ELSEVIER
Brain Research 952 (2002) 257–267
BRAIN RESEARCH
www.elsevier.com/locate/bres

Research report

Coupling between reaching movement direction and hand orientation for grasping

Nezha Bennis, Agnès Roby-Brami*

Neurophysique and physiology of the motor system, UMR 8119, CNRS and University Paris V, 45 rue des Saints Pères, F-75270 Paris Cedex 06, France

Accepted 2 May 2002

Abstract

In a previous work, we demonstrated that orientation of the hand in the horizontal plane (azimuth) at the time of grasping depends on the direction of the reaching movement in the horizontal plane. Here we report three experiments to further investigate the generality of this coupling. Azimuth of the hand for grasping was studied while subjects were reaching for objects placed at various locations on a horizontal board. Hand movements were recorded with an electromagnetic sensor giving information about hand 3D position and orientation. As expected, hand azimuth for grasping was coupled with movement direction in the central part of the workspace (but reached a limit for rightmost reaching directions). The coupling did not depend on the direction of where the object had to be put after grasping. Various initial positions and azimuths of the hand were compared to the most comfortable initial hand posture. The coupling between hand azimuth and movement direction remained whatever the initial hand azimuth. This demonstrates that reaching movement direction is coupled with azimuth at the time of grasping and not with a rotational hand movement. The coupling between hand azimuth and movement direction subsisted when the initial upper trunk orientation was changed. Thus our results cannot be explained by an invariance of the coupling coded in hand-centered or shoulder-centered coordinates. They rather suggest that the movement is produced in a frame of reference associated with the environment.

Theme: Motor systems and sensorimotor integration

Topic: Control of posture and movement

Keywords: Hand orientation; Reaching; Grasping; Posture; Goal-directed movement

1. Introduction

Prehension movements involve two components: transportation of the hand in vicinity of the object to be grasped (the reaching or transport component) and formation of the finger posture for grasping (the grasping component) [32]. The finger configuration for grasping varies with the intrinsic properties of the object such as size, shape and weight and can be described as an opposition axis along which the fingers exert forces on the object and ensure stable grasp [21,28]. The orientation of the opposition axis for grasping is known to depend on the shape and orientation of the object [7,10,11,24]. In addition, it has been demonstrated that, when it is not constrained by the shape or orientation of the object, the orientation of the opposition axis varies with the location of the object in the horizontal plane [14,31]. In a recent study, we confirmed that hand azimuth (i.e. the projection of the hand longitudinal axis in the horizontal plane) for grasping depends on the location of the object in the horizontal plane and we found that it also varied with the initial hand position [33]. We demonstrated that the variations of hand azimuth with either the object location or the initial hand position could be largely explained by a coupling of hand azimuth for grasping to movement direction in the horizontal plane (i.e. the vector joining the initial hand position to the object location). This result confirms that the control of hand orientation for grasping is strongly linked to the control of the reaching component, as proposed by Desmurget et al. [7,10].

---

*Corresponding author. Tel.: +33-1-4286-2287; fax: +33-1-4927-9062.
E-mail address: roby@biomedicale.univ-paris5.fr (A. Roby-Brami).

0006-8993/02/$ – see front matter
PII: S0006-8993(02)03250-X

The mechanisms of the control of goal-directed movements are still controversial. For some authors, goal-directed movements are first specified as a vector in the task space, thus defining the trajectory of movement of the end-point of the limb [1,13,17]. It is usually assumed that visuomotor coordination is achieved through a sequence of coordinate transformations between the visual space where the target is perceived and the motor space, which is defined in joint and muscle coordinates [30]. In particular, Soechting and Flanders proposed an intermediate coordinate system centered on the shoulder [38,39]. Other authors proposed that goal-directed movements are planned in joint space as sets of angles representing a desired or a reference posture [7,10,11,18,34,35]. Some differences between the results favoring the spatial motor control hypothesis and those favoring the postural motor control hypothesis could be due to different experimental constraints [9]. However, there is at present no agreement on the question of how the central nervous system chooses an upper limb posture that corresponds to a desired hand position and orientation in space. This question is not trivial since the mapping between the desired hand position and orientation in space and the upper limb joint configuration is not unique and since human subjects adopt a regular upper limb configuration for grasping despite anatomical redundancy [18].

The hypothesis is that movements are controlled by means of synergies, which reduce the number of available degrees of freedom [3]. One example was found in the oculomotor system since the orientation of the eyeball during fixation (3 degrees of freedom, df) is uniquely determined by gaze direction (2 df), each eye orientation having its rotation axis in a head fixed plane called Listing's plane [5,41]. This behavioral regularity, known as Donder's law, is probably linked to neural mechanisms. It has been proposed that the straight arm when pointing may be similar to the eye and achieve a constant orientation for a particular target, even if the rotation axes does not follow Listing's law [20]. However, Donder's law is not obeyed in more general upper limb movements, in particular when the task involves upper arm–fore arm coordination [26] or when considering movements from different initial positions [8,16,33,40].

Instead, we propose that reaching to grasp movements use the coupling between reaching movement direction and hand orientation as a simplifying synergic principle [33]. Such a coupling, which explains the differences in grasping posture due to both the target and the different initial hand positions, may simplify the planning of prehension and the coordination of reaching and grasping. Here, we report a series of three experiments aimed at further testing the generality of the coupling between movement direction and hand azimuth. In the previous study, subjects had to bring the object in front of them after having grasped it [33]. The first experiment compared this task condition to a lifting task, which imposes no horizontal movement direction after grasping. The second and third experiments were designed to test the hypothesis that the coupling of hand azimuth for grasping to movement direction could be explained by an invariance in hand-centered [17] or in shoulder-centered reference frames [38,39]. If this were the case, hand azimuth for grasping should vary with a modification of the initial posture with different orientations of the hand or the trunk, respectively. In addition, the workspace was wider than the previous one, in order to test the consequence of a conflict between movement direction and the need to preserve a comfortable posture for grasping [34,35]. In these three experiments, hand azimuth for grasping was tightly coupled to the reaching movement direction, at least within the central workspace. This coupling was not modified by the initial hand or trunk orientation, suggesting that it was not planned in hand- or shoulder-centered reference frame. The generality and robustness of this relationship suggests that the control of goal-directed gestures is more likely devoted to the orientation of the distal limb segment than to the trajectory of the hand in space.

2. Materials and methods

2.1. Subjects

A total of seven right-handed subjects, two men and five women, aged 26–46 years volunteered for this study. All subjects were professional colleagues or students who gave written consent to the experiment, in agreement with French regulations on ethical issues.

