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RESEARCH ARTICLE

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Orientation of the opposition axis in mentally simulated grasping

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Abstract Five normal subjects were tested in a simulated grasping task. A cylindrical container filled with water was placed on the center of a horizontal monitor screen. Subjects used a precision grip formed by the thumb and index finger of their right hand. After a preliminary run during which the container was present, it was replaced by an image of the upper surface of the cylinder appearing on the horizontal computer screen on which the real cylinder was placed during the preliminary run. In each trial the image was marked with two contact points which defined an opposition axis in various orientations with respect to the frontal plane. The subjects' task consisted, once shown a stimulus, of judging as quickly as possible whether the previously experienced action of grasping the container full of water and pouring the water out would be easy, difficult or impossible with the fingers placed according to the opposition axis indicated on the circle. Response times were found to be longer for the grasps judged to be more difficult due to the orientation and position of the opposition axis. In a control experiment, three subjects actually performed the grasps with different orientations and positions of the opposition axis. The effects of these parameters on response time followed the same trends as during simulated movements. This result shows that simulated hand movements take into account the same biomechanical limitations as actually performed movements.

Keywords Motor imagery · Visuomotor transformation · Prehension · Opposition axis · Coordination

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Introduction

It seems reasonable to consider that a close relationship should exist between the mental simulation of a motor task and its actual execution. Both activate common structures such as primary motor cortex and premotor cortex, as well as parietal areas, basal ganglia and lateral cerebellum (e.g., Decety et al. 1994). Patients suffering motor disorders, such as Parkinson's disease, experience difficulty in both executing motor tasks and mentally simulating them (Dominey et al. 1995). Mental simulations and actual executions of motor tasks share structures involved not only in the execution phase but also in the preparation phase of movements. Di Pellegrino et al. (1995) observed that monkey's premotor cortex neurons, usually activated during the movement preparation phase, are also activated when the animal witnesses the experimenter performing the same movement. These results suggest the existence of a mental mechanism capable of codifying the representation of movements independently of their actual execution and that this mechanism may be related to the motor task programming. Parsons (1987, 1994) suggests that mentally simulated motor tasks involve not only kinesthetic transformations of joint segments but also mechanical limitations of real movements. He showed a close relationship between the time required to decide whether a hand shown on a picture is the right or the left hand and the time required to imitate the hand configuration. This suggests that a mentally simulated movement could solve a visual task involving the action of a three-dimensional corporal segment. How similar simulated and executed actions really are is clearly illustrated by results obtained using mental chronometry. It is known, for example, that simulated actions take the same time as truly executed ones (for a review of previous work, see Jeannerod 1995) and replicate the classical speed-accuracy trade-off observed with real alternating movements (Sirigu et al. 1996). This approach to motor imagery, which focuses more on the brain mechanisms involved than on the content of motor images, complements experiments in which the only data were based on subjective reports. If a relationship between the motor image and the action it simulates actually exists, then properties inherent in the action should be expressed in the image.

In the current experiment normal subjects were instructed to judge whether a grasp was feasible while imagining a precision grip formed by both the right thumb and index finger. Our aim was to investigate the reference system for simulating movements to form the axis along which the two fingers transmit the opposite forces for grasping and lifting an object. This is a critical question when it comes to grasping objects. The definition of an opposition axis in the preparation phase of movements is demonstrated by analyzing the kinematics of prehensile movements. Paulignan et al. (1997) showed that the orientation axis for grasping cylindrical objects placed at different locations in the workspace was computed within an egocentric frame of reference: in other words, the upper limb kept the same configuration, hence limiting uncomfortable or awkward hand positions. If the simulated movements follow the rules which apply to motor behavior, the prospective evaluation of the feasibility of grasping an object displayed at different orientations would require the subject to choose an adequate frame of reference in order to be able to complete the task. This choice should reflect both the subject's feasibility judgements and the time required to give the response.

Materials and methods

Main experiment: simulated movements

Subjects

Five right-handed individuals (three men and two women), with ages ranging from 23 to 39 years and with no detected neurological disorders, participated in the experiment. They all gave their informed consent. Before the experiment, they received an explanation of the methods used. The purpose of the study was revealed once the experiment was over. The experiment was approved by the local ethics committee.

