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RESEARCH NOTE

Michel Desmurget · Hélène Gréa · Claude Prablanc

Final posture of the upper limb depends on the initial position of the hand during prehension movements

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Abstract The question of knowing how the nervous system transforms a desired position and orientation of the hand into a set of arm and forearm angles has been widely addressed during the last few decades. Despite this fact, it still remains unclear as to whether a unique posture of the arm is associated with every location and orientation of the hand in space. The main objective of the present study was to address this question. To this end, we studied a prehension task requiring human subjects to reach and grasp a cylindrical object presented at different locations, along variable orientations. In contrast to previous investigations, we considered the influence of the initial position of the hand. Results showed that the posture of the arm: (1) varied systematically as a function of the movement starting point; (2) was stereotyped for a particular subject given a configuration of the object and a movement starting location; (3) was altered at both the distal and proximal levels when the orientation of the object was changed; (4) was similarly influenced by the experimental factors in all the subjects, except one. When considered together, the previous results support three main conclusions: First, the nervous system solves the joint redundancy problem using fixed strategies. Second, these fixed strategies do not provide a single correspondence between hand configuration and arm posture. Third, the position and orientation of the hand in space are unlikely to be controlled through separate independent neural pathways.

Key words Upper limb · Posture · Initial position · Movement

M. Desmurget
Emory University School of Medicine, Department of Neurology, Atlanta, GA 30322, USA

H. Gréa · C. Prablanc (✉)
INSERM U94, Vision et Motricité, 16 av du Doyen Lépine, F-69500 Bron, France
e-mail: prablanc@lyon151.inserm.fr, Fax: +33-3-72-91-34-01

Introduction

Because the number of degrees of freedom (df) of the upper limb exceeds those necessary to completely specify the position and orientation of an object in space, any configuration of the hand can be theoretically associated with an infinite number of joint combinations (Bernstein 1967). Despite this fact, postural invariance has been reported in several studies dealing with both pointing and prehension movements (Cruse 1986; Strautman et al. 1991; Flanders et al. 1992; Hore et al. 1992; Soechting and Flanders 1993; Desmurget and Prablanc 1997; Paulignan et al. 1997). The generality of this result was recently questioned in two experiments showing that the final configuration reached by the upper limb presented significant variations when human subjects had to point from different starting locations toward a given visual target (Soechting et al. 1995; Gielen et al. 1997). Interestingly, by contrast to earlier studies describing postural singularities irrespective of the movement starting position (Cruse 1986; Strautman et al. 1991; Hore et al. 1992), these experiments involved unconstrained pointing performed in a three-dimensional (3-D) space with both the shoulder and the elbow joints. This observation may suggest that the level of constraint imposed on the movement is critical with regard to the existence of postural singularities. Another alternative explanation is, however, plausible, namely that the postural variations observed by Soechting et al. (1995) and Gielen et al. (1997) are related to the fact that unconstrained movements allow the subject to point using different parts of the index finger's extremity (fingertip, fingerpad, ...). For the sake of clarity, let us illustrate this remark with a simple example. Consider a subject required to point with their extended right index finger to their left shoulder from two starting configurations: (1) right upper limb horizontal and stretched rightward; (2) right upper limb vertical and stretched downward along the hip. In the first case, the subject will probably perform the task by flexing the shoulder and elbow joints: at the end of the movement, the right arm will lie in a horizontal plane and the index fingertip will be in contact with the target. In the second case, by contrast, he probably will flex the shoulder and rotate the upper arm around the humeral axis: at the end of the movement, the right arm will lie in a frontoparallel plane and the index fingerpad will be in contact with the target. Imagine now an additional constraint requiring the subject to perform the task by using a given part of the index finger (e.g., the fingertip) or, more generally, a given configuration of the hand. It is not clear whether postural variations would still be observed.

The main objective of the present study was to extend the pioneering observations of Soechting et al. (1995) and Gielen et al. (1997) by constraining not only the location of the hand but its spatial configuration as a whole. To this end we studied a prehension task requiring a subject to grasp a cylindrical object with a power grip. This situation strictly, but naturally, defined the location and orientation of the hand in space. During the experiment, three main factors were manipulated: (1) the object location, (2) the object orientation, (3) the movement starting point.

