

Posture of the arm when grasping spheres to place them elsewhere

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Received: 4 February 2010 / Accepted: 9 April 2010 / Published online: 22 June 2010
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Abstract Despite the infinitely many ways to grasp a spherical object, regularities have been observed in the posture of the arm and the grasp orientation. In the present study, we set out to determine the factors that predict the grasp orientation and the final joint angles of reach-to-grasp movements. Subjects made reach-to-grasp movements toward a sphere to pick it up and place it at an indicated location. We varied the position of the sphere and the starting and placing positions. Multiple regression analysis showed that the sphere's azimuth from the subject was the best predictor of grasp orientation, although there were also smaller but reliable contributions of distance, starting position, and perhaps even placing position. The sphere's initial distance from the subject was the best predictor of the final elbow angle and shoulder elevation. A combination of the sphere's azimuth and distance from the subject was required to predict shoulder angle, trunk-head rotation, and lateral head position. The starting position best predicted the final wrist angle and sagittal head position. We conclude that the final posture of the arm when grasping a sphere to place it elsewhere is determined to a larger extent by the initial position of the object than by effects of starting and placing position.

Keywords End-state comfort · Donders' law · Arm movement · Movement direction

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Introduction

The control of human prehensile movements has been widely studied (For reviews see Castiello 2005; Smeets and Brenner, 1999). The number of degrees of freedom in the arm exceeds the number of degrees of freedom necessary to specify the contact points of the digits. Moreover, for most objects, the contact points themselves can be chosen from many possibilities. Therefore, an object can theoretically be grasped in infinitely many ways. This redundancy makes the system flexible (Robertson and Miall 1997), so regularities in the postures that are observed when subjects perform reach-to-grasp tasks are not trivial.

Studies on 3D pointing have shown that final arm postures largely obey Donders' Law (Miller et al. 1992), although deviations of a few degrees are often observed (Gielen et al. 1997). Grasping postures toward objects in the sagittal plane are even very consistent after perturbations, suggesting that the central nervous system uses final posture as a control variable (Desmurget and Prablanc 1997; Grea et al. 2000). Final postures of reach-to-grasp movements also tend to be very consistent across repetitions in non-human primates (Helms et al. 1995).

Ideas that have been put forward for the choice of final postures for pointing movements are the minimization of travel costs (Rosenbaum et al. 1995), work (Soechting et al. 1995) or torque-change (Uno Kawato, et al. 1989), and avoiding extreme joint angles (Cruse and Bruwer 1987) to prevent degraded position signals (Rossetti et al. 1994). Studies on grasping have been interpreted as showing an invariant grasp orientation in body-centered coordinates (Paulignan et al. 1997) or as a function of movement direction (Bennis and Roby-Brami 2002; Roby-Brami et al. 2000, 2003). However, in these studies, only the grip orientation was measured and not the configuration of the

whole arm. Because the studies on whole-arm posture mentioned previously have focused on pointing and studies on grasping have been limited to the grasp orientation or to a small range of object positions, it remains unclear what determines the final arm posture in grasping.

In the current study, we set out to determine which factors determine the grasp posture in an unconstrained reach-to-grasp movement. We wanted subjects to be free to use all the degrees of freedom at their disposal including translating the shoulder and rotating the wrist. Therefore, we did not restrict torso movement and we did not use a splint on the wrist. We used a sphere as the target to leave the grasp orientation as free as possible. By varying the position of the sphere, as well as the starting position of the hand and the position at which the sphere was to be placed, the role of all these factors can be assessed simultaneously.

One might expect considerable effects of movement direction (e.g. starting and placing position) on the grip orientation and posture of the arm, because most theories state that movement-related costs are minimized. On the other hand, if the effect of starting position is as small as in pointing [only small deviations from Donders' Law (Gielen et al. 1997)], the effect of starting position may be small. We found that the latter prediction turned out to be correct; effects of movement direction were observed, but they were small compared to the effects of the position of the sphere.

Materials and methods

Subjects and setup

This study involved six subjects (two of whom were authors) and was part of a program that was approved by the local ethics committee. All subjects signed an informed consent form before participating. In the experiment, subjects made reach-to-grasp movements toward a glass opaque sphere with a 4.5 cm diameter. They were seated comfortably behind a table on which a board with indentations on a three by seven grid was mounted (Fig. 1). The indentations were spaced 10 cm apart and indicated the 21 possible target positions. Movements could start at one of two positions, with thumb and index finger touching each other. The starting position was either near the body (10 cm from the edge of the table) or far from the body (40 cm further away) at the same lateral position as the body midline. These positions were indicated by two additional indentations in the board. Because the workspace was quite large and the starting and placing positions were on opposite sides of the grid, we tested a wide range of movement directions. The largest gap between sampled movement directions was 37° (18.5° to either side of the lateral direction).