2.2. Task and experimental set-up

The task consisted in seizing a light cardboard cylinder (4 cm in diameter and 10 cm high) by using a precision grip between the thumb and other fingers. Fig. 1A shows the experimental set-up and the reference frame for position and orientation measurements. The subject sat in front of a horizontal wooden board on which the initial hand positions (P1–P3) and object locations (A–J) were marked within a 0.6×0.4-m space (against 0.35×0.25 m in Ref. [33]). The board was placed in front of the subject so that his/her right shoulder was located 30 cm posterior to the reference frame ($Y=-30$ cm). The trunk was immobilized by a harness and the subject was instructed to look straight ahead. The right hand was comfortably placed palm down on a molded gantlet, which maintained the hand and thumb without constraint (Fig. 2A). The gantlet was attached to the table at the initial positions P1–P3, by two brass screws passing through the gantlet and the table. The first screw, located near the wrist, was used to fix the hand position; the second screw, located at the level of the second phalanx of the third finger, was used to fix the slant

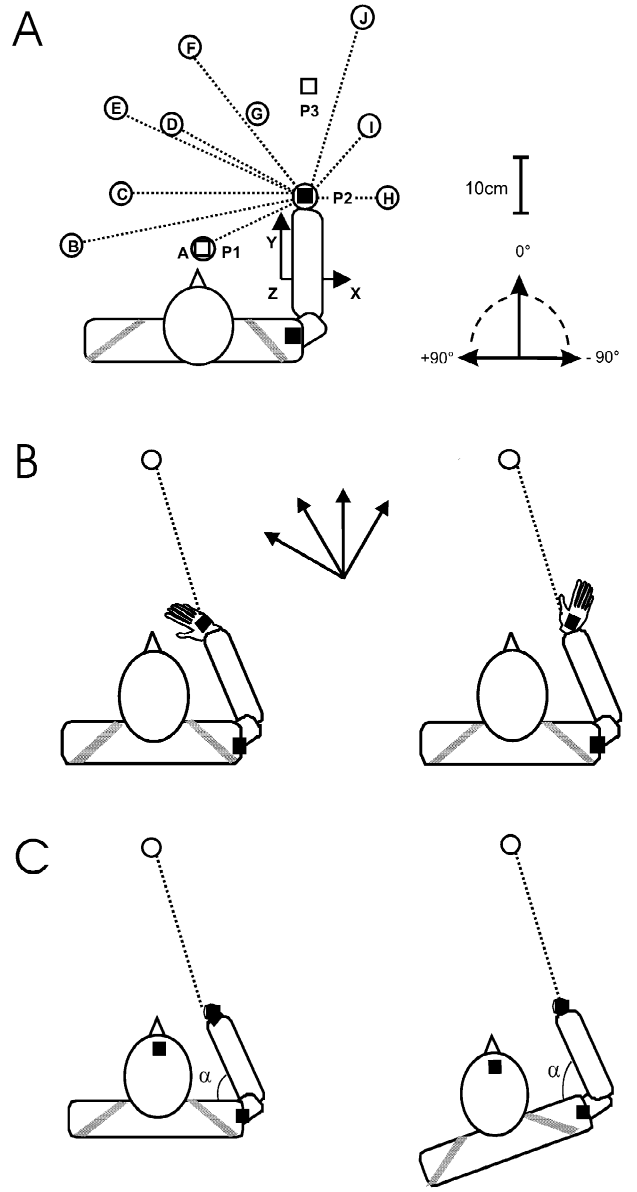

Fig. 1. (A) Experimental set-up. Horizontal board showing the object locations (circles: A–J) and the initial hand positions (open squares: P1–P3). The upper trunk was blocked by a harness. The position and orientation of the reference axes *X*, *Y*, *Z* are indicated. The solid squares indicate the sensors placed on the hand and acromion. The object location A, coinciding with P1, was studied for initial hand positions P2–P3 and was replaced by object location G for initial hand position P1. (B) Schema of the modifications of the initial hand orientation for an initial position at P1. The hand orientation was modified by a positive (counter-clockwise) or a negative (clockwise) slant of the gantlet, indicated by the black arrows. The black squares indicate the sensor locations, and the dotted line indicates movement direction. (C) Schema of the modifications of the upper trunk orientation. The hand initial position was P1. The upper trunk azimuth was modified by a +20° rotation. α is the horizontal abduction angle in the shoulder.

of the gantlet in order to modify the orientation of the longitudinal axis of the hand.

Two task conditions were compared in the first experiment. In the ‘grasp to lift’ task, subjects were asked to grasp the cylindrical object, to lift it to a height of 5 cm (indicated by a wooden paw) and to put it back in its original position. In the ‘grasp to bring’ task, subjects were asked to grasp the object and to place it on the board in front of their abdomen, at a constant final location. The initial hand position was in P2, with the hand longitudinal axis parallel to the *Y* reference axis. The movements were self-paced after a verbal signal; no emphasis was placed on the reaction or execution time. A total of five movements were performed for each object location.

In the second experiment, different initial postures were obtained by turning the gantlet on the table without modifying the position of the wrist (Figs. 1B and 2A). Four initial hand azimuths were studied for each hand position (P1–P3). Initially imposed gantlet slant was measured as the angle between the screw line and the *Y*-axis: right (−30°), median (0°), left (30°) and extreme left (60°). The subjects were asked to place the right hand in the gantlet in a position, which was indicated by the contour of the gantlet’s surface but not rigidly maintained. For each initial hand posture, the object location was randomly varied among nine locations. One movement was performed per object location. The task was to grasp and lift the object.

In addition, the most comfortable hand orientation for each initial position (P1–P3) was determined for each subject immediately after the experiment. The gantlet was fixed at the given location by the screw located at wrist level. The subject was asked to slowly turn the whole of the hand and gantlet until he/she felt that his/her posture was the most comfortable. The azimuth of the hand was then recorded after a verbal signal from the subject.

In the third experiment, two initial trunk postures were compared (Fig. 1C). In the control condition, the trunk was frontal and parallel to the reference *X*-axis, as in the previous experiments (‘frontal trunk’); in the second condition (‘rotated trunk’), the chair was moved and rotated so that the trunk azimuth made an angle of 20° with regard to the frontal plane, without change in the spatial location of the sensor fixed on the acromion. The subjects were instructed to look straight ahead. The position and configuration of the upper limb was the same in the two conditions, but the shoulder was more abducted in the rotated trunk condition (see α angle in Fig. 4A). Two initial hand postures were studied, both stated as comfortable (P1 with 30° slant, P2 without slant). The task was to ‘grasp and lift’ the object. A total of five movements were performed for each object location.