Experimental design

The subjects were comfortably seated in front of a 38-cm monitor lying flat. Its surface was perpendicular to the body axis at a distance of about 45 cm below the orbitomeatal line. They were asked to place a keyboard on their knees and hold it with the left hand. The experiment started with a preliminary run to clarify the instructions: an opaque cylindrical container filled with water (5 cm high, 3 cm diameter, 30 g weight) was placed on the center of the monitor screen at a distance of 50 cm from the body plane (see Fig. 1A, insert). Another plastic container was placed behind the first one. Subjects were asked to lift the plastic cylinder filled with water, pour the water into the other container and return it to its original position using a precision grip formed by the right-hand thumb and index finger (Napier 1956). Subjects were also asked to carefully observe the axis defined by the contact point of the fingers on the cylinder surface, along which the forces were applied during the grasp (the opposition axis). They were explicitly instructed not to use their left hand or any other fingers with the exception of the thumb and index finger of their right hand. They were also instructed not to stand up or use a vertical grip or perform any pronation/supination movement of the wrist to complete the grasping movement. This action was repeated at least 20 times at the beginning of the experiment before both objects were removed from the subject's view. During the experiment itself, the computer monitor was used to display the target stimuli (see Fig. 1A, B, insert). Each trial was made at a central 500-ms fixation point, followed by an image of the upper surface of the cylinder (a circle) which appeared for 5 s at the same location the real cylinder was placed during the preliminary run. Each circle was marked with two contact points (without the name of the fingers) which defined an opposition axis at 0°, 22°, 45°, 56°, 90°, –22° (338°), –45° (315°) and –56° (304°) with respect to the frontal plane. In addition, the contact points were placed in such a way that the opposition axis crossed the circle through its center, or at 3 or 6 mm with respect to its center. The subjects' task consisted, when shown a stimulus, in judging as quickly as possible whether the previously experienced action of grasping the cylinder full of water and pouring the water into the other container would be possible with the fingers placed according to the opposition axis indicated on the circle. No actual movement was allowed. The subjects had to rate the level of feasibility of the grasp with three levels (“easy”, “difficult”, “impossible”), for which they pressed keyboard keys with their right hand using the following code: *l* “easy”, *k* “difficult” and *j* “impossible”, with their annular, greater and index fingers, respectively. Before the formal task started, each subject went through a training period.

The task itself consisted of 56 random stimuli displayed 10 times each. For each stimulus the feasibility level and the response time, i.e., the time between the display of the stimulus and the key press, were monitored.

Data analysis

A within-subject 3 (feasibility: easy, difficult, impossible) × 3 (opposition axis: across center of stimulus, 3, 6 mm off center) and 3 (feasibility) × 8 (orientations of opposition axis) repeated measures ANOVA was performed for feasibility level according to the center and the angle of the grasp axis. A within-subject 1 (response time) × 3 (opposition axis: across center of stimulus, 3, 6 mm off center) and 1 (response time) × 8 (orientations of opposition axis) repeated measures ANOVA was conducted for response time level according to the center and the angle of the grasp axis. A significance level of 0.05 was chosen. A Newman-Keuls test was used as a post hoc test.

Control experiment: real movements

Subjects and procedure

This experiment was run on three of the five subjects who participated in the main experiment. The experiment was approved by the local ethics committee. The same procedure as the one used in the preliminary run of the main experiment was used. Subjects were instructed to grasp and lift the plastic cylinder filled with water, pour the water into the other container located behind the first one and return it to its original position using a precision grip formed by the right thumb and index finger. They were explicitly instructed not to use their left hand or other fingers with the exception of the right thumb and the right index finger. They were also instructed not to perform a pronation/supination movement of the wrist while performing the grasping movement. The onset of the hand movement was located 10 cm right of the sagittal axis. Before starting each trial, subjects kept their eyes closed until they heard an auditory signal. Once they opened their eyes, they could see the container marks on its top (without the name of the fingers), indicating to them where to place their two fingers in order to grasp the object. The two contact points defined an opposition axis at 0°, 22°, 45°, 56°, 90°, –22° (338°), –45° (315°) or –56° (304°) with respect to the subject's frontal plane. In addition, the contact points were placed in such a way that the opposition axis crossed the container through its center or at 3 or 6 mm with respect to its center. Stimuli were presented randomly 5 times each.

