RESEARCH ARTICLE

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Prehension of objects oriented in three-dimensional space

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Abstract When reaching for an object, the proximity of the object, its orientation, and shape should all be correctly estimated well before the hand arrives in contact with it. We were interested in the effects of the object's orientation on manual prehension. Subjects were asked to reach for an object at one of several possible orientations. We found that the trajectory of the hand and its rotation and opening were significantly affected by the object's orientation within the first half of the movement. We also detected a slight delay of the wrist relative to the forearm and a small bias of the orientation of the fingers' tips toward the orientation of the table on which the object lay. Finally, the aperture of the hand was proportional to the physical size of the object, which shows that size constancy was achieved from the variation of the object's orientation. Taken together, these results indicate that the three components of the movement – the transport, rotation, and opening of the hand – have access to a common visual representation of the object's orientation.

Key words Manual prehension · Visuomotor coordination · Three-dimensional orientation · Wrist joint · Human

Introduction

The coordination between the eye and the hand is exemplified by a large number of everyday activities, ranging from pointing to handwriting. Among these activities, the manual prehension of an object is a movement that involves both proximal and distal joint segments. Proximal joints (at the shoulder and elbow level) participate in the transportation of the hand to the vicinity of the object, while distal joints (at the fingers level) shape the hand appropriately for the object and its planned use. The distinction between proximal and distal joints led to the division of the prehension movement into a reaching and a grasping component (for a review, see Jeannerod 1988). According to this framework, the planning of the reaching movement is based on the extrinsic properties of the target object (primarily its spatial location), while grasping is solely concerned by the object's intrinsic properties (such as its shape, size, and weight).

If reaching and grasping are self-regulated, then the transportation of the hand should be independent of the shape or size of the object to be grasped, and the shaping of the hand should be independent of the location of the object (Jeannerod 1981; Jeannerod and Biguer 1982). Unfortunately, these predictions were not directly supported by studies in which either the location or the size of the object was perturbed at the movement onset. A sudden change in the position of the object not only affected the hand trajectory but also produced a reopening of the hand once the hand was directed toward the new object's location (Paulignan et al. 1991b). Conversely, changing the size of the object modified the grip formation, but also lengthened the final phase of the hand transportation, especially when the object's size varied from small to large (Paulignan et al. 1991a). In both studies, the first noticeable change in either the direction of the hand trajectory or the opening of the hand occured about 300 ms after the perturbation (although the analysis of the transport kinematics suggested a much earlier change when the object location was perturbed). In order to account for these results, one needs to acknowledge some kind of interaction between reaching and grasping, such as for instance a temporal coupling between these two components (Hoff and Arbib 1993).

There is, however, an alternative interpretation of the results on the interaction between reaching and grasping. It is indeed puzzling to find an asymmetry in reach duration depending on whether the object's size increases or decreases (Paulignan et al. 1991a; Jakobson and Goodale 1991). Such an asymmetry could not be explained by ap-

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pealing to a difference in the precision required for the movement (Fitts 1954), because reach duration increased with object's size. Instead, it is as if the subject confused a change in size with a change in proximity: as the object was perceived closer, the trajectory length was planned to be shorter, and the hand was inappropriately slowed down well before the object contact. In fact, the relationship between size and distance has been extensively studied in visual perception, in particular with respect to the phenomenon of size constancy according to which an object appears the same size independently of its distance to the observer (Kaufman 1974). To pretend that size and distance are processed independently would be to underestimate the complexity of the problem of size perception. In short, the interaction between reaching and grasping might reflect an early interaction between the visual processing of intrinsic and extrinsic object properties.

Telling apart intrinsic and extrinsic properties of an object will be even more elusive when one considers the object's orientation in space. While the orientation should be considered extrinsic to the object if it is described relative to the line of sight, one can argue that it should be intrinsic if it is instead described relative to the gravitation direction. Interestingly, both of these propositions have been suggested in the past (Arbib 1981; Jeannerod 1981). Moreover, a change in object orientation should produce a change in hand orientation, but it is again difficult to classify a priori the hand orientation as a distal or proximal segment given the diversity of the joints involved (i.e., the wrist and forearm). One escape to these uncertainties is to consider that the object and hand orientations constitute a third component of the movement, functionally coupled with the reaching and grasping components (Soechting and Flanders 1993; Stelmach et al. 1994; Desmurget et al. 1995).