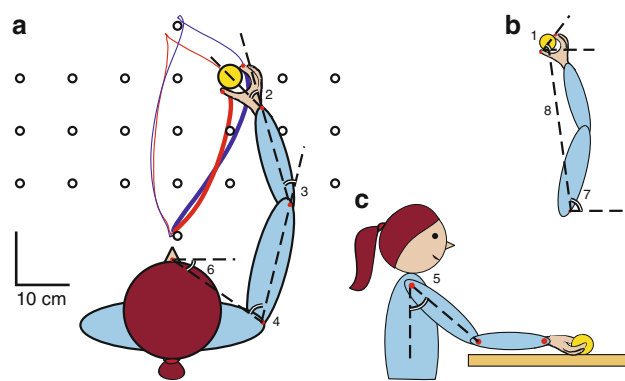


Fig. 1 Overview of the experiment. **a** Top view of a single trial: a subject moved her hand from the starting position to pick up a sphere (indicated in yellow) and put it at the placing position. If the placing position was different from the starting position, she then brought her hand back to the starting position. The movement path of the thumb is shown in red and the path of the index finger in blue. The thicker lines represent the initial reach-to-grasp segment. Also indicated are wrist angle 2, elbow angle 3, shoulder angle 4, and trunk-head rotation 6. **b** Definition of the grasp angle 1, azimuth from the shoulder (a), and distance from the shoulder (d). **c** Definition of shoulder elevation 5

Movements were recorded at 100 Hz with an Optotrak motion recording system (Northern Digital, Waterloo, Ontario, Canada). Clusters of three infrared emitting diodes (IREDs) were attached to the nails of the thumb and index finger. Single markers were attached to the outer edge of the acromion, the epicondylus lateralis humerus, the proc. styloideus ulnae and the forehead (about 4 cm above the nose). These markers (red dots in Fig. 1) indicate the shoulder, elbow, wrist and head position. A calibration trial was performed to be able to reconstruct the approximate positions of the contact points of the thumb and the index finger from the positions of the clusters of markers attached to the nails. During this trial, the subject held an IRED between thumb and index finger such that the IRED was approximately at the position of the contact points of the thumb and index finger with the sphere.

Procedure

Data were collected in two sessions. In the first session, if the starting position was near the body, the subject grasped the sphere at the target location and then placed it at the far location before returning to the starting position (as in Fig. 1), and if the starting position was far from the body, the sphere was to be placed at the near location before returning to the starting position. In the second session, the sphere was to be grasped and then placed at the starting position of the hand.

Each experimental session consisted of ten blocks. Five blocks with the starting position nearby and five blocks with the starting position far away. Each block consisted of

one trial for each possible position of the sphere, in random order. All 21 positions could be used in the blocks with the starting position close by. When starting far away, the trial starts with the arm reaching over the table. Positions that were occluded by the arm in the starting posture could not be used, so blocks with the starting position far away consisted of fewer than 21 trials.

Before a trial started, the subject moved his right hand to the starting position with thumb and index finger touching each other. The subject subsequently closed his eyes so that the starting posture could not be influenced by seeing the position of the sphere. After the experimenter placed the sphere at the target position, she gave a verbal signal to the subject. Upon this signal, the subject opened his eyes, grasped the sphere, and placed it at the appropriate location. In the first session, the subject then had to move his hand back to the starting position to start the next trial. In the second session, the subject had to put the sphere at the start position and wait for the experimenter to remove it before placing the hand for the next trial.

Data analysis

Data were analyzed offline using custom software. We used the relationship between the clusters of three markers attached to the nails and the single marker held between finger and thumb during the calibration to determine the position of the digits. The beginning of the reach-to-grasp movement was defined as the first moment the speed of the wrist exceeded 0.1 m/s. The end of the reach-to-grasp movement was determined using the MSI-method that has been described in detail elsewhere (Schot et al. 2010). This method finds the moment that can best be considered as the end of the movement. For this, we required the digits' sagittal position to be between 6 cm and 34 cm from the near starting position (the sphere could be placed at 10, 20 or 30 cm) and their height to be lower than the sphere's height. Additionally, the grip size should be decreasing and decelerating. From the time points that remained, the time point with the most convincing combination of a grip size close to the sphere's diameter (with an additional penalty on larger apertures) and a low speed of the wrist was selected as the movement endpoint. For a full account of how this was implemented and of the robustness of the method see Schot et al. (2010).

