (9), the movement task (3), or both (4) by guessing, because they showed less than 75% correct responses (chance level is 50% for both tasks). Forty individuals remained for data analysis and were distributed over the three experimental conditions in the following way: 10 subjects in the z-rotation, 11 in the translation, and 19 in the y-rotation conditions. The proportion of subjects dropped owing to their low accuracy (29%) corresponds to other mental rotation studies (e.g., Yuille & Steiger, 1982: 23%-44%).

Stimuli, Apparatus, and Design. The same five different cube array objects as those in Experiment 2 of Wohlschläger and Wohlschläger (1998; for details, see that article) were used to generate the stimuli. The stimuli were generated by rotating each object and its mirror shape about the *z*-axis in steps of 60°. Next, using central perspective, left-eye and right-eye views of the object were constructed for stereoscopic presentation (see below).

A matching-to-sample design was used. The two isomers of the cube array objects were presented at six different orientations (0°,

60°, 120°, 180°, 240°, and 300°) and combined with each of the two hand movement directions, resulting in 24 trials per block. Trials within each of the 11 blocks (resulting in a total of 264 trials) were randomized. The 1st block served as a warm-up and was excluded from data analysis.

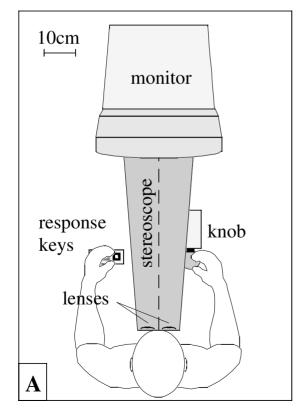
The probe stimuli were presented in the center of the display. The comparison stimuli were reduced in size by half and were presented in the upper left and right of the display (see Figure 1C). All the stimuli were presented three-dimensionally, using a special monitor stereoscope (see Figure 1A). Rotational hand movements were exerted on a knob (5.5 cm in diameter), fixed to either a vertical axis (*y*-rotation) or an axis pointing to depth (*z*-rotation). The center of the knob was in the same spatial position for both rotation conditions. The horizontal linear movements (translation) were exerted on a trackball that had approximately the same diameter as the knob. All movements were made with the right hand, whereas the response buttons had to be operated with the left hand.

Procedure. The procedure was an interlocked dual task procedure:

$$S_1 \rightarrow A_1 \rightarrow S_2 \rightarrow R_2 \rightarrow R_1$$
.

 S_1 is the cue stimulus for the movement direction, and A_1 is an unspeeded response affirming the recognition of S_1 . A_1 starts the presentation of S_2 , the stimulus for the mental object rotation task that is responded to with R_2 . Finally, R_1 is the response to S_1 ; in other words, R_1 is the execution of the hand movement planned and held in memory throughout the processing of the mental object rotation task.

At the beginning of each trial, the stimulus S_1 for the hand movement task was shown: an arched arrow pointing in either a clockwise (CW) or a counterclockwise (CCW) direction. The arrow indicated the direction in which the movement had to be made *after* the response to the mental rotation task. Next (A_1) , using their left hands, the subjects had to push the start button on the left, in order



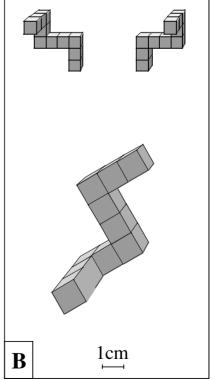


Figure 1. Experimental set-up and stimuli. For details, see the text.

to bring up the probe stimulus S2 for the mental rotation task, which replaced the arrow. Responses R2 to the mental rotation task had to be given with the left hand on the response keypad placed to the left. After one of the response buttons was pushed, the stimulus disappeared. The subjects now had to exert the movement (R₁) on the knob or trackball in the direction indicated by the arrow shown at the beginning of the trial. For the translation condition, a CW arrow indicated a rightward and a CCW arrow a leftward movement. After moving the knob or trackball for 1 sec, another arrow appeared, indicating that the next trial could be started. The probe stimulus of the mental rotation task also disappeared if no response was given within 12 sec after stimulus presentation. Although those trials were classified as unanswered, the subjects nevertheless had to move the knob or trackball for 1 sec in order to proceed to the next trial. The knob and trackball had to be operated by movements of the whole hand, and not by individual fingers.

Exerting any movement on the knob or trackball during the presentation of the probe stimulus of the mental rotation task caused the probe stimulus to disappear immediately. Stopping to move caused the stimulus to reappear. Responses to the mental rotation task were accepted only if the knob or the trackball was at rest—that is, if the probe stimulus was visible.

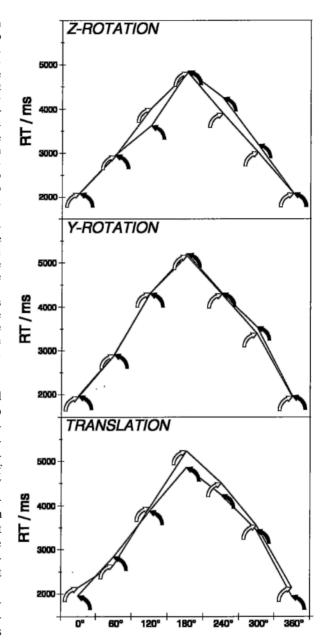
The subjects were asked to respond as quickly and accurately as possible to both tasks. That meant that they had to respond to the mental rotation task as soon as possible after the presentation of the probe stimulus, and they had to show the required movement as soon as possible after the response to the mental rotation task was given.