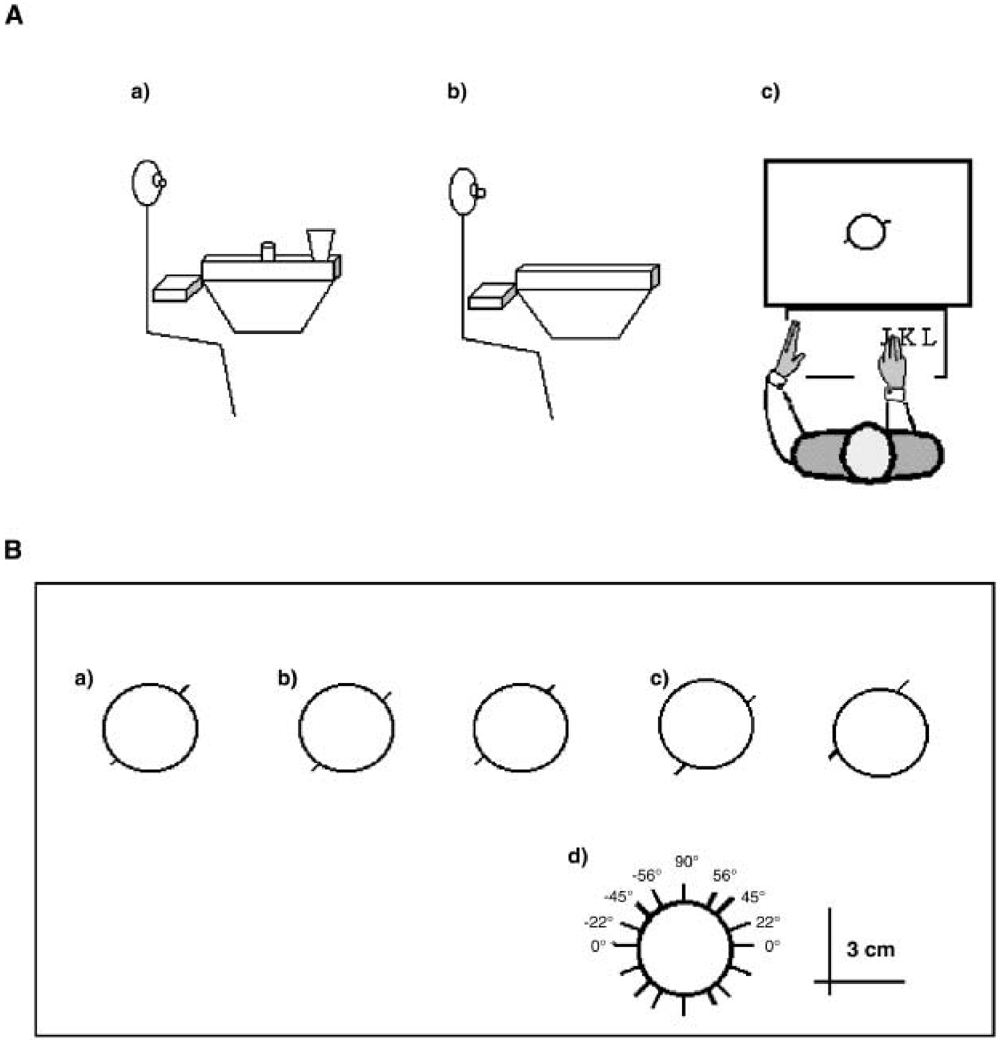


Fig. 1A,B Main experiment. **A** Schematic representation of the subject's position: *a* during the real movements; *b, c* during the imaginary movements. The subjects had to rate the level of feasibility of the grasp using three levels (“easy”, “difficult”, “impossible”), for which they pressed keyboard keys with their right hand using the following code: *l* “easy”, *k* “difficult” and *j* “impossible”, with their annular, greater and index fingers, respectively. **B** Example of an opposition axis located at 45° with respect to the frontal plane: *a* passing through the center; *b* at 3 mm from the center of gravity; *c* at 6 mm from the center of gravity; *d* the different orientations are presented together on the same scheme

Finally, ten unconstrained trials were carried out displaying an unmarked container. It was used to evaluate the subject's preferred opposition axis orientation.