We were interested in the posture at the end of the reach-to-grasp movement, so we calculated the grasp orientation, wrist angle, elbow angle, shoulder angle, shoulder elevation, trunk-head rotation, and sagittal and lateral head position at the end of the reach-to-grasp movement. All angle definitions are depicted in Fig. 1. Grasp orientation is defined as the angle in the horizontal plane between the projection of the opposition axis and the reference axis

pointing rightward. The wrist angle is the smallest angle *in space* between the forearm and the digits as defined by the positions of the elbow, wrist and the average position of the thumb and index finger (aligned is 0°, flexion is positive). The elbow angle is defined as the smallest angle *in space* between the upper arm and the forearm as defined by the positions of the shoulder, elbow and wrist (fully extended is 0°, flexion is positive). The shoulder angle is defined as the angle between the projection in the horizontal plane of the upper arm and the line connecting the shoulder and the head. Shoulder elevation is defined as the smallest angle between the upper arm (as defined by the shoulder and elbow positions) and the vertical (upper arm straight down is 0°). Finally, trunk-head rotation is defined as the angle in the horizontal plane between the projection of the vector from the shoulder to the head and the reference axis pointing rightward. Because one of the IREDS used to calculate trunk-head rotation was placed on the forehead and the other on the shoulder, this measure contains trunk rotation as well as head-on-trunk rotation. We estimated that the SD of the contribution of head-on-trunk rotation when calculating trunk-head rotation was 3.5° (see “Appendix” for details). This is much smaller than the within-subject SD for trunk-head rotation (11.2°), so this variation is mainly caused by trunk rotation rather than head-on-trunk rotation.

We wanted to examine how well grasp orientation, wrist angle, elbow angle, shoulder angle, shoulder elevation, trunk-head rotation, and sagittal and lateral head position at the end of the reach-to-grasp movement could be predicted from starting position, placing position, and the sphere's azimuth and distance from the subject before the movement. To achieve this, we encoded start position and place position as 0 (far) or 1 (close). The encoding is arbitrary, but using 0 and 1 has the advantage that the resulting coefficient directly matches the size of the effect. We used a binary value rather than a continuous one such as movement direction, because a continuous measure would correlate strongly with other variables such as target azimuth.

Azimuth is defined as the angle between the projection in the horizontal plane of the vector connecting the subject's shoulder position with the sphere, and a reference axis pointing rightward in the horizontal plane (*a* in Fig. 1b). Distance is the length of the vector from the subject's shoulder position to the sphere (*d* in Fig. 1b). In the definition of distance and azimuth, we used “shoulder position”. For this, we took each subject's average shoulder position at the beginning of the movement. We did so because as the position of the shoulder was not fixed, shoulder position at movement onset could vary systematically across conditions (e.g. the shoulder was further forward when the starting position was far from the

body). This would influence the calculation of azimuth and distance from the shoulder and therewith confound the analysis in terms of the positions relative to the chair. We therefore used the average of all shoulder positions at the beginning of the movement instead of the actual shoulder position in each trial.

For each subject, we performed a stepwise multiple regression analyses for each angle or position with starting position, placing position, azimuth and distance as independent variables. The distance and azimuth of the sphere expressed relative to the subjects' average shoulder position is obviously correlated with its distance and azimuth relative to the subjects' average head position. To be sure, we would not obtain a better fit by expressing azimuth and distance relative to the average head position rather than the average shoulder position, we also did the regression with azimuth and distance calculated relative to the average head position. Because it hardly mattered for the quality of the fits whether the azimuth and distance were expressed relative to the shoulder or relative to the head (the R^2 values were slightly larger when azimuth and distance were calculated relative to the shoulder, but the largest R^2 difference was only 0.06), we will only report the results of the analyses with the sphere's azimuth and distance defined relative to the shoulder (and refer to this as azimuth and distance). However, as we cannot clearly distinguish between the two accounts, it should be noted that we are not committed to the expression relative to the shoulder.

Results

The lengths of each subject's upper arm, forearm, and hand are shown in Table 1, as are the mean \pm SD of the grasp orientation, joint angles and head position. We see considerable differences in average postures across subjects but these cannot be easily attributed to differences in segment lengths.

The average grasp orientations for spheres at all 21 positions and the average postures at the end of reach-to-grasp movements to five of these positions are shown in Fig. 2 for one representative subject. Grasp orientations vary strongly and systematically across the different target positions. They were further counterclockwise when the sphere was further to the left and when the movement had started from far. Elbow angles are clearly smaller for objects that are closer to the subject. The wrist angles do not show a lot of variation across conditions. Note that the shoulder and head positions are not the same for all conditions. This can result in different positions of the more distal joints without differences in their joint angles.

To test to what extent the grasp orientation, wrist angle, elbow angle, shoulder angle, shoulder elevation, trunk-head rotation, and the lateral and sagittal position of the head could be predicted from the distance (d), azimuth (a), and starting and placing positions (s and p , respectively; with values of 0 for far and 1 for near), eight stepwise multiple regression analyses were performed for each subject to find the best coefficients for Eq. 1, where is the prediction of one of the dependent measures.

$$\hat{y} = y_0 + c_1s + c_2p + c_3a + c_4d \quad (1)$$

The mean \pm SD of the coefficients that we found by fitting Eq. 1 to the data of each subject are shown in Table 2 of the angular measures and in Table 3 for head position, as are the proportions of variance explained by the individual predictors (R^2), the total variance explained by the predictors (R_{total}^2), and the residual standard deviations after fitting Eq. 1. The R_{total}^2 values show that grasp orientation is very predictable, as are shoulder angle, trunk-head rotation, and elbow angle. The sizes of the mean individual R^2 values indicate how much a predictor contributed to the prediction of a particular angle or position. For instance, grasp orientation mainly depended on the objects' azimuth, followed by distance and starting position. Placing position only has a small contribution of 1.7° and does not reach significance in 2 out of 6 subjects.