2.3. 3D movement recording

The 3D motion analysis was performed with a Fastrack Polhemus system, which utilizes an electromagnetic field generated by a transmitter to determine the position (three Cartesian coordinates: *x*, *y*, *z*) and orientation (three nautical Euler’s angles) of two mobile sensors at a 30-Hz

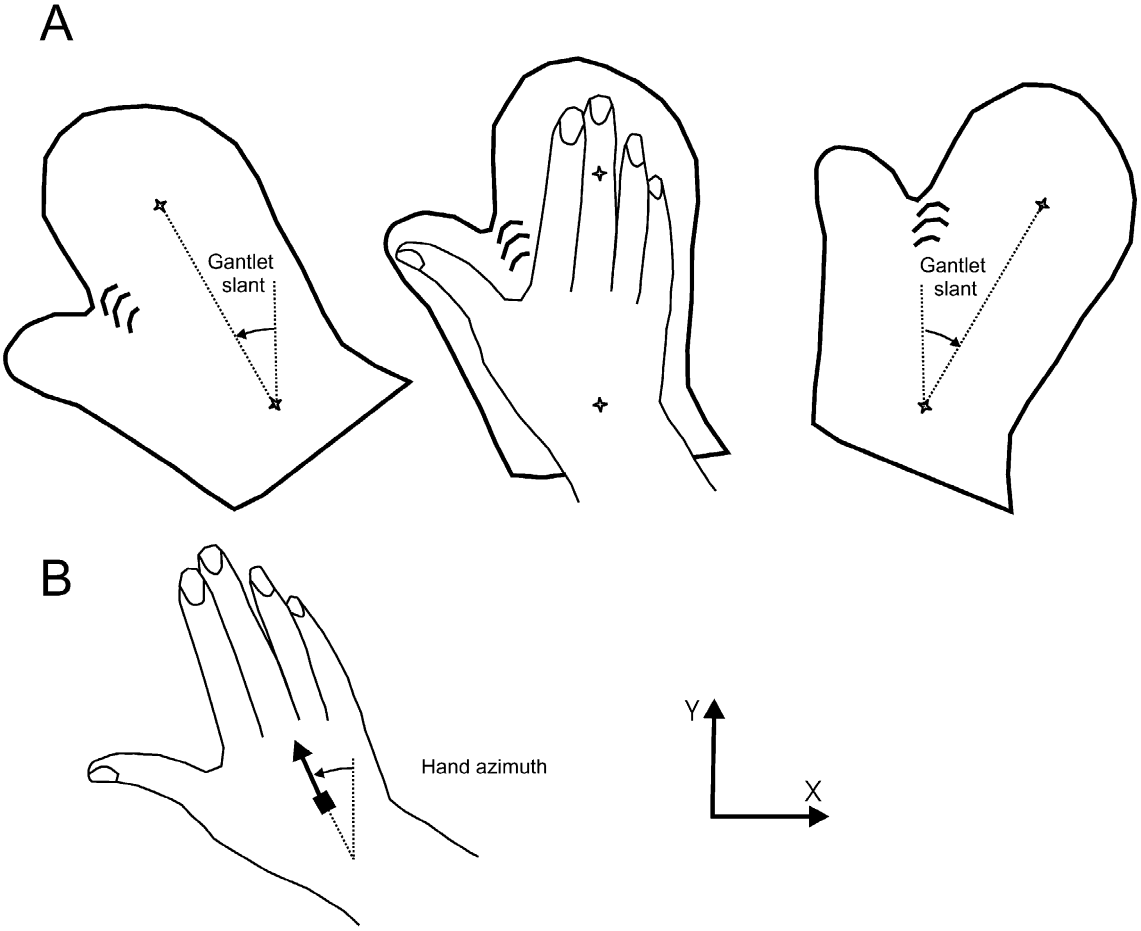

Fig. 2. Experimental set-up to constrain and measure hand orientation. (A) Schema of the molded gantlet, with the position of the two screws to fix the gantlet slant (30°, 0° and −30°, respectively, from left to right). The place of the hand is indicated. (B) Position and orientation of the marker on the dorsum of the hand, with its main axis along the third metacarpal bone. The marker is used to measure hand azimuth by reference to the *Y*-axis of the electromagnetic transmitter fixed on the table.

sampling rate. The magnetic transmitter fixed on the table provides the reference frame, *XYZ*. The hand sensor was fixed by adhesive tape on hand dorsum, with its main axis aligned with the third metacarpal bone (Fig. 2B). We concentrated on the azimuth which is the angle in the horizontal plane measured between the main axis of the sensor and the *Y*-axis of the reference frame. A second sensor was horizontally fixed on the ipsilateral acromion, with its main axis toward the right.

The experimental set-up and its environment were wooden, and metallic objects or electromagnetic sources were removed to avoid interference with the measurement system. A calibration procedure with two sensors fixed on a ruler showed that data were accurate (less than 1% error) within a 60-cm radius workspace around the magnetic transmitter. In the present study, the hand sensor always remained within less than 35 cm of the transmitter; the sensor fixed on the acromion was situated 35–52 cm from the transmitter, depending on the subject. Further analysis of the accuracy of the electromagnetic recording system for motor control and biomechanical analysis is provided in Ref. [4].

This study focused on the kinematics of the hand for reaching and on the relationship between hand azimuth at the time of grasping and movement direction. For convenience, hand azimuth was zero when the longitudinal axis of the hand was parallel to the reference *Y*-axis.

2.4. Data analysis

Tangential velocity of the hand sensor was computed by differentiation of the position signal. The onset of movement was determined as the first sample above the velocity threshold of 0.01 ms^{-1}. The time of grasping was defined as the time of minimum velocity between the reaching and return movements for the ‘grasp to bring’ task and as the time when the velocity vector became vertical in the ‘grasp to lift’ task. In both cases this time corresponded to the turning point of the hand trajectory between the first (reaching to grasp) and the second part of the movement (bring or lift). The position and orientation of the hand sensor were measured at the onset of movement (initial position and azimuth) and at the time of grasping.

Movement directions were calculated for each trial as the angle between the vector joining the initial hand position to the target and the *Y*-axis (i.e. forward movements with regard to the initial hand position have a null direction, outward movements have a negative direction and inward movements have a positive direction).

The mean values of five movements in each condition were statistically analyzed with repeated measures ANOVA, which included hand azimuth as a dependent parameter, the factor 'object location' and the factors 'task', 'gantlet slant' or 'initial trunk azimuth', depending on the experiment, with Tukey's post hoc test. When it was applicable to the whole range of the measures, regression analysis was used to test the linear relationship of hand azimuth to movement direction in individual subjects. A significance level of $P<0.05$ was used for all analyses.

3. Results

3.1. Modification of the task

Fig. 3A shows examples of the hand sensor velocity profile. In the 'grasp to lift' task, the velocity profile showed four peaks corresponding to movements of reaching, lifting and putting down the object and of replacing the hand on the gantlet. In the 'grasp to bring' task, the velocity profile showed three main peaks corresponding to movements of reaching, bringing and replacing the hand on the gantlet.