Movement recording

The spatial positions of two active markers placed on the nails of both right thumb and index finger were respectively sampled at 200 Hz by means of an Optotrak 3020 system. The camera was fixed 2.5 m above the workspace with its optical axis aligned with the vertical (Fig. 4, insert). Each trial was recorded for 5 s. After acquisition the position data were filtered with a second-order Butterworth filter with a forward and reverse pass. A cutoff frequency of 10 Hz was used.

Movement onset was determined as the first of seven consecutive measures of increasing amplitude on the fingers' speed. The movement endpoint was determined as the point where the interfinger distance stopped decreasing on the first cylinder. For each stimulus the reaction time (i.e., the time between the auditory signal and the first finger movement) and the movement time (i.e., the time between the first finger movement and the movement endpoint) were monitored. To reconstruct the opposition axis the position of the tips of the thumb and index finger was sampled at the end of the movement. The opposition axis was defined as the line connecting these two points. The opposition axis orientation was calculated in a head-centered reference frame as the angle between the opposition axis and the line crossing the center of the head and the object.

Data analysis

A within-subject 1 (reaction time) × 3 (opposition axis across from the center of cylinder, 3 mm, 6 mm off center) and 1 (reaction time) × 8 (orientations of opposition axis) repeated measures ANOVA was performed for reaction time according to the center and the angle of the grasp axis. A within-subject 1 (movement time) × 3 (opposition axis across center of stimulus, 3 mm, 6 mm off center) and 1 (movement time) × 8 (orientations of opposition axis) repeated measures ANOVA was conducted for movement time level according to the center and the angle of the grasp axis. A significance level of 0.05 was chosen. A Newman-Keuls test was used as a post hoc test.