Table 1 Various measures for each subject

Subject	Upper arm	Forearm	Hand	Grasp orientation	Wrist angle	Elbow angle	Shoulder angle	Shoulder elevation	Trunk-head rotation	Lateral head position	Sagittal head position
1	31.9	23.6	15.1	78.2 \pm 23.1	36.3 \pm 7.9	65.0 \pm 17.9	103.7 \pm 20.7	41.0 \pm 8.6	-29.5 \pm 12.3	-3.8 \pm 3.9	-12.5 \pm 8.5
2	31.8	26.4	17.3	55.8 \pm 25.4	27.6 \pm 6.1	68.9 \pm 16.3	92.7 \pm 21.5	45.0 \pm 5.8	-41.9 \pm 8.8	-10.4 \pm 5.1	-7.9 \pm 3.2
3	32.5	24.5	17.1	72.6 \pm 25.4	27.6 \pm 7.5	72.2 \pm 18.1	93.8 \pm 21.8	42.9 \pm 6.6	-34.7 \pm 11.0	-8.4 \pm 4.5	-10.5 \pm 3.6
4	28.5	21.7	14.4	72.7 \pm 26.5	24.7 \pm 5.7	68.8 \pm 15.9	97.5 \pm 17.6	54.3 \pm 3.9	-31.9 \pm 12.9	-4.4 \pm 5.3	-9.1 \pm 3.7
5	28.8	23.4	15.9	62.4 \pm 25.8	24.3 \pm 4.4	81.9 \pm 15.9	77.0 \pm 30.0	37.8 \pm 3.0	-32.3 \pm 11.6	-4.1 \pm 5.4	-3.7 \pm 2.0
6	33.6	27.6	19.3	62.5 \pm 22.4	24.6 \pm 4.6	71.4 \pm 14.7	87.2 \pm 20.6	43.4 \pm 4.9	-31.5 \pm 10.4	-6.2 \pm 4.1	-10.3 \pm 2.4

Upper arm, forearm, and hand length (in cm) and the means \pm SD's at the time of grasping of the angles (in degrees) and positions (in cm, from the near starting position)

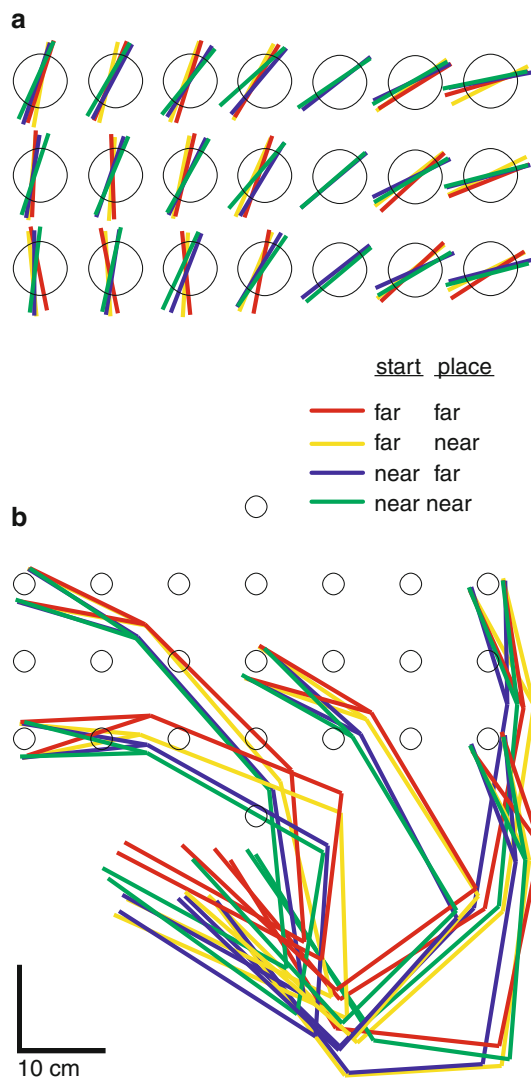


Fig. 2 Grasping postures of one subject. The four combinations of starting and placing positions are indicated by different colors. **a** Average axes connecting index finger and thumb for all object positions (not to scale) **b** Average postures for five selected positions. Lines connect the markers on the head, shoulder, elbow, and wrist and connect the marker on the wrist to the calculated positions of the thumb and index finger

Similarly, wrist angle mainly depended on starting position.