Fig. 3B displays the variations of the hand azimuth at the time of grasping as a function of the movement

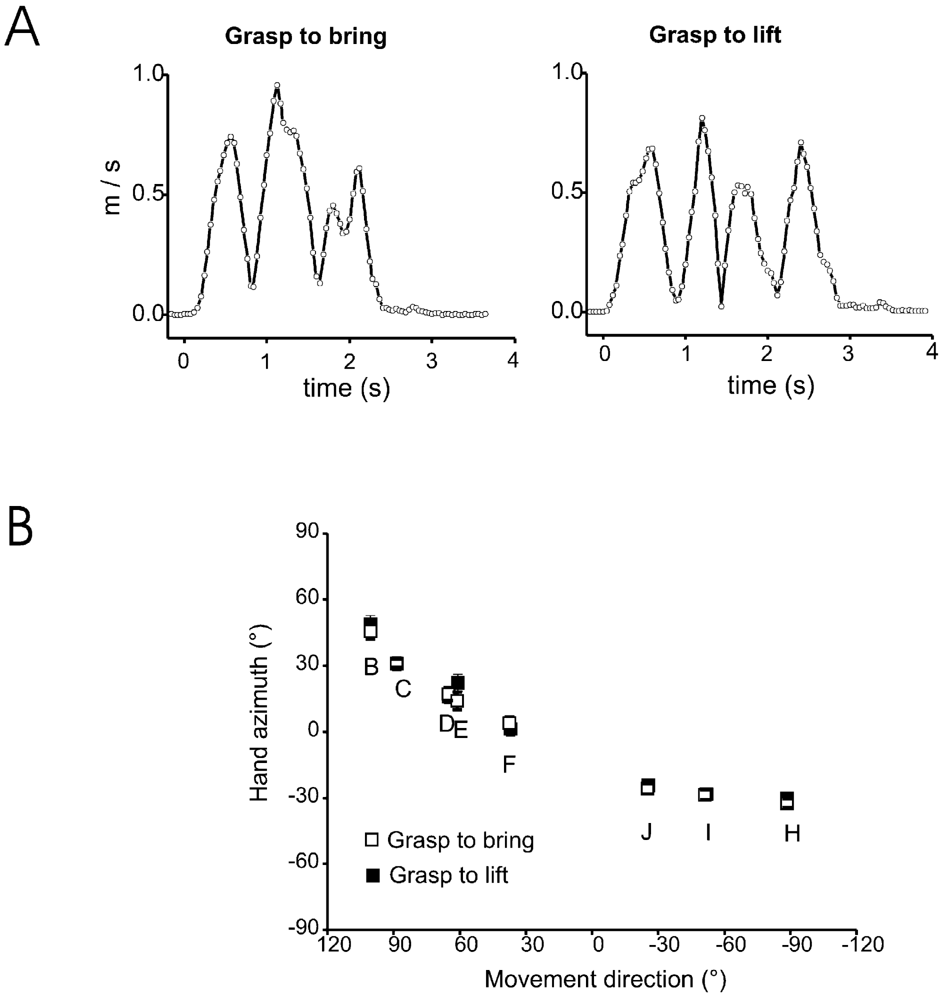

Fig. 3. (A) Velocity profiles of the hand sensor obtained in the 'grasp to bring' and 'grasp to lift' task conditions. Each trace represents one reaching movement toward an object placed at F. (B) Hand azimuth at the time of grasping as a function of movement direction (note that rightward directions are presented on the right of the graph). The initial hand position was P2. Each symbol represents the mean±S.E.M. of the values obtained for five trials in all the six subjects for a given object positions (B–J). The open squares represent the 'grasp to bring' and the solid ones the 'grasp to lift' task.

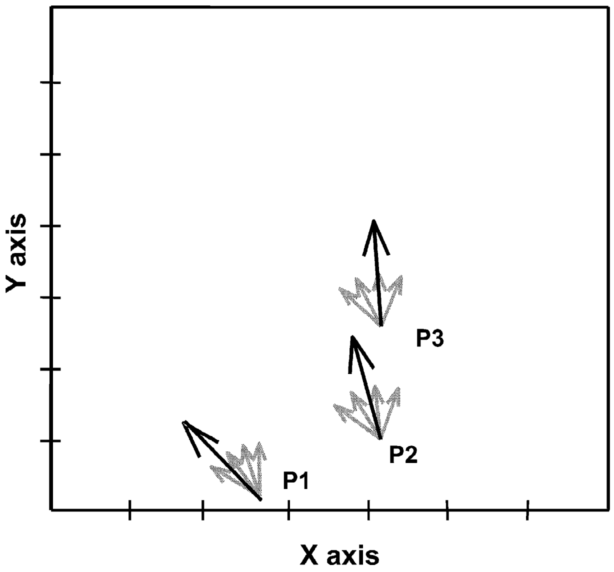

Fig. 4. Initial hand azimuth. The gray arrows indicate the effectively measured hand azimuths for the four imposed gantlet slants at P1–P3 hand positions. The longer black arrows indicate the comfortable posture at each initial hand position. Each arrow is the mean in the seven subjects.

direction, when the initial hand position was P2. For inward object locations (B–J), the azimuth at the time of grasping was linearly related to movement direction. For outward locations (H–I), the hand azimuth for grasping was around −30°. The hand azimuth at the time of grasping was not altered by change in the task, as shown by the similarity of the open (‘grasp to bring’) and filled (‘grasp to lift’) symbols.

ANOVA confirmed that the azimuth of the hand at the time of grasping significantly varied with the object location ($F(8,12)=162.7$, $P<0.0001$), and showed that there was no significant task effect ($F(1, 12)=1.97$, NS). Regression analysis showed that the azimuth at the time of grasping was linearly related to movement direction in all the subjects, in the two task conditions ($r^2=0.849$–0.935, $P<0.001$).

We verified that the displacement of the sensor fixed on the acromion during the reaching movement was less than 0.4 cm.

3.2. Modification of the initial hand azimuth

3.2.1. Initial hand postures

The initial hand azimuth was modified but not strictly constrained by the gantlet. As shown in Fig. 4 (gray arrows) and Table 1 which displays the mean azimuth in seven subjects, each 30° step in gantlet slant induced a roughly 20° deviation of the initial hand azimuth. ANOVA confirmed that the gantlet slant indeed modified the initial hand azimuth ($F(3,24)=208.3$, $P<0.0001$ for the initial hand position P1, $F(3,24)=144.9$, $P<0.0001$ for P2, $F(3,24)=157.6$, $P<0.0001$ for P3).

The azimuths chosen as comfortable for the different hand positions are shown in Fig. 4 (thick arrows) and Table 1. For an initial hand position at P1, the comfortable posture was close to that imposed by a left gantlet slant (30°), while for an initial hand position at P3 the comfortable posture was close to the median gantlet, without slant. For an initial hand position at P2 the comfortable posture was intermediate between the median and left gantlet slant.

Despite the obvious lack of postural comfort, subjects reproduced the initial hand posture determined by the orientation of the gantlet since the initial hand azimuth did not vary with object location (ANOVA: $F(8,24)=0.046$, NS for P1; $F(8,24)=1.6$, NS for P2; $F(8,24)=1.45$, NS for P3). The displacement of the sensor fixed on the acromion was limited during the reaching movement (less than 2.1 cm for P1, less than 1.6 cm for P2, less than 1.1 cm for P3).