Materials and methods

Subjects and apparatus

Nine right-handed subjects participated in this experiment. None of them had experienced visual or neurological deficit and they were naive about the purpose of the study. The apparatus was similar to that described in a previous publication (Desmurget and Prablanc 1997). In brief, the subject was seated comfortably in a chair. Their trunk was immobilized by a harness to prevent any displacement of the shoulder. An orthogonal frame of reference, centered on the subject's right shoulder, was defined for kinematic analyses (x was the sagittal axis, y the frontoparallel axis, and z the vertical axis). In front of the subject, a motor supported a translucent cylinder to be grasped (weight 400 g; diameter 5 cm; length 10 cm). The axis of rotation of the motor (R): (1) crossed the center of mass of the cylinder (C_{mass}); (2) was orthogonal to the y-z frontoparallel plane. During the experiment it was possible to displace C_{mass} by moving the motor along the x and y directions (this manipulation did not change the orientation of R, which always remained orthogonal to the y-z plane). Note that the cylinder was equipped with an electronic device allowing illumination from inside (when the ambient light was turned off, this illumination allowed the subject to see the object but not the environment).

Procedure

The experimental design resulted from the combination of three factors. The first factor, called *object location*, was related to the location of C_{mass} with respect to the subject. Three positions were studied: *sagittal (Sa)*: C_{mass} was located in the sagittal plane (x-z) at the same height as the subject's shoulder, and at a distance corresponding to 80% of the upper-limb length; *lateral (La)*: C_{mass} was located 20 cm to the right (y-axis) of Sa; *close (Cl)*: C_{mass} was located both 10 cm to the right (y-axis) and 17.5 cm in front (x-axis) of Sa.

The second factor, called *object orientation*, was related to the tilt of the cylinder axis with respect to the vertical axis. Three orientations were considered: 60° left (counterclockwise; *60*), 20° left (*20*), and 20° right (*–20*).

The third factor, called *hand initial location*, was related to the initial location of the center of mass of the hand. Three positions were considered: *down (Do)*: the upper arm was then roughly vertical and the hand was located at hip level in the sagittal plane crossing the shoulder; *middle (Mi)*: the hand was then located 35 cm above Do and 20 cm to the right; *high (Hi)*: the hand was then located 60 cm above Do and 35 cm to the right. Mean values of the upper-limb angles for each of these initial positions are reported in Table 1.

The whole experiment was carried out in the dark in order to prevent the subject from using retinal signals to correct the movement during its time course. A representative trial unfolded as follows. The subject initially focused on a red light-emitting diode (LED) placed in the sagittal plane at the same height and distance as those of Sa. During object positioning, the experimenter guided the subject's hand to its initial location (hand initial locations were indicated by means of small visual spots). After a randomly selected delay (1–3 s), a tone was given, the central LED was turned off, and the object was lit from inside, indicating that the subject had to grasp it. The only instruction was to grasp the object using a power grip. In this case, "the object is held in a clamp formed by the partly flexed fingers and the palm, counter-pressure being applied by the thumb lying more or less in the plane of the palm" (Napier 1956).

For technical reasons, the experiment was divided into three sessions, each corresponding to a different object location. These sessions were randomly ordered across subjects. During a session, the nine possible combinations of object orientation and hand starting point were presented in a random order. Each subject performed 270 movements (3 object positions × 3 object orientations × 3 starting points × 10 repetitions).

Recording technique and data analysis

Six infrared LEDs were placed on the right arm of the subjects in the following positions: (1) metacarpophalangeal joint of the index finger; (2) metacarpophalangeal joint of the auricular finger; (3) radial styloid; (4) ulnar styloid; (5) ulnar head of the elbow; (6) external extremity of the acromion. The x-, y-, and z-coordinates of these diodes were recorded at a frequency of 200 Hz, by a SELSPOT II system equipped with two cameras. For each diode, the position signals were filtered at 10 Hz with a zero-phase, finite impulse response filter using 33 coefficients. Arm posture was defined as the orientation angles of the upper- and lower-arm segments (for the sake of clarity, and because of their slight influence on the upper-limb posture, we did not consider wrist angles). Upper-limb angles are represented in Fig. 1 according to the following terminology (see Desmurget and Prablanc 1997 for computational details): *upper-arm azimuth* (UA); *upper-arm elevation* (UE); *upper-arm rotation* (UR); *elbow flexion* (EF); and *forearm rotation* (FR).