The results of the analyses show that even though there are differences between the individual subjects, the factors that have most predictive power have it in all the individual subjects. Correlating total limb length (the sum of upper arm, forearm, and hand length given in Table 1) with the coefficients obtained in the regression showed that differences between subjects could not easily be attributed to differences in limb size (all $p > 0.15$). Correlating the coefficients with upper arm, forearm or hand length did not give more significant results than could be expected by

Table 2 Results of the regression analyses for angular measures

Independent	Dependent	Grasp orientation		Wrist angle		Elbow angle		Shoulder angle		Shoulder elevation		Trunk-head rotation	
		Coefficient	R^2	Coefficient	R^2	Coefficient	R^2	Coefficient	R^2	Coefficient	R^2	Coefficient	R^2
y_0		-22.92 ± 16.93		40.84 ± 13.76		135.43 ± 10.55		22.66 ± 23.47		26.69 ± 9.89		-89.69 ± 8.76	
Start ($^\circ$)	c_1	$-9.50 \pm 6.04^{(6)}$	0.06	$-6.09 \pm 1.55^{(6)}$	0.25	$-5.40 \pm 6.59^{(5)}$	0.04	$3.35 \pm 6.38^{(5)}$	0.02	$0.94 \pm 3.84^{(5)}$	0.11	$0.74 \pm 5.26^{(5)}$	0.04
Place ($^\circ$)	c_2	$-1.70 \pm 2.96^{(4)}$	0.00	$-1.09 \pm 3.02^{(5)}$	0.04	$-2.42 \pm 2.26^{(4)}$	0.01	$1.05 \pm 3.82^{(5)}$	0.01	$1.84 \pm 2.02^{(4)}$	0.03	$0.16 \pm 2.72^{(4)}$	0.01
Azimuth	c_3	$1.06 \pm 0.10^{(6)}$	0.85	$0.01 \pm 0.04^{(4)}$	0.03	$0.21 \pm 0.06^{(6)}$	0.06	$0.46 \pm 0.05^{(6)}$	0.61	$0.00 \pm 0.02^{(2)}$	0.08	$0.26 \pm 0.04^{(6)}$	0.65
Distance ($^\circ/cm$)	c_4	$-0.39 \pm 0.12^{(6)}$	0.15	$-0.20 \pm 0.10^{(6)}$	0.08	$-1.62 \pm 0.13^{(6)}$	0.72	$1.24 \pm 0.37^{(6)}$	0.67	$0.30 \pm 0.12^{(6)}$	0.29	$0.53 \pm 0.11^{(6)}$	0.59
R^2_{total}			0.93		0.41		0.84		0.88		0.44		0.86
Residual ($^\circ$)		6.46 ± 1.37		4.54 ± 0.80		6.43 ± 1.57		7.00 ± 1.72		4.08 ± 1.53		3.88 ± 0.83	

Coefficients are the fit values in Eq. 1. The values are the means and standard deviations across the six subjects. The number in brackets indicates the number of subjects for whom this coefficient was statistically significant. R^2 gives the mean proportion of variance explained by each predictor. R^2_{total} gives the mean proportion of explained variance. Residual gives the standard deviations of the data's deviations from the predictions (mean \pm SD of the six subjects)

Table 3 Results of the regression analyses for head position

Independent	Dependent	Lateral head position		Sagittal head position	
		Coefficient	R^2	Coefficient	R^2
y_0		15.99 ± 23.99		-8.59 ± 34.33	
Start (cm)	c_1	$-0.16 \pm 0.49^{(3)}$	0.00	$-4.02 \pm 5.57^{(5)}$	0.23
Place (cm)	c_2	$-0.36 \pm 0.96^{(6)}$	0.01	$-1.58 \pm 1.12^{(5)}$	0.05
Azimuth (cm°)	c_3	$-0.13 \pm 0.02^{(6)}$	0.69	$-0.01 \pm 0.01^{(1)}$	0.01
Distance	c_4	$-0.14 \pm 0.03^{(6)}$	0.44	$0.06 \pm 0.08^{(2)}$	0.04
R^2_{total}			0.77		0.31
Residual (cm)		2.23 ± 0.38		2.65 ± 0.52	

See Table 2 for further details

chance (5%) either. The only significant correlation was of upper arm length and the coefficient of distance when predicting shoulder elevation.

The results of the regression analyses are shown graphically in Fig. 3. In this figure, we plot the measured angles and positions as a function of azimuth and distance. We also plot the average fit. As s and p are both binary variables, the equation describes four planes (one for each combination of starting and placing position). The separation between the planes indicates the predictive power of start and place position. The tilt indicates the predictive power of azimuth and distance. For example, Fig. 3a shows the average fit of Eq. 1 for grasp orientation. The separation between the

planes indicates that on average the grasp orientation is 9.5° more counterclockwise when the starting position was far rather than near, and only 1.7° more counterclockwise when the place position was far rather than near. The fact that the planes are only slightly tilted along the distance axis indicates that distance did not explain much of the variance (after considering the predictive power of the azimuth). Except in the case of the sagittal head position and the wrist angle, the separation between the planes is much smaller than the change in height along the distance and/or the azimuth axis. This means that most parameters are mainly determined by the sphere's position, independent of the start and place positions.