3.2.2. Effect of the initial gantlet slant on the relationship between hand azimuth and movement direction

Fig. 5A illustrates the variations of hand azimuth at the time of grasping as a function of movement direction from position P1. The measures obtained with the four initial gantlet slants are almost identical and are linearly related to movement direction. Regression analysis confirmed that the azimuth at the time of grasping was linearly related to movement direction in all the subjects, in all the different postural conditions ($r^2=0.757$–0.987; $P=0.0001$ excepted in two cases where $P=0.002$ and $P=0.004$). ANOVA performed with the ‘initial slant’ and ‘object location’ factors confirmed the ‘object location’ effect ($F(8,24)=$

Table 1
Mean azimuth in seven subjects

		Recorded hand orientations (°)		
		P1	P2	P3
Imposed gantlet slant (°)	−30	0.3±1.5	−18.2±1.5	−19.5±1.2
	0	16.8±1.4	5.6±1	2.3±0.9
	30	33.9±1.1	30.1±0.6	25.7±0.6
	60	56.9±0.8	49.2±0.8	44.4±0.6
Comfortable postures (°)	41±6.4	14.8±5.8	3.7±2.9	

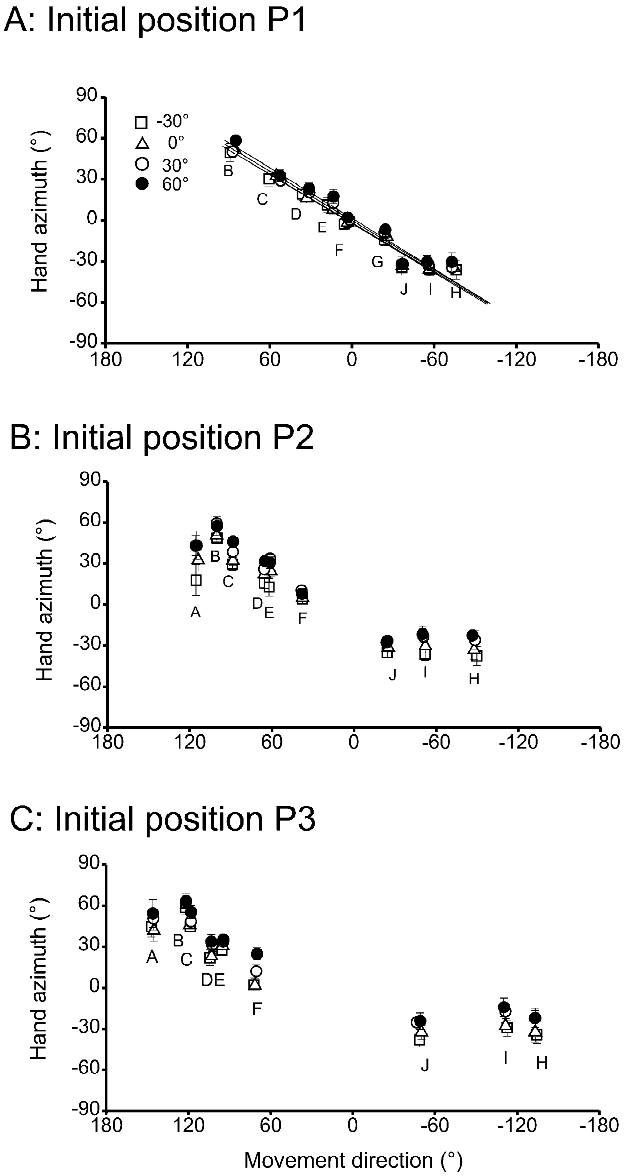

Fig. 5. Effect of the modifications of the initial orientation of the hand on the hand azimuth at the time of grasping. (A) Initial position P1, (B) initial position P2, and (C) initial position P3. Hand azimuth at the time of grasping is represented as a function of movement direction. Each symbol represents the mean±S.E.M. in seven subjects for a given object position (A–H). The different initial hand orientations are indicated in the legend. The regression lines for P1 are indicated. Equations for a $-30°$ gantlet slant: $y=0.56x-2.4$, $r^2=0.822$; for a 0° gantlet slant $y=0.60x+3.9$, $r^2=0.826$; for a 30° gantlet slant $y=0.57x+0.8$, $r^2=0.868$ and for a 60° gantlet slant $y=0.57x-1.4$, $r^2=0.858$.

272.2, $P<0.0001$) and showed a slight ‘initial slant’ effect ($F(3,24)=3.24$, $P=0.05$).

The variations of hand azimuth as a function of movement direction for positions P2 and P3 are shown in Fig. 5B,C. As observed in the first experiment, hand azimuth remained around $-30°$ for rightmost movement directions. ANOVA was used with the ‘initial slant’ and ‘object location’ factors. For P2, ANOVA showed a significant ‘object location’ effect ($F(8,24)=142.3$, $P<0.0001$) and a significant ‘initial slant’ effect ($F(3,24)=12.2$, $P=0.0001$). For P3, there was a significant ‘object location’ effect ($F(8,24)=16.18$, $P<0.0001$) and a significant ‘initial slant’ effect ($F(3,24)=6.98$, $P=0.002$).

Although the different hand postural conditions induced significant differences in hand azimuth at the time of grasping, this effect was small in comparison with the initial differences imposed by the gantlet. To further analyze this point, we compared the azimuth values obtained with a slanted gantlet to those obtained with a straight gantlet. Hatched bars in Fig. 6B represent the differences in hand azimuth at the time of grasping due to the gantlet slant (Tukey’s post-hoc test of the above ANOVA). Each 30° step slant induced very small differences in hand azimuth for grasping (mean 1.6° for P1; 4.8°