Results

All the subjects reported that it was surprisingly hard to remember the arrow direction. During the warm-up trials, we could observe all of them developing the following strategy to solve this problem: They made preparatory hand movements consisting of turning or shifting the hand in the direction opposite to the direction of the instructed movement. This meant that when a CCW arrow appeared, they rotated their hand CW in the rotation conditions (or moved it to the right in the translation condition) without moving the knob (or trackball), just as one rotates the hand without touching the knob before opening a door. When asked in the postexperimental interview, all the subjects reported that they had used that strategy throughout the whole experiment.

Besides the first 24 trials, which served as practice trials, a total of 107 unanswered trials (1.27%) were discarded prior to statistical analysis. In addition, 374 trials were discarded (4.51% of the remaining trials), in which the preparatory movement was executed in the wrong direction, which meant that the movement proper was probably planned in the wrong direction. Mean error rates and mean correct RTs for each stimulus angle and arrow direction were computed for each subject. Means of these means are shown in Figure 2 and Table 1.

Response times. The subjects' mean correct mental rotation RTs were submitted to an analysis of variance (ANOVA) with within-subjects factors of movement direction (MD) and stimulus orientation (SO) and a between-subjects factor of experimental condition (EC) that had three levels (z-rotation, y-rotation, and translation). As was expected with mental rotation experiments, a strong overall effect of SO was found [F(5,185) = 143.56, p < .0001], which was identical for all the experimental con-



stimulus orientation

Figure 2. Experiment 1: Mental rotation response time (RT) as a function of stimulus orientation and direction of various planned hand movements. Note that all hand movements were performed with the right hand and that they were not executed until the response to the mental rotation task was given with the left hand. The movement condition is indicated in the upper left of each panel. See the text for details. Arrows along curves indicate the direction in which the hand movement was planned to be made (clockwise vs. counterclockwise in the y-rotation and z-rotation conditions, rightward vs. leftward in the translation condition). Arrows shown with sample stimuli indicate the shortest mental rotation direction. Note that the shortest path is ambiguous with 180° and that no mental rotation is required at 0°.

Table 1
Mean Error Rates (%) for Experimental Conditions,
Arrow Directions, and Orientations in Experiment 1

Movement	Arrow Direction	Orientation						
Condition		0°	60°	120°	180°	240°	300°	
z-rotation	CW	0.0	7.4	17.7	22.5	13.3	5.2	
	CCW	4.8	4.0	15.2	24.2	14.9	8.5	
y-rotation	CW	3.9	6.1	15.7	19.4	12.5	7.7	
	CCW	4.4	8.5	13.4	19.6	12.5	10.4	
Translation	CW	4.6	3.6	12.3	14.5	11.7	9.5	
	CCW	3.4	2.0	6.1	16.3	12.3	8.3	

Note—CW, clockwise; CCW, counterclockwise.

ditions [F(10,185) < 1]. Also, the overall RT level was identical for all the experimental conditions [F(2,37) < 1], and it was independent of MD [F(1,37) < 1] in each experimental condition [F(2,37) = 1.53, p = .23]. There was no interaction between MD and SO [F(5,185) = 1.45, p = .21]. However, the three-way interaction reached significance [F(10,185) = 1.94, p < .05]. The significant three-way interaction made separate analyses for each experimental condition necessary (Keselman & Keselman, 1993).

In all conditions, SO had a strong effect on RT [translation, F(5,50) = 44.88; z-rotation, F(5,45) = 79.54; y-rotation, F(5,90) = 65.69, p < .0001 in all cases]. MD did not influence overall RT level in any condition [translation, F(1,10) = 1.86, p = .20; z-rotation, F(1,9) < 1; y-rotation, F(1,18) < 1]. The MD \times SO interaction was significant in the z-rotation group [F(5,45) = 2.49, p < .05], but not in the translation condition [F(5,50) = 1.90, p = .11], or in the y-rotation condition [F(5,90) < 1].

In order to test the interference effect directly, planned interaction contrasts⁶ were calculated for each EC, using the respective error terms of the above ANOVAs. The interference effect was highly significant in the z-rotation condition [F(1,45) = 8.38, p < .01], but not in the translation condition [F(1,50) = 3.83, p = .06] or in the y-rotation condition [F(1,90) < 1]. An inspection of the mean RT of the z-rotation condition suggests that the interference effect is larger for 240° and 120° than for 300° and 60° (for the latter orientation, the interference effect is, in fact, slightly reversed). For a post hoc test of that linear trend of the interference effect, the contrast weights for SO were set to 0, 1, 2, 0, -2, and -1 for 0°, 60°, 120°, 180°, 240°, and 300°, respectively. The linear trend was highly significant in the z-rotation condition [F(1,45) = 11.13, p <.005] but was absent in the translation condition [F(1,50) =2.86, p = .10] and the y-rotation condition [F(1,90) < 1].

Errors. Errors were submitted to the same type of ANOVA as that used to analyze RTs. The overall error level did not depend on MD [F(1,37) < 1], EC [F(2,37) = 1.24, p = .30], or the MD × EC interaction [F(2,37) = 1.59, p = .22]. Errors significantly increased with SO [F(5,185) = 23.46, p < .0001], but this increase was independent of EC [F(10,185) = 1.13, p = .34], MD [F(5,185) = 1.38, p = .24], and the MD × EC interaction [F(10,185) < 1].