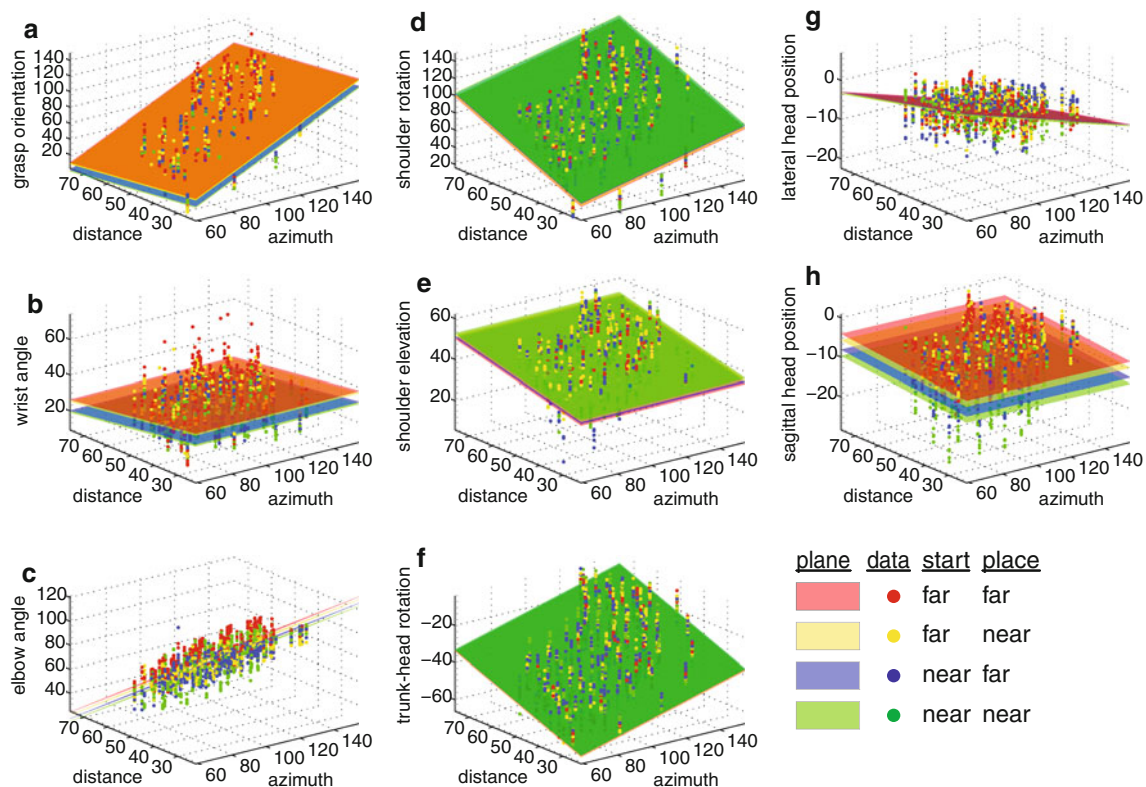


Fig. 3 Visualization of the means of the eight regression analyses done per subject. As there are four combinations of starting and placing position, we drew a plane for each combination

Because the difference in movement direction between the two starting positions is larger for the central part of the workspace, one might expect that the effect of starting position on grasp orientation was larger for movements to targets that were in the center of the workspace. To test this, we did a regression analysis using only the nine most central target positions. The result showed that for the center of the workspace, the effect of starting position on grasp orientation was slightly larger (12.2°) than the effect over the whole workspace (9.5°).

Discussion

In this study, we explored the factors that determine the posture of the arm when grasping a sphere in order to place it elsewhere. We tested whether grasp postures were more predictable when the sphere's position was expressed relative to the subject's head or shoulder. We found that both methods yielded about the same R^2 for all angles and positions we wanted to predict. Given this result, we only report to what extent the grasp orientation, wrist angle, elbow angle, shoulder angle, shoulder elevation, trunk-head rotation, and the lateral and sagittal position of the head were predictable given the sphere's position in terms of the azimuth and distance from the shoulder and the starting and placing positions. However, as we could not distinguish between the two accounts, we would like to mention again that we are not committed to the expression of azimuth and distance relative to the shoulder.

We found only small effects of placing position on the final posture of the reach-to-grasp movement. This suggests that a subsequent movement is only very modestly taken into account when people plan the final posture of the previous movement. This is in seeming contrast with observations that subjects adjust the grip orientation of a movement by 180° in order to avoid uncomfortable postures in a subsequent movement (Rosenbaum et al. 1990). Our results suggest that a considerable effect of a subsequent movement may only have considerable effects when the movement involves uncomfortable postures.