In addition to the previous angles, we also computed the elevation angle of the plane of the arm (EPA; angle between the vertical

Table 1 Values of the upper-limb angles for each of the movement starting points (mean + interindividual SD)

	Upper-arm azimuth (deg)	Upper-arm elevation (deg)	Upper-arm rotation (deg)	Elbow flexion (deg)	Forearm rotation (deg)
Down	99.6	–67.9	16.4	123.9	–20.2
	(15)	(5)	(13)	(12)	(11)
Middle	98.9	–59.2	37.9	97.8	–25.2
	(7)	(6)	(12)	(11)	(7)
High	78.8	–14.9	73.9	135.7	–19.4
	(5)	(4)	(15)	(10)	(14)

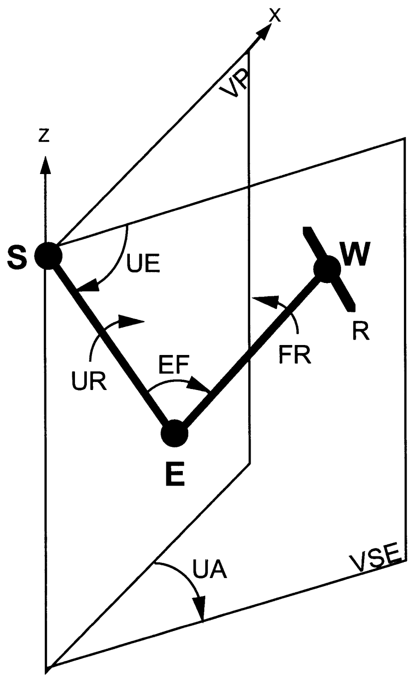

Fig. 1 Angles defining the posture of the arm. Define *x* and *z* as the sagittal and vertical axes crossing the shoulder; define *VP* as the vertical plane containing the *x*-axis and *VSE* as the vertical plane containing the shoulder-elbow axis. The Upper-arm Azimuth (*UA*) defines the angle between VP and VSE (UA is equal to 0° when the upper arm is in VP and to 90° when it is in the vertical plane containing the *y*-axis). The upper-arm elevation (*UE*) defines the angle separating the horizontal and the shoulder-elbow axis (UE is equal to 0° when the upper arm is horizontal and to –90° when it is directed vertically downward). The upper-arm rotation defines the rotation of the upper arm around its axis (internal rotations are considered as positive and external rotations as negative). The elbow flexion (*EF*) defines the angle between the elbow-wrist and elbow-shoulder vectors (EF is equal to 180° when the upper limb and the forearm are collinear and to 90° when they are orthogonal). The forearm rotation (*FR*) defines the rotation of the forearm around its axis, with the same sign convention as for UR (*S* shoulder, *E* elbow, *W* wrist, *R* radioulnar axis)

axis and the plane of the arm). This parameter, which represents the pivot angle of the upper limb around the horizontal line joining the shoulder to the object, can be considered as an economical way to describe the variations of the arm posture according to the hand initial location factor (Helms-Tillery et al. 1995; Desmurget et al. 1996. When the hand position and hand orientation are determined – as is the case for a power grip – and when the shoulder is fixed – as is the case in the present experiment, the angular configuration of the upper limb is uniquely determined once EPA is determined.)

To test the influence of the experimental conditions on the final postural configuration of the arm, analyses of variance with repeated measures (ANOVA), were performed for all the upper-limb angles. The repeated-measure factors were: "object location", "object orientation", and "hand initial location". Threshold for statistical significance was set at 0.05.

Results

All the dependent variables considered in the present experiment (UA, UE, UR, EF, FR) were significantly influenced by the "hand initial location" factor ($P < 0.0001$). This indicated that the posture reached by the arm was not the same for the different starting points. An illustration of this result is provided in Fig. 2, which displays the angular differences observed between the Do and Hi starting locations. As shown in the figure, UA, UE, and EF tended to increase for Hi with respect to Do. At the same time, UR and FR tended to decrease. Interestingly, the influence of the movement starting point on the final upper-limb posture was not homogeneous, and a significant interaction was observed, for all arm angles, between the hand initial location factor and the spatial characteristics of the object (orientation, position; $P < 0.02$). As shown in Fig. 2, the least amount of postural variation was noticed for the –20°/lateral target. At the same time, the greatest amount of postural variation was observed for the 20°/close target. This observation was not really surprising considering that the –20°/lateral and 20°/close combinations corresponded to the object configurations for which the ranges of potentially usable postures were minimal and maximal respectively (for the –20°/lateral target, the upper limb was almost fully stretched, and the magnitude of the angular variations mechanically allowed was small; by contrast, for the 20°/close target, the elbow was consistently flexed, and the magnitude of the angular variations mechanically allowed was large).