Discussion

Experiment 1 replicated the standard mental rotation findings: RTs and errors increased with angular stimulus disparity. SO was the only factor influencing error rates, and thus speed—accuracy tradeoffs can be excluded from the interpretation of RT results.

An interference between planned hand movements and mental object rotation was found only in the condition involving the planning of hand rotations about the z-axis. RTs for concordant rotational directions were, on average, about 230 msec shorter than RTs for discordant trials. In addition, a post hoc test showed that the size of the interference effect depended on the stimulus disparity—that is, the amount of mental object rotation that had to be done.

Although the effect was somewhat weaker (230 vs. 380 msec), the overall pattern of the results was parallel to that in our previous experiment (Wohlschläger & Wohlschläger, 1998) with simultaneously executed rather than planned hand movements. Planning hand movements interferes with mental rotation only if the movements are rotational and if the hand rotation is about an axis parallel to the mental rotation axis.

It thus can be concluded that the planning of rotational hand movements is sufficient to cause interference with mental object rotation. The fact that the planning of rotational hand movements interferes with mental object rotation only if the planned spatial operation is suitable for reorienting the objects in an adequate way underlines the idea that mental object rotation is a planned (covert) action.

However, the unexpected preparatory movements observed in Experiment 1 pose two problems for our interpretation. As was reported above, at the beginning of each trial—after the presentation of the arrow indicating the direction in which the movement had to be planned, but before pushing the start button—all the subjects spontaneously made preparatory movements in the direction opposite to the arrow. The hand remained in that preparatory position throughout the whole trial and thus served as an external memory for the movement direction.

The first problem is that, although preparatory hand movements are a clear sign of movement planning—and that is what we wanted our subjects to do—preparatory hand movements are also a clear sign of the completion of planning. The preparatory hand movements—and thus the planning—were clearly completed by the time the mental rotation stimuli were shown. Hence, it was not the planning phase proper that caused interference with mental rotation but, rather, the maintenance or memorization of the movement plan, which is similar to (if not the same as) holding a spatial operation in working memory (in the following, we sometimes write movement planning or action planning for short when we mean maintenance of a movement plan or maintenance of an action plan). However, although the cues for the hand movements were identical for all three movement conditions, the type of action executed in response to the cue (and, hence, the spatial operation that was planned and held in working

memory) did matter: The interference effect was observed only with hand rotations about the z-axis. Thus, the possibility can be excluded that it was simply the memorization of the cue that led to interference with mental rotation.

The second problem is that the preparatory hand movements may provide an alternative explanation for the interference effect found, because preparatory hand positions were completely confounded with planned movement direction. It thus might be that sensing these hand positions, rather than the planning of a movement, caused the interference with mental rotation, perhaps in a kind of cross-modal interaction between proprioceptive information and visual-spatial imagery. Experiment 2 was designed to rule out this alternative explanation.

EXPERIMENT 2

Experiment 2 was designed to show that it is solely the planning of hand movements that causes the interference with mental object rotation and to exclude the possibility that preparatory hand positions—as a side effect of movement planning—were responsible for the interference effect. Two conditions were designed to show that preparatory hand positions are neither a sufficient nor a necessary condition for the interference effect observed in Experiment 1.

- 1. The fixed-hand condition. As above, subjects had to plan a rotational hand movement about the z-axis. To prevent preparatory movements, subjects had to push down and hold two buttons simultaneously with the ring and index fingers of their right hands. If an interference with mental object rotation were to be observed in this condition, preparatory hand positions could no longer be considered a necessary condition for the interference effect.
- 2. The pseudopreparation condition. Subjects in this condition were asked to make hand movements similar to the preparatory hand movements observed in Experiment 1 and to maintain this *pseudopreparatory* hand position during the mental rotation task. The hand position was pseudopreparatory because the subjects were not instructed to plan or execute a subsequent rotational hand movement. Instead, they were instructed to release the knob at the end of each trial. If an interaction with mental object rotation were to be observed in this condition, preparatory hand positions would have to be considered a sufficient condition for interference with mental object rotation. On the other hand, if the pseudopreparatory hand positions were not sufficient, the interference effect found in Experiment 1 could clearly be ascribed to the mental process of planning rotational hand movements.

Method

Subjects. Forty right-handed students from different fields at LMU participated in Experiment 2. Remuneration was the same as in Experiment 1. About two thirds of the students were women, and care was taken to distribute men and women equally over the experimental conditions. Five subjects in the fixed-hand and 3 subjects in the pseudopreparation conditions were suspected to have solved

the mental rotation task by guessing, because they showed less than 75% correct responses. In the fixed-hand condition, 1 additional subject had more than 25% errors in the movement task, and another subject made more than 25% errors in both tasks. Thirty individuals remained for data analysis, and they were equally distributed over the two experimental conditions. The proportion of dropped subjects was 25%.

Stimuli, Design, Apparatus, and Procedure. The stimuli and design were similar to those in Experiment 1. The apparatus was the same as that in the *z*-rotation condition in Experiment 1, except for slight modifications depending on the experimental condition.