We have therefore decided to investigate the effects of object orientation on manual prehension. For this purpose, we asked human adults to reach for a simple object placed in front of them. The orientation of the object was manipulated between trials. The prehension movements were recorded by following the positions of several markers placed on the subjects' arm. In the next three sections, we analyze separately the transportation of the hand, its rotation, and its opening. In the final section of the paper, we discuss the results and their implication for the visuomotor coordination.

Hand transportation

Woodworth (1899) first noted the stereotyped pattern of prehension movements, consisting of a fast-rising acceleration followed by a slower deceleration. Therefore, the velocity of the hand presents only one maximum, which typically occurs in the first half of the movement (Jeannerod 1984). In addition, the hand "pre-shapes" well before seizure of the object, that is, the fingers are displaced in anticipation of the chosen grip, and the grip aperture correlates with the object's size (Jeannerod 1981). The maximum aperture of the hand during its transportation occurs in the second half of the movement (Jeannerod 1984; von Hofsten and Rönnqvist 1988).

In this section we analyze the effects of object orientation on hand displacement. Subjects were asked to reach for an object lying on a table in front of them. In a first experiment, the orientation of the object varied from trial to trial, while its location and size were kept constant. In order to minimize the effects of global movement speed (Wing et al. 1986; Wallace and Weeks 1988), each subject was prompted to achieve the prehension in a fixed time. The analysis focuses on the position of the wrist just before grasping the object and on the trajectory of the wrist to attain this position.

Materials and methods

Subjects

Three subjects participated in this experiment, aged between 25 and 32 years. All subjects were right-handed, and naive to the purposes of the experiment.

Apparatus

The recording device was an OPTOTRAK/3020 (Northern Digital, Waterloo, Canada), which consists of three lens systems mounted within a 1.1-m-long bar. This device can compute the three-dimensional positions of up to 24 markers, which are small (4-mm radius), infrared-emitting diodes (IREDs). The field of view of the OPTOTRAK is about 34° by 24°, with a range of about 6 m. One important constraint of this apparatus is that a marker should be in view of the three cameras to be informative. The error for each marker's position was estimated to be about 1 mm over a 50-cm trajectory (standard deviation less than 0.5 mm). Seven markers were placed on the arm of the subjects in the following arrangement: two markers on the forearm (one close to the wrist, the other close to the elbow), two on the dorsal part of the hand, and the remaining three at the tips of the thumb, index, and middle fingers. Except for the two markers on the forearm, the markers were fixed on a lightweight cotton glove. The marker positions were updated at 200 Hz.

Stimulus

The stimulus consisted of a rectangular polyhedron, of size 70×50×8 mm. This object was made of black polyvinyl chloride (PVC), and uniformly textured with small white dots. The object rested on a small, spherical joint enabling any orientation within a cone of semiangle 45°. The spherical joint was designed such that changing the orientation of the object would not change the position of its center of gravity. The object and spherical joint were placed on a table 1 m wide and 0.8 m long.

Seven orientations for the object were selected, as shown schematically in Fig. 1. First, a baseline condition, called *flat*, where the object laid parallel to the tabletop, its long edge parallel to the line passing through the shoulders of the subject. The six other orientations were rotations by ±20° of the object from the baseline condition: the *front*, *back*, *left*, and *right* conditions slanted the object toward, away, to the left, and to the right of the subject, respectively, and the *clockwise* and *counterclockwise* conditions were rotations of the object in the plane parallel to the tabletop.

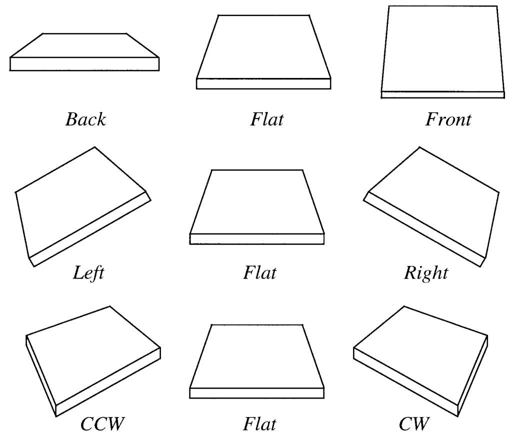

Fig. 1 The object was either placed parallel to the tabletop or rotated by 20° away from this *Flat* baseline condition. Four orientations were obtained by slanting the object away, toward, to the left or to the right of the subject (producing the *Back*, *Front*, *Left*, and *Right* conditions). The last two conditions were obtained by rotating the object counterclockwise (*CCW*) or clockwise (*CW*)