The existence of a relation between arm posture and the movement starting point was confirmed by additional analyses involving the EPA. As shown by these analyses, the complex angular modifications observed when the initial hand location was modified could be summarized as follows: (1) the tilt of the plane of the arm varied systematically as a function of the movement starting point: at the end of the movement, the upper limb verticality was maximum for Do, intermediate for Mi, and minimum for Hi; (2) the variations in the upper-limb orientation were compensated by concomitant variations in the forearm rotation. The modifications of EPA according to the hand initial location factor are represented in Fig. 3.

In addition to the finding that the posture of the arm was not completely constrained by the configuration of the hand in space, three important points need to be mentioned. *First*, the variations of the upper-limb posture actually observed in response to the experimental modifications were consistently smaller than the variations anatomically allowed. *Second*, given a configuration of the object and a movement starting location, the intraindividual standard deviations were quite small for all the upper-limb angles (Fig. 2). This indicated that the posture of the arm was, to a large extent, stereotyped when the object position, the object orientation, and the movement starting point were specified. A further illustration of this point is provided in Fig. 3, which shows individual trials performed by one subject from the different starting points toward the 20°/close target. *Third*, as indicated by the significance of the within-subjects ANOVAs, the postural variations observed according to the experimental factors presented consistent similarities from subject to subject (Maxwell and Delaney 1989). In order to estimate these similarities more accurately, we submitted EPA to a