In the fixed-hand condition, an additional keypad was placed slightly above and behind the knob. The procedure was identical to that in Experiment 1, except that the subjects had to push and hold down both buttons of the additional keypad with the index and ring fingers of their right hands throughout the mental rotation taskthat is, until the response to the mental rotation task was given with the left hands. Releasing either one of the buttons caused the mental rotation stimulus to disappear, as did any movement of the knob. Also, responses to the mental rotation task were accepted only if both buttons were pushed and if the knob was at rest. In addition, trials could be started only if both buttons were pushed. Consequently, the procedure was slightly different from that of Experiment 1. After the presentation of the arrow, the subjects first had to push and hold both buttons of the additional keypad with the index and ring fingers of their right hands. Next, they had to push the start button with their left hands in order to bring up the probe stimulus. The subjects had to hold down the buttons of the additional keypad until after the response to the mental rotation task was given. Then they had to release both buttons and turn the knob in the required direction as soon as possible with their right hands. After turning the knob for 1 sec, the next trial began with the presentation of another

In the pseudopreparation condition, after the presentation of the arrow, the subjects had to turn the knob with their right hands at least 70° in the direction opposite to the arrow. The subjects had to hold the knob in that position until after the response to the mental rotation task was given. A small load was mounted eccentrically on the disk at the other end of the rotational axis of the knob. This load caused the knob to turn back to the 0° position as soon as the subject released the knob. Releasing the knob caused the probe stimulus to disappear immediately. It reappeared as soon as the knob was brought back to the required angular position. Responses to the mental rotation task were accepted only if the knob was in the required angular position. After the response was given, the subjects had to release the knob, and the next trial began with the presentation of another arrow as soon as the knob reached the 0° position, owing to the load.

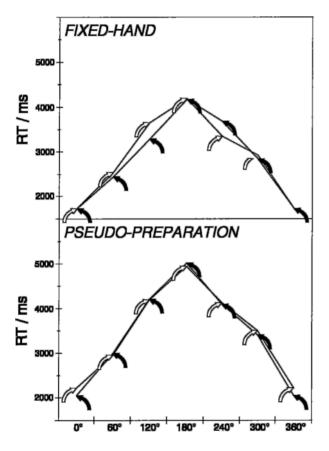
In order to control the subjects' hand movements, we videotaped the movements of the subjects' right hands. In addition, an experimenter supervised subjects' hand movements on a monitor outside the experimental chamber.

Results

As was revealed by the on-line supervision of the subjects' hand movements and the postexperimental inspection of the videotapes, the subjects in the fixed-hand condition did not show any sign of preparatory hand movements, whereas the subjects in the pseudopreparatory condition exerted the pseudopreparatory hand movements in the requested manner. All the subjects in the fixed-hand condition reported that it was surprisingly hard to remember the arrow direction. One subject reported that she lifted the toes corresponding to the arrow direction (e.g., left toes for CCW and right toes for CW).

Besides the practice trials, in total 14 unanswered trials (0.44%) were discarded prior to statistical analysis. In addition, in the fixed-hand condition, 105 trials were discarded (3.35% of the remaining trials), in which the hand movement was executed in the wrong direction, which meant that the movement was probably also planned in the wrong direction. Mean error rates and mean correct RTs for each stimulus angle and arrow direction were computed for each subject. Means of these means are shown in Figure 3 and Table 2.

Response times. The subjects' mean correct mental rotation RTs were submitted to the same type of ANOVA



stimulus orientation

Figure 3. Experiment 2: Mental rotation response time (RT) as a function of stimulus orientation and direction of hand movements. Hand movements were performed with the right hand, whereas responses to the mental rotation task were given with the left hand. The experimental condition is indicated in the upper left of each panel. Arrows along curves indicate the arrow presented at the beginning of a trial. In the fixed-hand condition clockwise (counterclockwise) arrows indicates the planning of a clockwise (counterclockwise) rotational hand movement. In the pseudopreparation condition clockwise (counterclockwise) arrows indicate that a counterclockwise (clockwise) pseudopreparatory movement was made. See the text and Figure 2 for details.

Table 2
Mean Error Rates (%) for Experimental Conditions,
Arrow Directions, and Orientations in Experiment 2

Movement	Arrow	Orientation						
Condition	Direction	0°	60°	120°	180°	240°	300°	
Fixed-hand	CW	5.2	5.3	10.9	19.3	13.5	5.8	
	CCW	2.8	6.5	16.6	16.5	14.2	8.2	
Pseudo-	CW	5.5	10.6	16.9	30.3	20.4	10.2	
preparation	CCW	3.6	9.3	16.0	28.4	17.7	9.4	

Note—CW, clockwise; CCW, counterclockwise.

as that in Experiment 1, except that the between-subjects factor EC now had only two levels (fixed-hand vs. pseudo-preparation). A strong overall effect of SO was found [F(5,140)=141.87,p<.0001], which was identical for both experimental conditions [F(5,140)<1]. The overall RT level was higher in the pseudopreparation condition [F(1,28)=5.49,p<.05], but it was independent of MD [F(1,28)<1] in each experimental condition [F(1,28)<1]. There was no interaction between MD and SO [F(5,140)<1.61,p=.16]. However, the three-way interaction was significant [F(5,140)=2.85,p<.05], making separate analyses for the two experimental conditions necessary (Keselman & Keselman, 1993).