Results

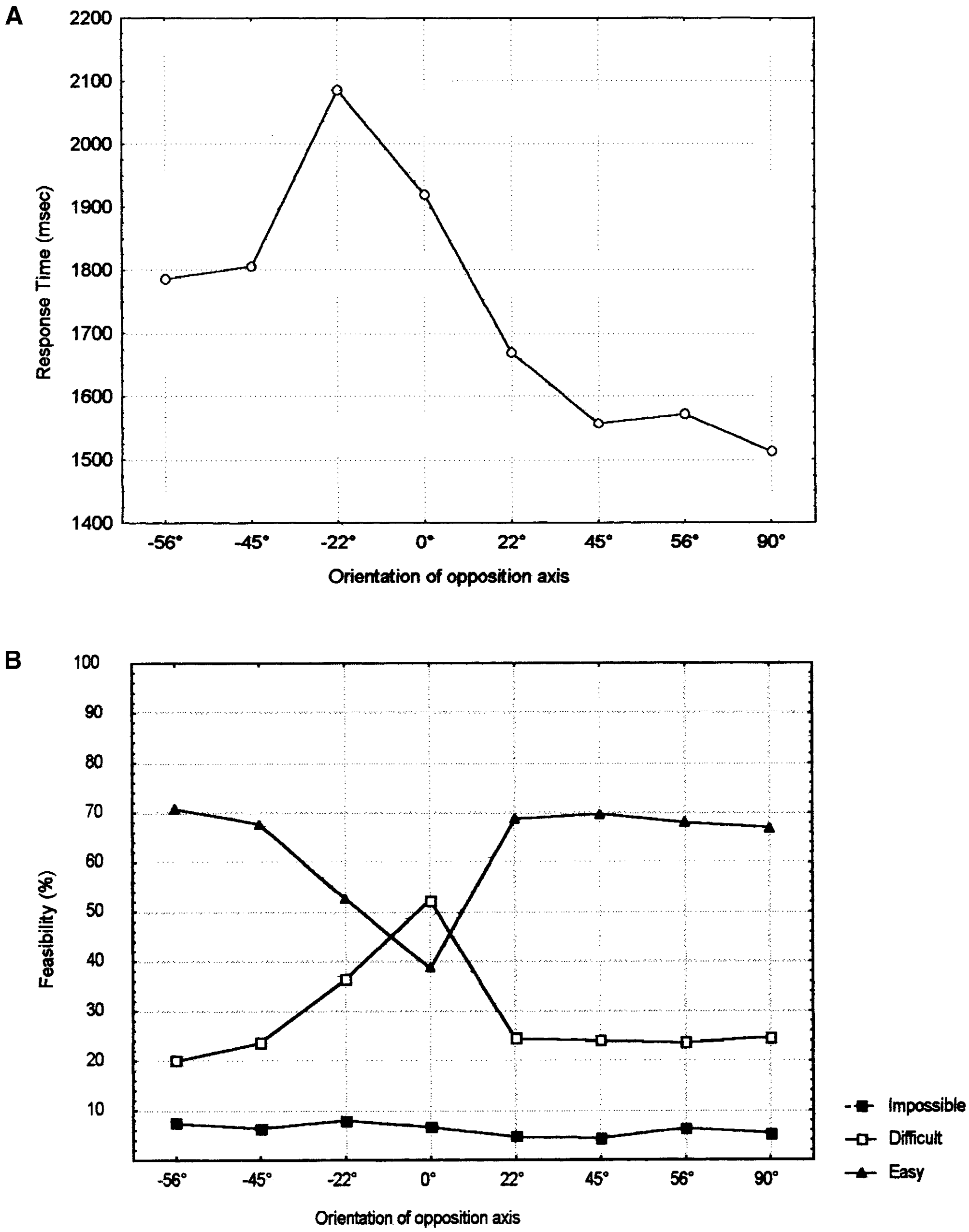
Main experiment

Influence of orientation of opposition axis

Response time

A significant effect of the orientation was observed on the RTs [$F_{(7,28)}$=7.12, P<0.0001]. The shortest RTs were observed at –56° (1787 ms), –45° (1806 ms), 22°

Fig. 2A,B Simulated movements. Response times **(A)** were longer for the grasps judged to be more difficult due to the orientation of the opposition axis **(B)**



(1670 ms), 45° (1557 ms), 56° (1572 ms) and 90° (1512 ms) (Fig. 2A, insert). The longest RTs were found for –22° (2086 ms) and 0° (1919 ms). These long RTs significantly differed from the RTs for 45°, 56° and 90°.

Feasibility level

A significant effect of the orientation [$F_{(14,56)}$=3.63, P<0.0003] on the feasibility level was observed. The post hoc test revealed that this effect was mostly due to the –56°, -45°, 22°, 45°, 56° and 90° angles, which were considered as "easy" (in 67–70% of cases) (Fig. 2B, insert). The 0° angle was considered the least "easy" (39%) and the most "difficult" (in 52%), a percentage which was found to be significantly different from those for the other angles.

The –22° angle was considered "easy" in 53% of cases and "difficult" in 36%, but with no significant difference with the other angles. The "impossibility" level was similar for all the explored angles (5–8%).

Influence of position of opposition axis with respect to object center

Response time

A significant effect of the position of the opposition axis with respect to the center was found on response time