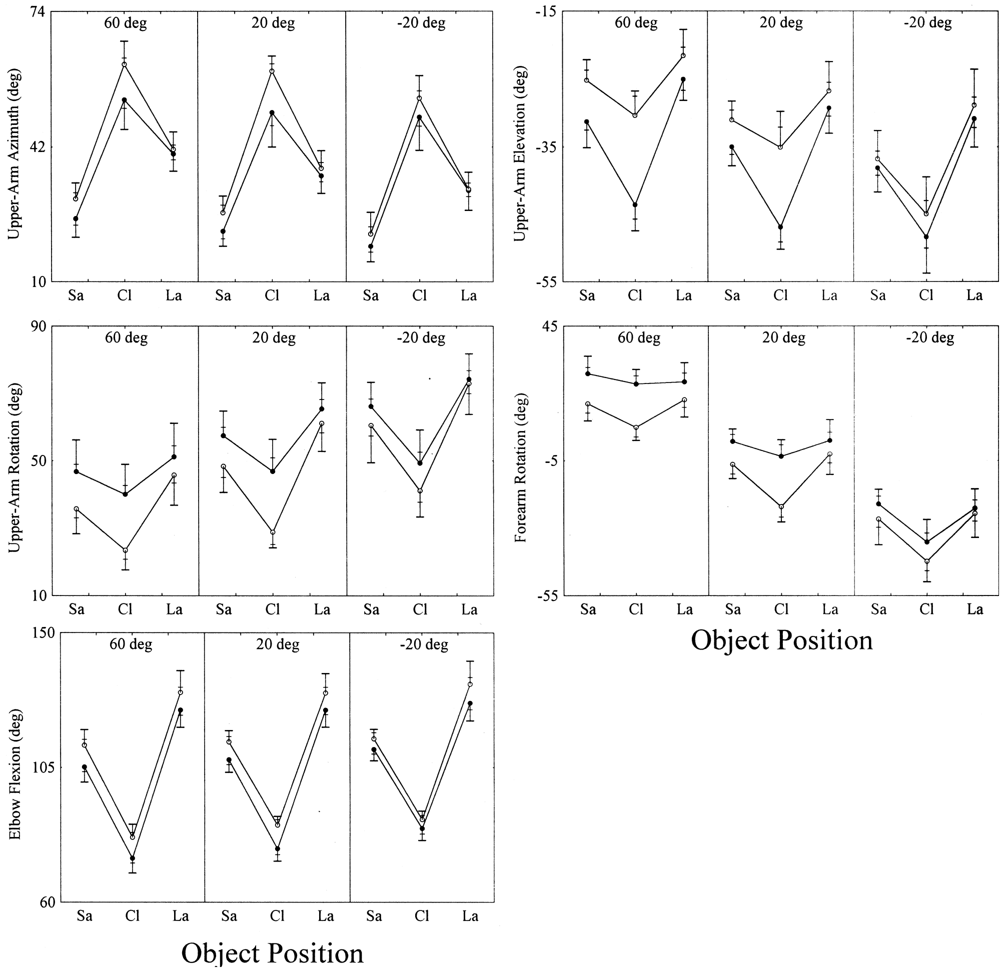

Fig. 2 Variations of the upper-limb angles according to the object position (*Sa* sagittal, *Cl* close, *La* lateral), the object orientation, and the movement starting point (high, *white circles*; down, *black circles*). For each experimental configuration, the mean values, mean intraindividual SD (*small bars*), and interindividual SD (*large bars*) are represented

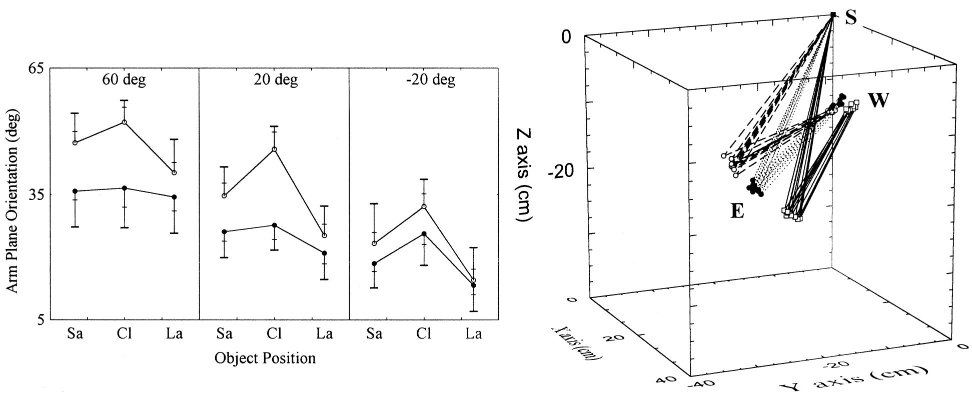

Fig. 3 *Left panel* Variations of the elevation of the plane of the arm (EPA) according to the object position (*Sa,* sagittal; *Cl,* close; *La,* lateral), the object orientation, and the movement starting point (high, *white circles*; down, *black circles*). For each experimental configuration, the mean values, mean intraindividual SD (*small bars*), and interindividual SD (*large bars*) are represented. *Right panel* Variations of the EPA according to the movement starting point for subject S8 (high, *dashed lines/white circles*; middle, *dotted lines/black circles*; down, *continuous lines/white squares*). Individual trials performed toward the 20°/close target. *S*, *E*, and *W* represent the locations of the shoulder, elbow and wrist, respectively

principal component analysis (nine variables, one per subject; 27 observations per variable: one per starting point, object position, and object orientation; Johnson and Wichern 1982). As shown in Fig. 4, eight of the nine subjects were clustered into a homogeneous group. This agreed with the conclusion that the postural variations exhibited by these subjects presented a high degree of similarity (NB: the intercorrelations involving any two of these eight subjects were higher than 0.90).

Before reaching the Discussion, the last important result we would like to stress here concerns the existence

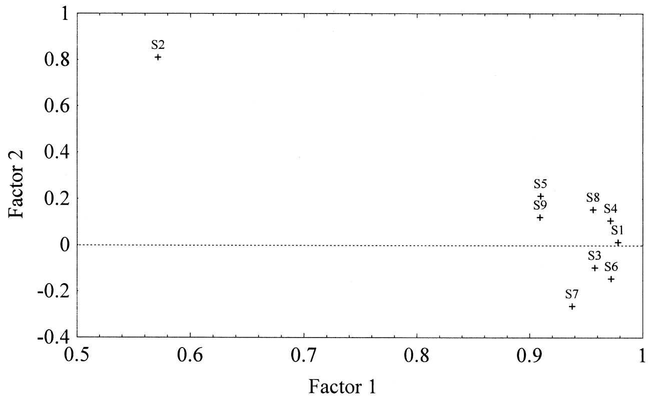

Fig. 4 Results of the principal component analysis performed, with respect to EPA, to estimate the degree of consistency in the behavior of the different subjects (nine variables: one per subject; 27 observations per variable: one per starting point, object position, and object orientation). As shown, eight of the nine subjects were clustered into a homogeneous group. This indicated that the postural variations exhibited by these subjects according to the experimental factors were very similar

of significant interactions between the object orientation and object position factors, for all the upper-limb angles ($P < 0.035$). As shown in Fig. 2, the excursion of the shoulder angles depended not only on the object position but also on the object orientation. Such a result would not have been expected if the neural transformations dealing with these two parameters were independent.