Some other relationships were not inevitable but quite intuitive. For instance, although all objects could be reached using fixed angles of elbow and shoulder (by moving the trunk to different positions), it makes sense to extend the elbow and rotate and elevate the shoulder to reach objects that are further away (see Table 2).

Some of the relationships that we found are less intuitive than those described earlier. We found that the variance in the wrist angle could best be explained by the starting position. The effect of start position on sagittal head position arises because subjects leaned forward more

when starting far away (not shown) and did not completely move back to grasp the sphere. Starting position had a marginal effect on shoulder elevation; trunk-head rotation and shoulder angle are slightly smaller when the start position was near. These effects indicate that the elbow was positioned further forward (which is clearly visible in Fig. 2) and less wrist flexion was needed. The relationship between sagittal head position (presumably caused by hip flexion) and wrist angle implies that there are synergies between joints that are quite distant from each other.

When reaching for targets at different positions, the flexibility of the wrist was hardly used (see Table 1). Rather, people used the freedom in their shoulder and elbow to reach the different targets. The tendency not to use the full range of motion of the wrist has been reported previously in pointing in the horizontal plane and grasping in the sagittal plane (Cruse 1986; Wang 1999). It is in contradiction with the idea that the final posture is planned to minimize the work (Soechting et al. 1995) or travel costs (Rosenbaum et al. 1995) because in most cost functions wrist movements are associated with lower costs than elbow movements (Soechting et al. 1995; Wang 1999), so wrist movements should be preferred over elbow movements. It may be that people prefer to move the elbow (rather than the wrist) because they need a smaller angular displacement at the elbow to obtain the same amount of hand displacement. Similar violations of minimizing work have been found in pointing in the sagittal plane (Vaughan et al. 1998).

We found that grasp orientation can be predicted from the azimuth from the shoulder. This is in line with results of Paulignan et al. (1997), but seemingly in contradiction with the study by Bennis and Roby-Brami (2002) who found a strong correlation between grasp orientation and movement direction. The latter authors also found that rotating the trunk has no effect on the grasp orientation. They therefore concluded that grasp orientation cannot be planned in a shoulder-centered frame of reference fixed to the trunk, because rotating the trunk gives the same grasp orientations. Rather, grasp orientation seemed to be planned in relation to the movement direction. Based on our results, we suggest an alternative explanation for their results. We propose that it is not a shoulder-centered frame of reference fixed to the trunk, but rather the direction of the line connecting the shoulder and the object (azimuth) that determines the grasp orientation. As was stated in the *data analysis* section, the shoulder position is not an ego-centric reference that varied with the initial posture of the subject. By taking the average shoulder position of each subject at the beginning of the trial, it is an allocentric reference that is adjusted to the subject's morphology. This proposal is in line with Bennis and Roby-Brami's finding

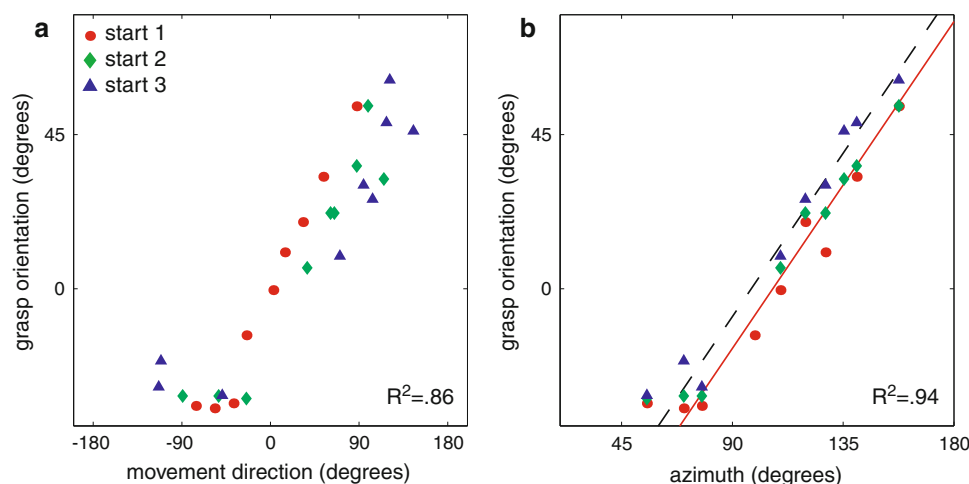


Fig. 4 Our interpretation of the data presented by Bennis and Roby–Brami (2002) **a** The relationship between grasp orientation and movement direction as reported by Bennis and Roby–Brami (replotted from their Fig. 5). **b** Same data showing the relationship between grasp orientation and azimuth (angle between the projection in the *horizontal plane* of the vector from the shoulder to the sphere and a reference axis pointing rightward in the *horizontal plane*). The solid line has the slope that we obtained for this relationship from the

regression analysis on our data (0.98). Since grasp orientation was defined differently in their study and could not easily be converted, the intercept was fit to the data points for their start 1 (this starting position was close to our near starting position; *solid line*). The grasp orientation in our study was roughly 9° further counterclockwise when the starting position was further away (*dashed line*). This nicely fits Bennis and Roby–Brami’s (2002) data for start 2 and 3 which were further away than their start 1

that rotating the body without moving the shoulder relative to the body has no effect on grasp orientation.