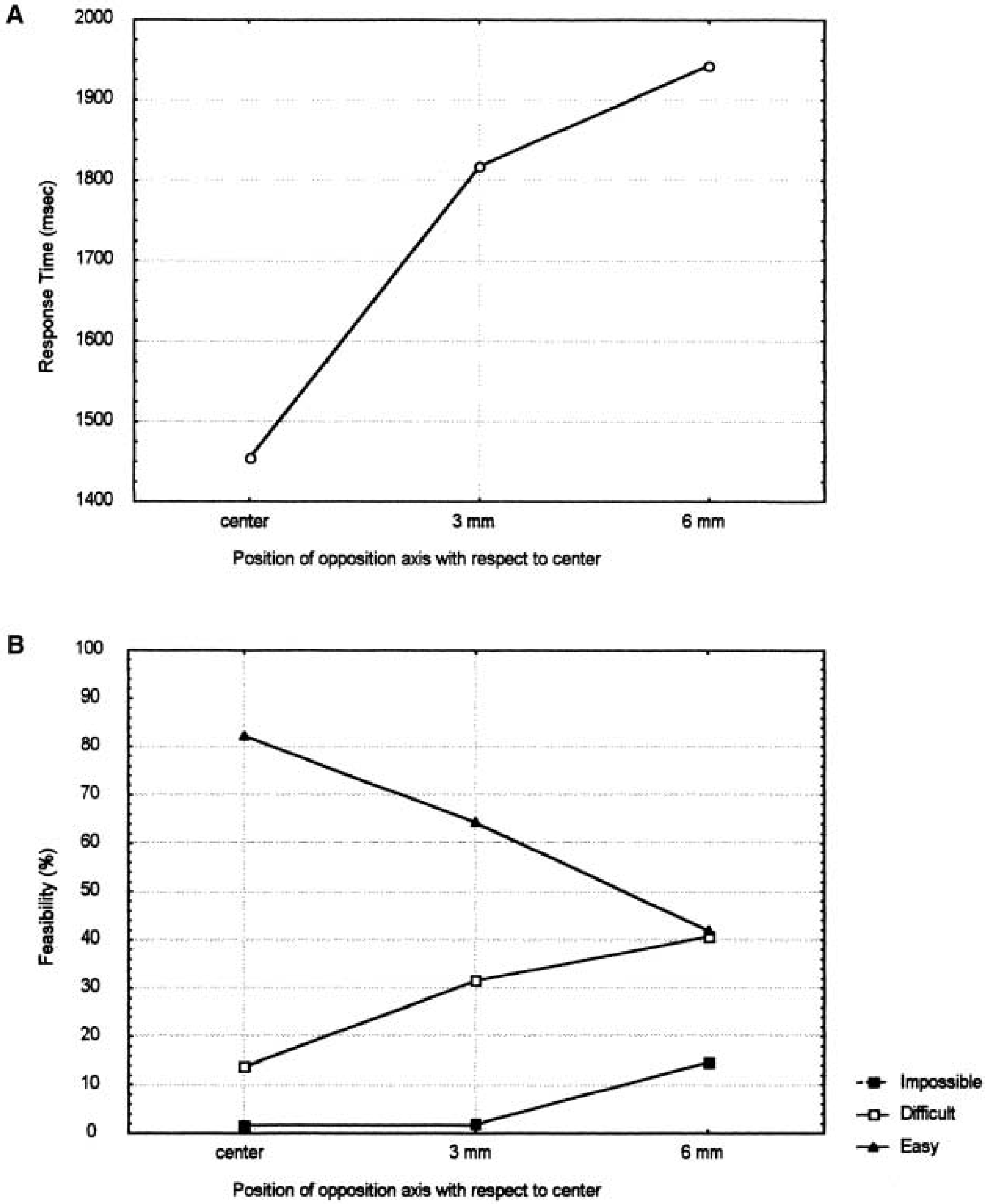


Fig. 3A,B Simulated movements. The response times **(A)** were longer for the grasp judged to be more difficult **(B)** as the presented opposition axis moves away from the center of gravity of the object

[$F_{(2,8)}$=5.32, P<0.0339]. When the opposition axis passed through the center, the shortest RTs (1470 ms) were observed (Fig. 3A, insert). They were significantly different from the RTs obtained when the axis passed 3 mm (1821 ms) and 6 mm (1963 ms) from the center.

Feasibility level

A significant effect of the position of the opposition axis on the feasibility of the grasp was found [$F_{(4,16)}$=5.48, P<0.0056]. The subjects considered the grasp "easy" in 82% of cases when the axis passed through the center, in 64% when it passed 3 mm from the center and in 42% when it passed 6 mm from the center. Conversely, they rated the grasp "difficult" in 14% of cases when the axis passed through the center, 32% 3 mm from the center and 41% at 6 mm (Fig. 3B, insert). The post hoc analysis showed a significant decrease in the "easy" ratings as the imaginary opposition axis moved away from the center. The proportion of "impossible" ratings was 2% for an axis passing through the center as well as for an axis passing 3 mm from it but it jumped to 15% at 6 mm from the center.

Control experiment

Preferred orientation of opposition axis

During the unconstrained trials, the mean orientation in the three subjects was 77.17° (SD 14.76). Orientations ranged from 44.73° to 102.72°.