In both conditions, SO had a strong effect on RT [pseudopreparation, F(5,70) = 83.49; fixed-hand, F(5,70) =59.53, p < .0001] in both cases. MD did not influence overall RT level in any condition [F(1,14) < 1] for both conditions]. The MD × SO interaction was significant in the fixed-hand group [F(5,70) = 3.98, p < .01], but not in the pseudopreparation condition [F(5,70) < 1]. Planned interaction contrasts (see the results section of Experiment 1) for the interference effect and its linear trend showed that the interference effect was significant in the fixed-hand condition [F(1,70) = 4.78, p < .05] but was insignificant in the pseudopreparation condition [F(1,70)]1.71, p = .19]. Likewise, the linear trend of the interference effect was significant in the fixed-hand condition [F(1,70) = 8.53, p < .01], but not in the pseudopreparation condition [F(1,70) = 1.78, p = .19].

Errors. Errors were submitted to the same type of ANOVA as that used to analyze RTs. More errors were made in the pseudopreparation group [F(1,28) = 8.15, p < .01]. Errors significantly increased with SO [F(5,140) = 28.83, p < .0001] but did not depend on MD [F(1,28) < 1]. None of the interactions between the three factors was significant $[MD \times EC, F(1,28) < 2.01, p = .17; SO \times EC, F(5,140) = 2.03, p = .08; MD \times SO, F(5,140) = 1.02, p = .41; MD \times SO \times EC, F(5,140) < 1].$

Discussion

Experiment 2 again replicated standard mental rotation findings: RTs and errors increased with angular stimulus disparity. Overall RT level was about 570 msec higher in the pseudopreparation condition. Because the overall error level also was about 4% higher in the pseudopreparation condition and, apart from that, only stimulus orientation influenced error rates, speed—accuracy tradeoffs can be excluded in the interpretation of RT results.

An interference between planned hand movements and mental object rotation was found in the fixed-hand condition, but not in the pseudopreparation condition. In the fixed-hand condition, RTs for concordant rotational directions were again about 230 msec shorter than RTs for discordant trials. Also, the finding that the interference effect was larger for larger angles paralleled the results of Experiment 1. From these results along with the lack of an interference effect in the pseudopreparation condition, it can be concluded that planning rotational hand movements—or, to be more precise, the maintenance of a movement plan or spatial operation in working memorycauses interference with mental object rotation and that this interference is not caused by preparatory hand movements or positions. Mental object rotation is, thus, obviously influenced by the mere planning of rotational hand movements: Their execution is not a necessary condition for this influence.

The increased overall RT level in the pseudopreparation condition was an unexpected effect, and thus an explanation is restricted to post hoc speculations. We tend to believe that an inhibitory process might be responsible for the increased RT. The subjects in the pseudopreparation condition had to hold the knob at a given angular position and to suppress turning it. It is known that the speed of mental object rotation is influenced by the speed of simultaneously executed rotational hand movements (Wexler, Kosslyn, & Berthoz, 1998). Perhaps an inhibition to turn also communicates itself to the mental rotation process. In contrast, in the fixed-hand condition, rather than an inhibition to turn, an inhibition to release the keys was required. In other words, in this case there was no suppression of a rotational movement. We want to repeat explicitly that this explanation for the increased overall RT level in the pseudopreparation condition is very speculative and that a more systematic investigation is definitely necessary.

We nevertheless want to point out again that the present results (and the recent results in Wohlschläger & Wohlschläger, 1998) show that mental object rotation is influenced by movement planning and/or movement execution, as long as the movements are rotational and the axes of rotation are parallel.

GENERAL DISCUSSION

In Experiment 1, we showed that planning subsequent rotational hand movements (or better, maintaining the movement plan) leads to an interference with mental object rotation, provided that the axes of rotation coincide in space. RTs were shorter if mental object rotation and rotational hand movements went in the same direction than they were in the opposite, discordant case. Experiment 2 showed that this is a consistent effect, because it was replicated despite methodological differences. In addition, Experiment 2 could exclude the possibility that the preparatory hand movements—as a side effect of

movement planning—were responsible for the interference effect observed in Experiment 1: Movement planning without preparatory movements led to an interference effect of the same size as that in Experiment 1, whereas pseudopreparatory hand positions without subsequent movements did not cause any interference. In both experiments, the size of the effect depended on the size of the mental rotation angle. This can be seen as evidence for interference of hand movement planning with the mental rotation process proper, and not with processes that are independent of stimulus orientation, such as stimulus identification, decision making, or response preparation, because the latter processes are known to be independent of stimulus orientation.

Although the interference effect in the present experiments was somewhat weaker (230 msec, as compared with 380 msec), the results were perfectly parallel to our recent interference experiment (Wohlschläger & Wohlschläger, 1998, Experiment 2), in which hand movements were executed (rather than planned) simultaneously with a mental object rotation task. Both the planning and the execution of hand movements interfere with mental object rotation, but only if the movements are rotational in nature and if the axes of rotation are parallel in space. The parallel results allow us to conclude that the planning of rotational hand movements is sufficient and that simultaneous execution is not necessary to cause interference with mental object rotation. Obviously, it is mainly the movement plan and its maintenance—or one might also say, the intention to move—that causes interference, although movement execution enhances it. Alternatively, one might say that holding a spatial operation in working memory interferes with the execution of another spatial operation—mental rotation—if the operations have opposite signs along the same spatial dimension.