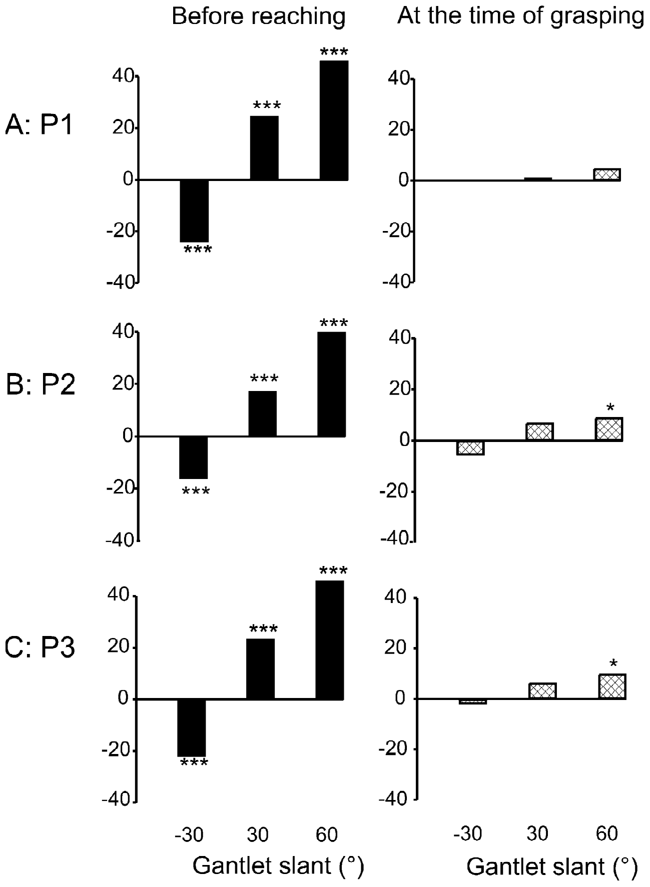

Fig. 6. Effect of the imposed gantlet slant on the orientation of the hand. Each histogram represents the difference between the azimuth value obtained with a gantlet slant (-30, 30° or 60°) and that obtained without slant (median gantlet orientation). Each bar represents the mean in seven subjects at each initial position P1–P3. (A) Black bars: differences in the initial hand azimuth before reaching. The differences are obtained from the values displayed in Fig. 4. ***$P<0.0001$, significant difference with Student’s t-test. (B) Stippled bars: differences in the hand azimuths at the time of grasping. The differences are obtained from a Tukey’s post-hoc test of the ANOVA including the factors ‘gantlet slant’ and ‘object location’, see text (*$P<0.05$).

for P2; 4° for P3). This effect was particularly small when compared to the different initial hand azimuths imposed by the gantlet (black bars in Fig. 6A; Table 1).

The difference between initial azimuth before reaching (Fig. 6A) and azimuth at the time of grasping (Fig. 6B) shows that the hand made a mean clockwise (negative) or counter-clockwise (positive) rotation during reaching (independently of the variations due to different object locations). This hand rotation during reaching tends to preserve the relationship linking hand azimuth at the time of grasping to movement direction.

3.3. Modification of the initial trunk posture

3.3.1. Initial trunk posture

Modification of the initial trunk posture was obtained by a displacement of the chair and was measured by the data obtained from the sensor fixed on the acromion. In the 'frontal trunk' conditions, this sensor was located at $X=-7\pm0.2$ cm, $Y=-27.8\pm0.1$ cm (mean and S.E.M. for all subjects) and its azimuth was $-74.8\pm0.9°$. In the 'rotated trunk' conditions, the sensor fixed on the acromion was located at $X=-9.7\pm0.1$ cm, $Y=-28.4\pm0.1$ cm and its azimuth was $-54.0\pm1.6°$. As expected, the deviation of the trunk azimuth was close to 20°, with similar positions of the acromion sensor (~2.7-cm distance).

The modification of the trunk posture brought the head backward, but the subjects obeyed the instruction to look straight ahead and this was verified with the help of a third sensor fixed on the head. Its azimuth was $4.4\pm1.6°$ in the 'frontal trunk' conditions and $-1.8\pm1.9°$ in the 'rotated trunk' conditions.

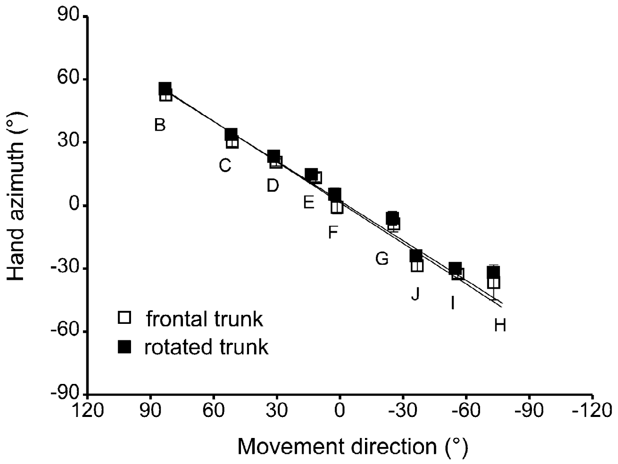

Fig. 7. Effect of the modifications of the initial orientation of the trunk. Hand azimuth at the time of grasping is represented as a function of movement direction. Each symbol represents the mean±S.E.M. in six subjects for a given object position (B–H). The open squares represent the 'frontal trunk' condition and the solid ones the 'rotated trunk' condition. The regression lines are indicated. Equations for the 'frontal trunk' condition: $y=0.59x+1.9$, $r^2=0.923$ and for the 'rotated trunk' condition: $y=0.59x+4.8$, $r^2=0.958$.

3.3.2. Relationship between hand azimuth at the time of grasping and movement direction

When the hand initial position was P1, ANOVA showed the significant effect of object location ($F(8,8)=38.36$, $P<0.0001$), without significant effect of initial trunk posture ($F(1, 8)=2.678$, NS, Fig. 7). The azimuth at the time of grasping was correlated to movement direction in all the subjects, in the two task conditions ($r^2=0.891$–0.990, $P<0.0001$).

When the initial hand position was P2, ANOVA showed the significant effect of object location ($F(8,8)=167.48$, $P<0.0001$), without significant effect of initial trunk azimuth ($F(1, 8)=0.023$, NS).

We verified that the displacement of the acromion sensor during the reaching movement was less than 1.7 cm for P1 and 1.5 cm for P2.

4. Discussion

As expected according to previous studies, hand azimuth at the time of grasping was linearly related to reaching movement direction within the central workspace [33]. This result is important, first because the geometry of the object (with a circular section) did not constrain the azimuth of the hand for grasping, and second, because the anatomy of the upper limb was redundant for this task. Indeed, five degrees of freedom (df) are needed to grasp a cylindrical object and our experimental set-up allowed the subjects to use all 7 df of the upper limb.

However, this relationship does not apply for outward movement directions. For the rightmost object positions (H–J), when the initial hand position was P2 or P3, hand azimuth for grasping remains oriented around −30°. This limit is probably related to the physiological range of joint movements [22] and to the need to preserve a comfortable posture for reaching and grasping [6,34,35]. Thus, subjects probably reached these locations by translating the hand backward (for example by associating arm retropulsion and elbow flexion) without further modifying hand azimuth.

The experiments performed in the present study demonstrate that the coupling of hand azimuth to movement direction for inward movement directions was particularly robust since it persisted when the direction to move the object was changed or when the initial hand and trunk posture was modified.

In previous experiments [33], subjects were instructed to seize the object and to transfer it to a specified position in front of them. There was a possibility that the direction of the subsequent movement influenced the azimuth of the hand at the time of grasping. Indeed, it has been shown that in a complex action composed of several sub-movements (such as taking an object in one place to put it in another place) the kinematics of the first reaching to grasp movement can be influenced by the parameters of the subsequent ones [15,25]. This is why, in the present experiment, we used a lifting task, which does not imply a particular movement direction in the horizontal plane after grasping. However, hand azimuth at the time of grasping was the same in the two conditions, demonstrating that it was not influenced by the direction of the subsequent movement.