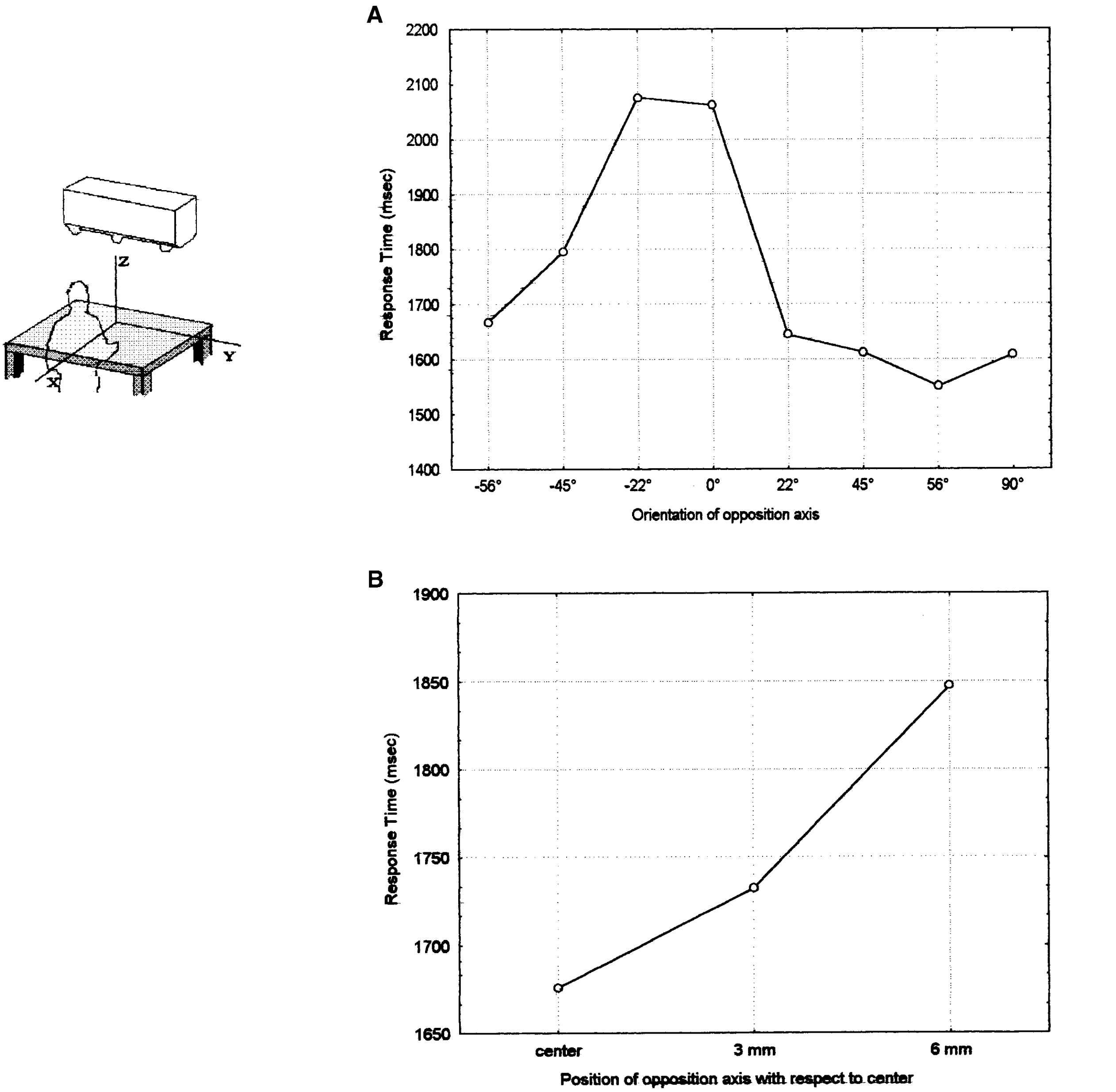


Fig. 4A,B Real movements were recorded by means of an Optotrak 3020 system. The response times were longer due to the orientation **(A)** and position **(B)** of the opposition axis

Influence of the opposition axis orientation

In order to compare with the main experiment results, a single time value (the sum of reaction time and movement time, henceforth “response time”) was used. A significant effect of the orientation could be observed on response times [$F_{(7,14)}$=8.43, P<0.0004]. The shortest values were observed at –56° (1668 ms), –45° (1795 ms), 22° (1645 ms), 45° (1613 ms), 56° (1551 ms) and 90° (1608 ms). The longest values were found for –22° (2076 ms) and 0° (2061 ms). These long values differed significantly from those found with other orientations (Fig. 4A, insert).

Influence of position of opposition axis with respect to object center

A significant effect of the position of the opposition axis with respect to the center was found on response time [$F_{(2,4)}$=31.79, P<0.0035]. When the opposition axis passed through the center (1676 ms) and at 3 mm from the center (1733 ms), the shortest values were observed. They were significantly different from the values obtained when the axis passed at 6 mm (1847 ms) from the center (Fig. 4B, insert).