Recent neurophysiological findings seem to agree with our behavioral results. It is commonly accepted that parietal areas are highly active during spatial tasks like mental rotation (see, e.g., Deutsch, Bourbon, Papanicolaou, & Eisenberg, 1988; Ditunno & Mann, 1990; Mehta, Newcombe, & Damasio, 1987; Ratcliff, 1979). More recently, however, functional neuroimaging studies were able to show that, in addition to parietal areas, premotor areas also are active during mental rotation, when human hands are used as stimuli (Bonda, Petrides, Frey, & Evans, 1995; Parsons et al., 1995). Although there is not much evidence that the same is true when abstract objects are used as stimuli (Cohen et al., 1996; Parsons & Fox, 1995), one might nevertheless be tempted to speculate that mental rotation involves premotor processes or processes of action planning. It is important to note here that the equation premotor areas = premotor processes is no longer true. A considerable part of premotor neurons are visuomotor neurons rather than pure motor neurons (for a review, see Jackson & Husain, 1997; Wise, DiPellegrino, & Boussaoud, 1996). Also, parietal neurons are not purely visual—some of them show motor-dependent properties

(Mountcastle, Lynch, Georgopoulos, Sakata, & Acuna, 1975; Taira, Mine, Georgopoulos, Murata, & Sakata, 1990), and it has been shown that parietal area 7 is also active during motor imagery tasks (Parsons et al., 1995). Thus, the old concept of the central sulcus as the dividing line between sensory and motor areas has eroded more and more. As has already been mentioned in the introduction, parietal and premotor areas form together a system for visually guided, object-oriented actions (Gallese et al., 1996; Graziano et al., 1994; Jeannerod et al., 1995; Rizzolatti et al., 1988). The interference between mental object rotation and the planning of rotational hand movements observed in the present experiments makes it quite likely that both mental object rotation and the planning of object-oriented (here, the knob) hand movements make use of that system.

We would like to suggest that mental object rotation is perhaps better considered an imagined (covert) action than either a pure visual-spatial imagery task or a visual imagery task involving movement planning. At this point, we have to come back to our differentiation between movement and action. Overt actions always have at least two components: a motor component consisting of the executed movements and an effect component consisting of the perceivable consequences of the movements. The latter component is the goal of the action. If the same is assumed for covert actions, this would mean that they consist of both motor imagery (an image of the movement) and visual—or more generally, perceptual—imagery (an image of the action goal). Our view of mental object rotation as a covert action is based in part on the fact that mental object rotation has been shown to interact with both hand movement planning (as is shown here) and the perception of object rotation (as was shown by Jolicœur & Cavanagh, 1992). However, because it is unclear whether the nature of motor imagery is purely motoric or perceptual and motoric (see Annett, 1995), in the case of planned hand movements it remains unclear whether motor codes or visuospatial codes are interfering with mental object rotation. In other words, we cannot decide whether the imagined movement or the imagined goal of the planned hand action is causing the interference effect. In accordance with the common-coding approach of Prinz (1990, 1997), we would like to suggest that there is an additional (perhaps higher) level of representation⁷ at which action plans and events are represented by common codes. As has already been suggested by William James (1890), the movements an action requires might be evoked by simply imagining the goal (i.e., the desired perceivable effect) of the particular action. If—as in the experiments reported here—the action (i.e., the hand movement) must be planned but its execution is postponed, the image of the action goal must be maintained for the period between action planning and action execution. We would like to suggest that the interference between mental object rotation and the planning of rotational hand movements is grounded in an interference

between the goal of an overt action (the hand movement) and the goal of a covert action (mental object rotation).