Current observations on reaching to grasp movements supported the hypothesis that a change in initial hand azimuth should modify the hand azimuth for grasping. First, it has been demonstrated that the initial posture of the hand may affect the kinematics of a reaching movement [23]. In addition, Wing and co-workers have proposed that reaching is controlled as a displacement of the thumb. Indeed, the path of the thumb movement for prehension is straight [42] and less variable that the path of the wrist movement [19]. Other authors proposed that the reaching component is organized in a way that optimizes both thumb and index finger displacements [27,37]. According to these hypotheses, the initial position of the fingertips before reaching should influence the position of the thumb and fingers on the object and thus hand azimuth for grasping.

The second experiment was therefore designed to test the effect of a modification of initial hand azimuth on hand azimuth for grasping. The constraints induced by the gantlet imposed different general upper limb postures and some were far from comfortable, which may have influenced the subsequent movements [36]. Despite the fact that the subjects tended to get closer to the comfortable posture, the imposed hand azimuths were clearly different (~20° steps) and proved to be stable during the experiment. The main result is that the hand rotated during reach so that hand azimuth at the time of grasping almost overtook the initial deviation of hand azimuth. This result contradicts the hypothesis that reaching movement is planned in a way that optimizes the thumb or index trajectory [19,27,37,42]. Indeed, a simple geometric construct shows that hand rotation during reaching increases the length of the path followed by the fingers. In addition, this experiment demonstrates that movement direction is directly coupled to hand azimuth at the time of grasping and not to a rotational movement of the hand.

Our observations strongly support the idea that the control of grasping orientation is tightly integrated to the one of reaching. According to the ‘visuo-motor channels’ hypothesis (reviewed in Ref. [32]), the control of prehension is subserved by two separate components for reaching and grasping, activated in parallel by specific visual inputs and controlling a specific part of arm musculature [21]. Accordingly, Paulignan et al. [31] proposed that grasp orientation was invariant in head-centered coordinates. This finding is probably secondary to the radial disposition of their target objects, inducing a strong correlation between head-centered target directions and movement directions. In our previous study, which used a greater variety of object locations and different hand initial positions, we demonstrated that hand azimuth was indeed related to movement direction and not to target direction in head-centered coordinates [33]. The present results, as the previous ones, demonstrate that the control of hand orientation cannot be managed by the grasping component but is most probably related to the reaching component. Desmurget et al. [7,10] came to the same conclusion after recording movements directed to objects with various orientations.

The coupling between hand orientation and movement direction may provide a simple synergistic rule for upper limb coordination [3]. Several authors have shown that reaching to grasp movements where characterized by a reproducible and regular posture despite the redundancy of the upper limb [7,8,10,40]. It has been proposed that the choice of the final posture could be predicted by minimization of the energetic cost to achieve the movement [29,35,40]. Minimization of the energetic cost cannot explain our results since hand orientation for grasping was not changed when the initial posture was modified, even if this implied an extra hand rotation. Rather, we propose that the posture for grasping is due to geometrical constraints expressed by coupling between hand orientation and movement direction. Indeed, this coupling, together with the upper limb geometry in the horizontal plane, constrains the shoulder and elbow angles and thus may solve the question of redundancy, providing that the wrist is stabilized in a neutral position regardless of movement direction.

Several studies mainly based on pointing tasks support the idea that goal-directed movements are coded as vectors in space. In particular, Gordon et al. [17] proposed that 2D pointing movements could be coded as a function of distance and direction with regard to the hand. Our second experiment was performed to test the hypothesis that the coupling between movement direction and hand azimuth can be explained by an invariant relationship planned in hand-centered coordinates. If hand azimuth for grasping were coupled to the movement direction expressed in hand-centered coordinates, it should have followed the modifications of the initial hand azimuth. The results contradict this hypothesis since the hand azimuth at the time of grasping did not depend on the different initial hand postures.

Soechting and Flanders [38,39] proposed that the control of pointing movements uses a shoulder-centered coordinate system that is intermediate between visual and intrinsic coordinate systems. In this system, the target is coded as a function of distance, azimuth and elevation with regard to the shoulder [38] and the upper limb posture is coded as a function of azimuth and elevation of the upper and lower arm [39]. They suggested that pointing movements are planned primarily as an approximation between such extrinsic and intrinsic coordinates. For approximated pointing movements made in the dark, they observed a quasilinear relationship between azimuth of the target and azimuth of the upper and lower arm [39]. However, this effect was not tested with various initial postural conditions. Our third experiment was performed to test the hypothesis that the coupling between movement direction and hand azimuth can be explained by an invariant relationship planned in shoulder-centered coordinates. The same reasoning as above shows that the coupling between movement direction and hand azimuth cannot be directly explained by a relationship planned in a shoulder-centered coordinate system fixed to the trunk.

Hand azimuth for grasping was coupled to movement direction as expressed by reference to the environment. This strongly suggests that goal directed movements are produced in a frame of reference associated with the environment. This is consistent with the observation of Adamovich et al. [2] who demonstrated that hand trajectory was invariant in the external frame of reference whether or not the trunk was involved in reaching or if it was unexpectedly arrested. As proposed by Feldman and Levin, movements are generated by a shift between the actual posture and a referent posture, which has the dimension of a body configuration (a set of joint angles) [12]. The hypothesis that movements are generated by a shift of this referent configuration in a frame of reference associated with the environment, and not to a particular point of the body, may explain our observation that the coupling of hand orientation with movement direction was not modified when the initial posture was changed.

Acknowledgements

We are grateful to Léna Jami and Pierre Baraduc for fruitful comments and discussion, to Sylvain Hanneton for help with the statistics and to Gilles Hoffmann for the revision of the English. This work was partly supported by a grant of the French Ministry of Research (ACI Cognitique 2000). Nezha Bennis received a post-doctoral grant from Institut Garches. Agnès Roby-Brami is supported by INSERM.

References

[1] W. Abend, E. Bizzi, P. Morasso P, Human arm trajectory formation, Brain 105 (1982) 331–348.

[2] S.V. Adamovich, P.S. Archambault, M. Ghafouri, M.F. Levin, H. Poizner, A.G. Feldman, Hand trajectory invariance in reaching movements involving the trunk, Exp. Brain Res. 138 (2001) 288–303.

[3] N. Bernstein, The Co-ordination and Regulation of Movements, Pergamon, London, 1967.

[4] E.V. Biryukova, A. Roby-Brami, A.A. Frolov, M. Mokhtari, Kinematics of human arm reconstructed from spatial tracking system recordings, J. Biomech. 33 (2000) 985–995.

[5] J.D. Crawford, T. Villis, How do motor systems deal with the problems of controlling three-dimensional rotations?, J. Motor Behav. 27 (1995) 89–99.

[6] H. Cruse, E. Wischmeyer, M. Bruwer, P. Brockfeld, A. Dress, On the cost functions for the control of the human arm movement, Biol. Cybern. 62 (1990) 519–528.