Discussion

During a real grasp, the final finger position defines an opposition axis (or an opposition space if more than two fingers are involved) through which opposite forces operate on the object (Napier 1955; Iberall et al. 1986). Obviously, the orientation of this axis is constrained by the biomechanics of the arm, in such a way that certain orientations will be systematically avoided in order to prevent end-position discomfort or even failure of the grasp (Stelmach et al. 1994). This is what we observed in our previous work (Paulignan et al. 1997) in which subjects tended to adopt an invariant posture of the upper limb while grasping objects placed at different locations in the workspace. Paulignan et al.'s study showed that orientations of the opposition axis during real grasps involving a cylindrical object (i.e., in the absence of constraints inherent in the object's shape) are best represented within a body-centered frame of reference. In the current experiment, the grasps' execution required different degrees of shoulder rotation and flexion-extension of the wrist according to the orientation of the proposed opposition axis. An opposition axis at 0° requires an extreme flexion of the wrist with an internal rotation of the shoulder or an extreme extension of the wrist with an external rotation of the shoulder. Similarly, an opposition axis at –22° also appears to be near the limits of wrist flexion and internal shoulder rotation. Indeed, in the control experiment, where spontaneous orientations of the opposition axis were recorded, subjects tended to adopt postures roughly between 45° and 90°, the average being 75°. During simulated grasps, although no angular position was interpreted as impossible, orientations outside this 45°–90° range were considered uneasy, with a consistent rejection of –22° – 0° orientations across all conditions. In other words, the subjects' pattern of responses followed the limitations that the geometry of the upper limb would have imposed on real motor performance, which implies that, although they received no instruction to do so, subjects simulated the movement before giving the response. The fact that response times increased with the estimated difficulty of the task, as shown in Fig. 2, also points in the same direction. This implicit process would be the motor counterpart of the classical mental rotations or displacements used for giving responses about visual objects. Unlike 3D shapes, which can be rotated at the same rate in any direction, rotation of one's hand is limited by the biomechanics of the upper limb joints (Wexler et al. 1998). According to Parsons and Fox (1998), the response times reflect simulated biomechanically compatible trajectories, at the same rate as for executed movements. Thus the time to give the response may reflect the degree of mental rotation needed to bring one's hand into an adequate position to achieve the task. Subjects would then use the various degrees of freedom of the upper limb to mentally calculate the possible grasp angle within a body-centered reference frame. This view is supported by the fact that, in the control experiment in which the movements were actually performed, response times (i.e., including reaction time and movement time) for the different orientations were very close to those observed during mental simulation. Comparison of Figs. 2 and 4A clearly shows that it took the subjects the same amount of time to both plan an orientation of the opposition axis in order to perform a movement and to make a judgement about its feasibility. In both conditions, the most difficult orientations (0°, –22°) needed response times in the 2-s range or higher, though significantly longer than the ones measured for other orientations. This result therefore confirms and adds to previous results showing similar durations for executed and mentally simulated actions (Decety and Jeannerod 1996; Sirigu et al. 1996) as well as similar response times while making judgements requiring hand rotations or actually performing them (Parsons 1994; Johnson 2000).

We also found that the position of the proposed opposition axis with respect to the center of gravity of the object greatly influenced the pattern of responses. Whenever the subjects had to judge the feasibility of the grasp for different positions of the opposition axis, the proportion of “easy” responses decreased while the response time increased significantly as the opposition axis was moved away from the center of gravity (Fig. 3A, B, insert). This finding demonstrates that, in grasping objects, the opposition axis is not only determined by limb biomechanics, but also by the visual characteristics of the object itself. Finger positions appear to be normally computed so as to ensure a stable grasp, a necessary precondition for transport and manipulation. Indeed, an opposition axis which does not pass through the center of gravity of the object will reveal itself inadequate because the object will slip and fall (Iberall et al. 1986). When the proposed axis was offset from center in our study, it made it more likely that the computation of opposition forces prior to the grasp became more difficult and required a longer time. This was also true for simulated as well as actually performed movements (Fig. 4B, insert), which indicates that mentally simulated movements require the same amount of computation of movement constraints as executed ones.

The present results reinforce the theory that simulated movements are closely related to actual motor execution (for a recent review see Jeannerod and Frak 1999). Simulated movements may therefore represent a useful model for studying the motor system and its disorders.

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