REFERENCES

- Annett, J. (1995). Motor imagery: Perception or action? *Neuropsychologia*, 33, 1395-1417.
- BONDA, E., PETRIDES, M., FREY, S., & EVANS, A. (1995). Neural correlates of mental transformations of the body-in-space. *Proceedings of the National Academy of Sciences*, 92, 11180-11184.
- CARPENTER, P. A., & JUST, M. A. (1978). Eye fixations during mental rotation. In J. W. Senders, D. F. Fisher, & R. A. Monty (Eds.), Eye movements and higher psychological functions (pp. 115-133). Hillsdale, NJ: Erlbaum.
- COHEN, M. S., KOSSLYN, S. M., BREITER, H. C., DIGIROLAMO, G. J., THOMPSON, W. L., ANDERSON, A. K., BOOKHEIMER, S. Y., ROSEN, B. R., & BELLIVEAU, J. W. (1996). Changes in cortical activity during mental rotation: A mapping study using functional MRI. *Brain*, 119, 89-100.
- COOPER, L. A. (1976). Demonstration of a mental analog of an external rotation. *Perception & Psychophysics*, **19**, 296-302.
- COOPER, L. A., & PODGORNY, P. (1976). Mental transformations and visual comparison processes: Effects of complexity and similarity. *Journal of Experimental Psychology: Human Perception & Performance*, 2, 503-514.
- COOPER, L. A., & SHEPARD, R. N. (1973). Chronometric studies of the rotation of mental images. In W. G. Chase (Ed.), Visual information processing (pp. 75-176). New York: Academic Press.
- CORBALLIS, M. C. (1986). On imagined revolutions. In D. F. Marks (Ed.), *Theories of image formation* (pp. 151-168). New York: Brandon House.
- CORBALLIS, M. C. (1988). Recognition of disoriented shapes. Psychological Review, 95, 115-123.
- CORBALLIS, M. C., & McLAREN, R. (1982). Interaction between perceived and imagined rotation. *Journal of Experimental Psychology:* Human Perception & Performance, 8, 215-224.
- CORBALLIS, M. C., & McLAREN, R. (1984). Winding one's Ps and Qs: Mental rotation and mirror-image discrimination. *Journal of Experimental Psychology: Human Perception & Performance*, 10, 318-327.
- CORBALLIS, P. M., & CORBALLIS, M. C. (1993). How apparent motion affects mental rotation: Push or pull? *Memory & Cognition*, **21**, 458-466. DE'SPERATI, C., & STUCCHI, N. (1997). Recognizing the motion of a grasp-
- able object is guided by handedness. *NeuroReport*, **8**, 2761-2765.
- DEUTSCH, G., BOURBON, W. T., PAPANICOLAOU, A. C., & EISENBERG, H. M. (1988). Visuospatial tasks compared via activation of regional cerebral blood flow. *Neuropsychologia*, **26**, 445-452.
- DITUNNO, P. L., & MANN, V. A. (1990). Right hemisphere specialization for mental rotation in normals and brain damaged subjects. *Cortex*, 26, 177-188.
- FÖRSTER, B., GEBHARDT, R., LINDLAR, K., SIEMANN, M., & DELIUS, J. D. (1996). Mental rotation effect, a function of elementary stimulus discriminability? *Perception*, **25**, 1301-1313.
- GALLESE, V., FADIGA, L., FOGASSI, L., & RIZZOLATTI, G. (1996). Action recognition in the premotor cortex. *Brain*, 119, 593-609.
- GARVILL, J., & MOLANDER, B. (1977). Effects of interference on intramodal and cross-modal matching of form (Umeå Psychological Reports No. 124). Umeå, Sweden: Umeå University, Department of Psychology.
- Georgopoulos, A. P., Lurito, J. T., Petrides, M., Schwartz, A. B., & Massey, J. T. (1989). Mental rotation of the neuronal population vector. *Science*, **243**, 234-236.
- GRAZIANO, M. S. A., YAP, G. S., & GROSS, C. G. (1994). Coding of visual space by premotor neurons. Science, 266, 1054-1057.
- HEIL, M., BAJRIC, J., RÖSLER, F., & HENNIGHAUSEN, E. (1997). A rotation aftereffect changes both the speed and the preferred direction of mental rotation. *Journal of Experimental Psychology: Human Perception & Performance*, 23, 681-692.
- JACKSON, S. R., & HUSAIN, M. (1997). Visuomotor functions of the lateral pre-motor cortex. Current Opinion in Neurobiology, 6, 788-795.

- JAMES, W. (1890). The principles of psychology. New York: Holt.
- JEANNEROD, M., ARBIB, M. A., RIZZOLATTI, G., & SAKATA, H. (1995). Grasping objects: The cortical mechanisms of visuomotor transformation. *Trends in Neurosciences*, 18, 314-320.
- JOLICŒUR, P., & CAVANAGH, P. (1992). Mental rotation, physical rotation, and surface media. *Journal of Experimental Psychology: Human Perception & Performance*, 18, 371-384.
- JUST, M. A., & CARPENTER, P. A. (1976). Eye fixations and cognitive processes. *Cognitive Psychology*, 8, 441-480.
- Keselman, H. J., & Keselman J. C. (1993). Analysis of repeated measurements. In L. K. Edwards (Ed.), *Applied analysis of variance in behavioral science* (pp. 105-145). New York: Marcel Dekker.
- KORIAT, A., & NORMAN, J. (1985). Mental rotation and visual familiarity. Perception & Psychophysics, 37, 429-439.
- KOSSLYN, S. M. (1994). *Image and brain*. Cambridge, MA: MIT Press. MEHTA, Z., NEWCOMBE, F., & DAMASIO, H. (1987). Visuospatial processing. *Cortex*, 23, 447-461.
- METZLER, J., & SHEPARD R. N. (1974). Transformational studies of the internal representation of three-dimensional objects. In R. L. Solso (Ed.), *Theories in cognitive psychology: The Loyola Symposium* (pp. 147-201). Potomac, MD: Erlbaum.
- MOUNTCASTLE, V. B., LYNCH, J. C., GEORGOPOULOS, A. P., SAKATA, H., & ACUNA, C. (1975). Posterior parietal association cortex of the monkey: Command functions for operations within extrapersonal space. *Journal of Neurophysiology*, **38**, 871-908.
- Parsons, L. M. (1987a). Imagined spatial transformation of one's body. Journal of Experimental Psychology: General, 116, 172-191.
- Parsons, L. M. (1987b). Imagined spatial transformations of one's hands and feet. *Cognitive Psychology*, **19**, 178-241.
- PARSONS, L. M. (1987c). Visual discrimination of abstract mirrorreflected three-dimensional objects at many orientations. *Perception & Psychophysics*, 42, 49-59.
- PARSONS, L. M. (1995). Inability to reason about an object's orientation using an axis and angle of rotation. *Journal of Experimental Psychology: Human Perception & Performance*, 21, 1259-1277.
- PARSONS, L. M., & Fox, P. T. (1995). Neural basis of mental rotation. Society for Neurosciences Abstracts, 116, 172-191.
- Parsons, L. M., Fox, P. T., Downs, J. H., Glass, T., Hirsch, T. B., Martin, C. C., Jerabeck, P. A., & Lancaster, J. L. (1995). Use of implicit motor imagery for visual shape discrimination as revealed by PET. *Nature*, **375**, 54-58.
- PRINZ, W. (1990). A common coding approach to perception and action. In O. Neumann & W. Prinz (Eds.), *Relationships between perception and action* (pp. 167-201). Berlin: Springer-Verlag.
- PRINZ, W. (1997). Perception and action planning. European Journal of Cognitive Psychology, 9, 129-154.
- RATCLIFF, G. (1979). Spatial thought, mental rotation and the right cerebral hemisphere. *Neuropsychologia*, 17, 49-54.
- RIZZOLATTI, G., CAMARDA, R., FOGASSI, L., GENTILUCCI, M., LUPPINO, G., & MATELLI, M. (1988). Functional organization of inferior area 6 in the macaque monkey: II. Area F5 and the control of distal movements. *Experimental Brain Research*, 71, 491-507.
- ROLAND, P. E., LARSEN, B., LASSEN, N. A., & SKINHØJ, E. (1980). Supplementary motor area and other cortical areas in organization of voluntary movements in man. *Journal of Neurophysiology*, 43, 118-136.
- ROSENTHAL, R., & ROSNOW, R. L. (1985). Contrast analysis. Cambridge: Cambridge University Press.
- Sekiyama, K. (1982). Kinesthetic aspects of mental representations in the identification of left and right hands. *Perception & Psychophysics*, **32**, 89-95.
- Sekiyama, K. (1983). Mental and physical movements of hands: Kinesthetic information preserved in representational systems. *Japanese Psychological Research*, **25**, 95-102.
- SHEPARD, R. N., & COOPER, L. A. (1982). Mental images and their transformations. Cambridge, MA: MIT Press.
- SHEPARD, R. N., & JUDD, S. A. (1976). Perceptual illusion of rotation of three-dimensional objects. *Science*, 191, 952-954.
- Shepard, R. N., & Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science*, **171**, 701-703.
- TAIRA, M., MINE, D., GEORGOPOULOS, A. P., MURATA, A., & SAKATA, H. (1990). Parietal cortex neurons of the monkey related to