[7] M. Desmurget, C. Prablanc, Postural control of three-dimensional prehension movements, J. Neurophysiol. 77 (1997) 452–464.

[8] M. Desmurget, H. Grea, C. Prablanc, Influence of object position and size on human prehension movements, Exp. Brain Res. 119 (1998) 511–516.

[9] M. Desmurget, M. Jordan, C. Prablanc, M. Jeannerod, Constrained and unconstrained movements involve different control strategies, J. Neurophysiol. 77 (1997) 452–464.

[10] M. Desmurget, C. Prablanc, M. Arzi, Y. Rossetti, Y. Paulignan, C. Urquizar, Integrated control of hand transport and orientation during prehension movements, Exp. Brain Res. 110 (1996) 265–278.

[11] M. Desmurget, C. Prablanc, Y. Rossetti, M. Arzi, Y. Paulignan, C. Urquizar, J.C. Mignot, Postural and synergic control for three-dimensional movements of reaching and grasping, J. Neurophysiol. 74 (1995) 905–910.

[12] A.G. Feldman, M. Levin, The origin and use of positional frames of reference in motor control, Behav. Brain Sci. 18 (1995) 723–806.

[13] T. Flash, N. Hogan, The coordination of arm movements: an experimentally confirmed mathematical model, J. Neurosci. 5 (1985) 1688–1703.

[14] M. Gentilucci, E. Daprati, M. Gangitano, M.C. Saetti, I. Toni, On orienting the hand to reach and grasp an object, Neuroreport 7 (1996) 589–592.

[15] M. Gentilucci, A. Negrotti, M. Gangitano, Planning an action, Exp. Brain Res. 115 (1997) 116–128.

[16] C.C.A.M. Gielen, E.J. Vrijenhoek, T. Flash, S.F.W. Neggers, Arm position constraints during pointing and reaching in 3D space, J. Neurophysiol. 78 (1997) 660–673.

[17] J. Gordon, M.F. Ghilardi, C. Ghez, Accuracy of planar reaching movements. I. Independence of direction and extent variability, Exp. Brain Res. 99 (1994) 97–111.

[18] H. Gréa, M. Desmurget, C. Prablanc, Postural invariance in three-dimensional reaching and grasping movements, Exp. Brain Res. 134 (2000) 155–162.

[19] P. Haggard, A. Wing, On the hand transport component of prehensile movements, J. Motor Behav. 29 (1997) 282–287.

[20] J. Hore, S. Watts, T. Vilis, Constraints on arm position when pointing in three dimensions: Donder’s law and the Fick gimbal strategy, J. Neurophysiol. 68 (1992) 374–383.

[21] T. Iberall, M. Arbib, Schemas for the control of hand movements. An essay on cortical localization, in: M.A. Goodale (Ed.), Vision and Action: The Control of Grasping, Ablex, Norwood, NJ, 1990, pp. 204–242.

[22] D.G. Kamper, Z.W. Rymer, Effects of geometric joint constraints on the selection of final arm posture during reaching: a simulation study, Exp. Brain Res. 126 (1999) 134–138.

[23] A. Kritikos, G.M. Jackson, S.R. Jackson, The influence of initial hand posture on the expression of prehension parameters, Exp. Brain Res. 119 (1998) 9–16.

[24] P. Mamassian, Prehension of objects oriented in three-dimensional space, Exp. Brain Res. 114 (1997) 235–245.

[25] R.G. Marteniuk, C.L. MacKenzie, M. Jeannerod, S. Athenes, C. Dugas, Constraints on human arm movement trajectories, Can. J. Psychol. 41 (1987) 365–378.

[26] W.P. Medendorp, J.D. Crawford, D.Y.P. Henriques, J.A.M. Van Gisbergen, Kinematic strategies for upper-arm fore arm coordination in three dimensions, J. Neurophysiol. 84 (2000) 2301–2316.

[27] M. Mon-Williams, R.D. McIntosh, A test between two hypotheses and a possible third way for the control of prehension, Exp. Brain Res. 134 (2000) 268–273.

[28] J.R. Napier, The prehensile movements of the human hand, J. Bone Joint Surg. Br. 38B (1956) 902–913.

[29] K.C. Nishikawa, S.T. Murray, M. Flanders, Do arm postures vary with the speed of reaching?, J. Neurophysiol. 81 (1999) 2582–2586.

[30] J. Paillard, Knowing where and how to get there, in: J. Paillard (Ed.), Brain and Space, Oxford University Press, Oxford, 1991, pp. 461–481.

[31] Y. Paulignan, V.G. Frak, I. Toni, M. Jeannerod, Influence of object position and size on human prehension movements, Exp. Brain Res. 114 (1997) 224–226.

[32] Y. Paulignan, M. Jeannerod, The visuomotor channels hypothesis revisited, in: A.M. Wing, P. Haggard, J.R. Flanagan (Eds.), Hand and Brain: The Neurophysiology and Psychology of Hand Movements, Academic Press, San Diego, 1996, pp. 265–282.

[33] A. Roby-Brami, N. Bennis, M. Mokhtari, P. Baraduc, Hand orientation for grasping depends on the direction of the reaching movement, Brain Res. 869 (2000) 121–129.

[34] D.A. Rosembaum, L.D. Loukopoulos, R.G.J. Meulenbroek, J. Vaughan, S.E. Engelbrecht, Planning reaches by evaluating stored postures, Psychol. Rev 102 (1995) 28–67.

[35] D.A. Rosenbaum, R.G.J. Meulenbroek, J. Vaughan, C. Jansen, Coordination of reaching and grasping by capitalizing on obstacle avoidance and other constraints, Exp. Brain Res. 128 (1999) 92–100.

[36] Y. Rossetti, C. Meckler, C. Prablanc, Is there an optimal arm posture? Deterioration of finger localization precision and comfort sensation in extreme arm-joint postures, Exp. Brain Res. 99 (1994) 131–136.

[37] J.B.J. Smeets, E. Brenner, A new view on grasping, Motor Control 3 (1999) 237–271.

[38] J.F. Soechting, M. Flanders, Sensorimotor representations for pointing to targets in three dimensional space, J. Neurophysiol. 62 (1989) 582–594.

[39] J.F. Soechting, M. Flanders, Errors in pointing are due to approximations in sensorimotor transformations, J. Neurophysiol. 62 (1989) 595–608.

[40] J.F. Soechting, C.A. Bunéo, U. Herrmann, M. Flanders, Moving effortlessly in three dimensions: does Donders' law apply to arm movement, J. Neurosci. 15 (1995) 6271–6280.

[41] D. Straumann, T. Haslwanter, M.C. Hepp-Reymond, K. Hepp, Listing's law for eye, head and arm movements and their synergistic control, Exp. Brain Res. 86 (1991) 209–215.

[42] A.M. Wing, C. Fraser, The contribution of the thumb to reaching movements, Q. J. Exp. Psychol. 35 (1983) 297–309.