To test whether our proposal can really explain their data, we reanalyzed their data expressing the grasp orientations as a function of azimuth from the shoulder; we find an R^2 of 0.94 (Fig. 4b). This is higher than when expressing the grasp orientation as a function of movement direction ($R^2 = 0.86$; Fig. 4a). This indicates that grasp orientation can be predicted even better from the direction of the line connecting the shoulder to the object than from the movement direction. The relationship between grasp orientation and azimuth conforms to the slope that we found in the present study (1.06; slope of lines in Fig. 4b). The effect of movement direction expected based on the present results is the difference between the two lines. Thus, as in the present study (see Fig. 3a), azimuth had a strong influence and starting position a weak but reliable influence on grasp orientation. As Bennis and Roby–Brami used different starting positions, a cylinder rather than a sphere as a target, and a different task (subjects were to grasp and lift the cylinder rather than place it somewhere else), this suggests that our result holds for a wider variety of tasks than the one we let the subjects perform.

The 9.5° effect of start position on grasp orientation is rather small compared to the 10–30° effect observed by Roby–Brami et al. in another study (2000). This could be caused by the smaller workspace they used, consistent with our finding that the effect of starting position was slightly larger in the center of the workspace. It could also be due to the fact that they used another object. They used a 17-cm-

high cylinder rather than a 4.5-diameter sphere. For some movement directions, this might mean that subjects have to move around the cylinder in order to avoid knocking it over. In another study, we found evidence that the effect of starting position is indeed larger for a tall cylinder than for a smaller sphere (Voudouris et al. 2010). Altogether, the results offer some support for the idea that the final posture is planned on the basis of the target’s position (Cruse 1986). This hypothesis predicts no influence of the starting and placing positions. Although this does not hold for any of the angles or positions measured, for all but wrist angle and sagittal head position, the effects of movement direction (starting and placing position) were much smaller than those of object position (distance and azimuth from the shoulder). Taken together, our data suggest that the choice of grasping points and the final posture after a reach-to-grasp movement toward a spherical object to place it elsewhere can be predicted from the position of the object that is to be grasped. Additionally, there are smaller but consistent influences of starting and placing position. This is in line with studies on 3D pointing that have shown that movements largely obey Donders’ law, but with deviations of a few degrees (Gielen et al. 1997).

Acknowledgments This research was funded by NWO/MaGW under grant number 400-03-021.

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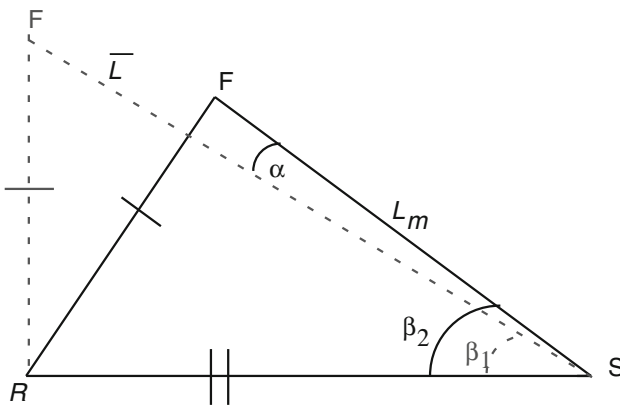


Fig. 5 Illustration of the values used to calculate the error in the measure of trunk rotation introduced by head on trunk movement

Appendix

To measure trunk-head rotation, we used the IRED's on the subjects' shoulder and forehead to measure trunk rotation. This measure accurately reflects trunk rotation when subjects do not rotate their heads (i.e. when the angle between the center of rotation (R), shoulder (S), and forehead (F) in Fig. 5 is constant). When subjects do rotate their heads, a contribution of head-on-trunk rotation (α) is added to the measure of trunk-head rotation. Also, the length of the vector between the forehead and the shoulder changes from \bar{L} to L_m . We used this to estimate the contribution of head-on-trunk rotation to head-trunk rotation. We calculated the average distance (\bar{L}) between the forehead and the shoulder in the horizontal plane for the first sample of the measurement for each subject). This is well before movement onset when the subjects still had their eyes closed and were assumed to 'look' straight ahead. From this we could estimate the length of the vectors connecting the shoulder and the forehead to the center of rotation. Given these lengths, we could calculate the angles β_1 and β_2 for each trial. The difference between these angles gives the estimated contribution of head-on-trunk rotation (α). The standard deviation of all these contributions was 3.5° . This is small compared to the mean within-subject standard deviation in trunk-head rotation of 11.2° (see Table 1) so trunk-head rotation is mainly caused by trunk rotation rather than by head rotation.

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