Discussion

The question of knowing how the nervous system transforms a desired configuration of the final effector into a set of arm and forearm angles has been widely addressed during the last decade (for a review, Gielen et al. 1995). Despite this fact, however, it remains unclear whether every orientation and location of the hand in space corresponds to a unique posture of the upper limb. The main purpose of the present experiment was to investigate this question. To this end we studied goal-directed movements, requiring human subjects to grasp a cylinder with a power grip. In contrast to previous studies (Helms-Tillery et al. 1995; Desmurget et al. 1996, Desmurget and Prablanc 1997; Paulignan et al. 1997), we did not only consider the influence of the spatial attributes of the cylinder to be grasped (position, orientation). We also examined the effect of the movement starting point. Our analyses demonstrate that the posture of the arm is not invariant for a given location and orientation of the hand in space. As shown in the Results section, when the movement starting point was modified, systematic variations of the upper-limb angles were noticed. This finding complements and generalizes the results obtained by Soechting et al. (1995) and Gielen et al. (1997) in pointing experiments, which required subjects to control the location of the final effector, but at the same time allowed large variations in the hand configuration. It also suggests that the postural stabilities reported in several pioneering studies depends on the existence of specific constraints. With respect to this point, it is worth noting that the studies describing postural invariance irrespective of the movement starting location involved a restricted set of experimental situations such as pointing at distant targets with an outstretched arm (Strautman et al. 1991; Hore et al. 1992) or pointing in a horizontal plane using a three-degrees-of-freedom manipulandum (Cruse 1986).

Beyond the previous observations, it is noteworthy that the behavior of the motor system was not random, but quantitatively deterministic both between and within subjects. Modifying the object configuration and/or the hand initial location had a similar effect from subject to subject. In addition, for a given subject and a particular initial state, the motor system evolved toward a single and predictable final state (the variability in the final posture of the arm was quite low given a subject, a starting point, and a configuration of the object to be grasped; see, for a similar result: Helms-Tillery et al. 1995; Desmurget et al. 1996, Desmurget and Prablanc 1997; Paulignan et al. 1997). From a theoretical point of view, these observations suggest that the nervous system solves the redundancy problem using fixed strategies. As indicated by the systematic relationship existing between the upper-limb angles and the movement starting point, these fixed strategies do not provide a single correspondence between hand configuration and arm posture. This result agrees with recent models suggesting that kinetic factors are taken into account during movement planning (Uno et al. 1989; Rosenbaum et al. 1995; Soechting et al. 1995). The estimation of the congruence existing between the quantitative predictions of each of these models and the behavioral data reported in the Results section is, however, beyond the scope of the present study.

Computationally, a possible way to reduce the complexity of the inverse mapping procedures consists of grouping the upper-limb degrees of freedom into independent functional modules, each dealing with a given spatial attribute of the object to be grasped (Hollerbach 1988). This hypothesis, initially proposed to account for the parallelism existing during prehension movements between grip formation and hand transport (for a review, Paulignan and Jeannerod 1996), has been recently generalized to hand orientation (Jeannerod 1992; Stelmach et al. 1994). According to this generalization, the proximal angles of the upper limb (shoulder, elbow) should only be related to the object location, whereas the distal angles (wrist, radioulnar joint) should only be related to the object shape and orientation. Clearly, our experimental observations do not support these predictions. As shown in the Results section, indeed, both the proximal and distal angles were affected when the object orientation was modified. In addition, a strong interaction was observed between the postural modifications induced by the object position and object orientation. These findings indicate, in agreement with other studies (Soechting and Flanders 1993; Desmurget et al. 1996), that the position and orientation of an object to be grasped are not treated as separate attributes by the nervous system. This suggests that the final configuration of the hand (position, orientation) is controlled as a whole during prehension movements and pleads against the notion of modularity as a general simplifying rule for solving the problem of joint redundancy. Note, however, that the latter observation does not mean that modularity cannot be used in some cases. In particular, our data cannot be considered as conclusive with regard to the existence of an independent control of the most distal part of the limb (finger movements; Paulignan and Jeannerod 1996).

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