- the visual guidance of hand movements. Experimental Brain Research, 83, 29-36.
- WEXLER, M., KOSSLYN, S. M., & BERTHOZ, A. (1998). Motor processes in mental rotation. *Cognition*, **68**, 77-94.
- Wise, S. P., DiPellegrino, G., & Boussaoud, D. (1996). The premotor cortex and nonstandard sensorimotor mapping. *Canadian Journal of Physiology & Pharmacology*, **74**, 469-482.
- WOHLSCHLÄGER, A., & WOHLSCHLÄGER, A. (1998). Mental and manual rotation. *Journal of Experimental Psychology: Human Perception & Performance*, **24**, 397-412.
- YUILLE, J. C., & STEIGER, J. H. (1982). Nonholistic processing in mental rotation: Some suggestive evidence. *Perception & Psychophysics*, 31, 201-209.

NOTES

- Also, monotonous curvilinear trends are sometimes observed (Koriat & Norman, 1985).
- 2. The term *mental object rotation* is used here to make a clear distinction between mental rotation of two-dimensional or three-dimensional stimuli and other kinds of mental rotation, such as, for example, the mental rotation of an intended movement direction. Accordingly, *manual object rotation* is used for rotatory object manipulations, and *manual rotation* for the rotatory hand movements per se (with or without an object held in hand).
- 3. An oblique axis showed substantially different RT functions for mental and manual object rotation. As was discussed in Wohlschläger and Wohlschläger (1998), these differences are probably caused by the restrictions of the apparatus used for the manual rotation condition. Our apparatus allowed only single-axis rotations. There is good reason to assume that objects rotated about a single oblique axis are mentally not rotated back about that single axis. They are rather rotated back by successive rotations about Cartesian axes or by spin-precession—that is, a rotation about an axis which instantaneously changes its orientation in space (Parsons, 1987c). Recently, Parsons (1995) was able to show that, in the case of oblique axes, there is a general inability to conceive the position of axis and angle of rotation. This agrees with our observation (Wohlschläger & Wohlschläger, 1998) that clockwise and counterclockwise manual rotations were equally probable. Owing to the construction of our apparatus, the subjects were forced to use single axis rotation in the manual rotation condition, whereas they probably used a different transformation in mental rotation.
- 4. Meanwhile, our results were replicated with two-dimensional stimuli (Wexler, Kosslyn, & Berthoz, 1998). In addition to the compatibility effect, they showed that mental object rotation speed correlates with the speed of simultaneously executed rotational hand movements.
- 5. As a side effect, showing that the planning of a rotational movement is sufficient to cause interference with mental object rotation would also demonstrate that it is really the action—whether planned or actually executed—that causes interference. Then, it can be excluded that the interference observed when moving one's hand simultaneously with a mental object rotation task is based on a cross-modal interference between visual-spatial imagery and the kinesthetic feedback elicited by the movements. Although this alternative explanation of the interference effect in Wohlschläger and Wohlschläger (1998) was overlooked, it is nevertheless possible in principle from a cognitive point of view (Garvill & Molander, 1977), as well as from a neurophysiological standpoint (Mountcastle, Lynch, Georgopoulus, Sakata, & Acuna, 1975).
- 6. The contrast weights were 0, +1, +1, 0, -1, and -1 for the 0° , 60° , 120° , 180° , 240° , and 300° SOs, respectively. The contrast weights for MD were +1 and -1 for CW and CCW directions, respectively. Interaction contrast weights were calculated by multiplying the contrast weights of the main factors (Rosenthal & Rosnow, 1985). In addition, the overall $\alpha = .05$ significance level was adjusted according to the Bonferoni approach.
- This level of representation comes close to the concept of a visualspatial working memory.