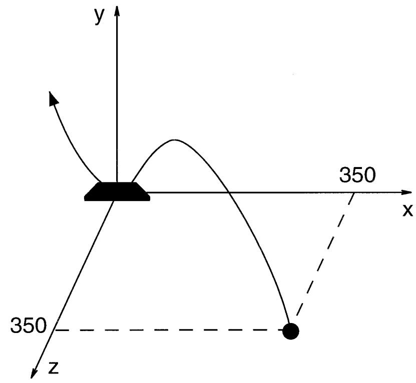

Fig. 2 The hand started from a resting dome located 350 mm in front and 350 mm to the right of the object to be grasped

Design

Each subject was asked to grasp the object placed in front of him, and to lift it up by about 20 cm in a direction approximately parallel to the normal of the object's surface. The object was located in the mid-sagittal plane of the subjects, 60 cm in front and 50 cm below their eyes. The subjects started each trial with their right hand resting on a half-sphere, whose radius was about 10 cm. This resting dome was itself fixed on the table, 35 cm in front and 35 cm on the right of the object to be grasped (Fig. 2). Therefore, the actual distance to be traveled by the hand to reach the object was about 50 cm.

The subject was instructed to pick up the object always with the same precision grip (Napier 1956). This grip consisted of the thumb placed on the left edge of the object, the index and middle fingers on the far long edge, and the remaining two fingers on the close right corner in order to stabilize the grip. This positioning of the fingers was quickly learned by all subjects. There were about ten practice trials before the actual experiment started, so that, together with the time during the calibration of the system, the subject was feeling comfortable with the overall apparatus.

The subject was instructed to close his eyes before each trial to allow the experimenter to adjust the orientation of the object. Three computer-generated sound signals were then generated sequentially. The first signal indicated that the subject could open his eyes and the second signal (2 s later), that he could start the reach. In order to obtain comparable grasping strategies across subjects and across trials, the duration of the reach was chosen to be 1 s; it was the purpose of the third signal (produced 1 s after the second one) to inform the subjects of this temporal constraint. There were four repeated trials per object orientation. All of the 28 trials were randomized and run in a single session, which lasted altogether about 45 min.

Data processing

The transport of the hand to the vicinity of the object can be analyzed by following the instantaneous position of the wrist. The position of the wrist is here defined as the position of the center of rotation of the hand relative to the forearm; this center of rotation can be computed from the four markers placed on the forearm and on the back of the hand. The distances between the center of rotation of the wrist and the four markers were determined during the calibration period with a gradient descent technique, using the fact that the center of rotation is the only point from which the four markers keep a constant excentricity while the hand is moving freely.

The wrist velocity was computed by numerical temporal derivation of the wrist positions. The *start* and *end* times of the reach can then be obtained from the troughs of the wrist velocity; the reach duration is simply the difference between end and start times (6 of 84 trials were removed from this analysis because at least one marker was occluded during the hand displacement). Finally, the trajectory length was computed from the spatial integration of the wrist positions (therefore the trajectory length is necessarily longer than the distance between the start and end wrist positions).

Results

Prehension events

We first checked that subjects succeeded in completing their reach in the time constraint prescribed by the experimenter. The mean reach duration was 1011 ms (SD 120 ms), which is indeed not different from the demanded 1 s (t_{77}=0.83, P>0.1). Across the seven orientations, there were some small fluctuations of reach duration about the mean, but these fluctuations did not reach significance: $F_{6,71}$=1.23, P>0.1. Similarly, neither the time

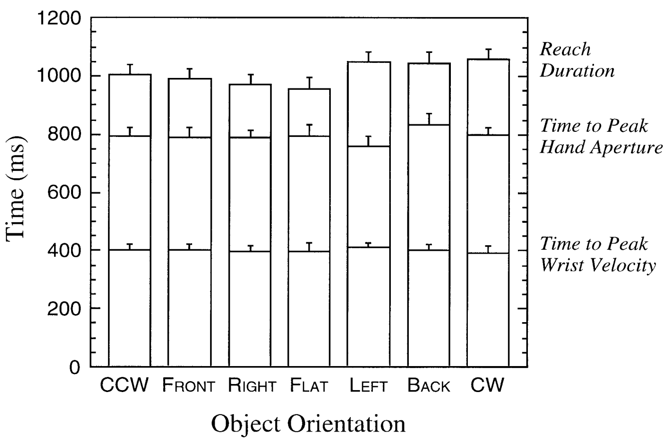

Fig. 3 The mean reach duration was close to 1 s, as imposed by the experimenter. The times to peak wrist velocity and peak hand aperture averaged 400 ms and 794 ms, respectively

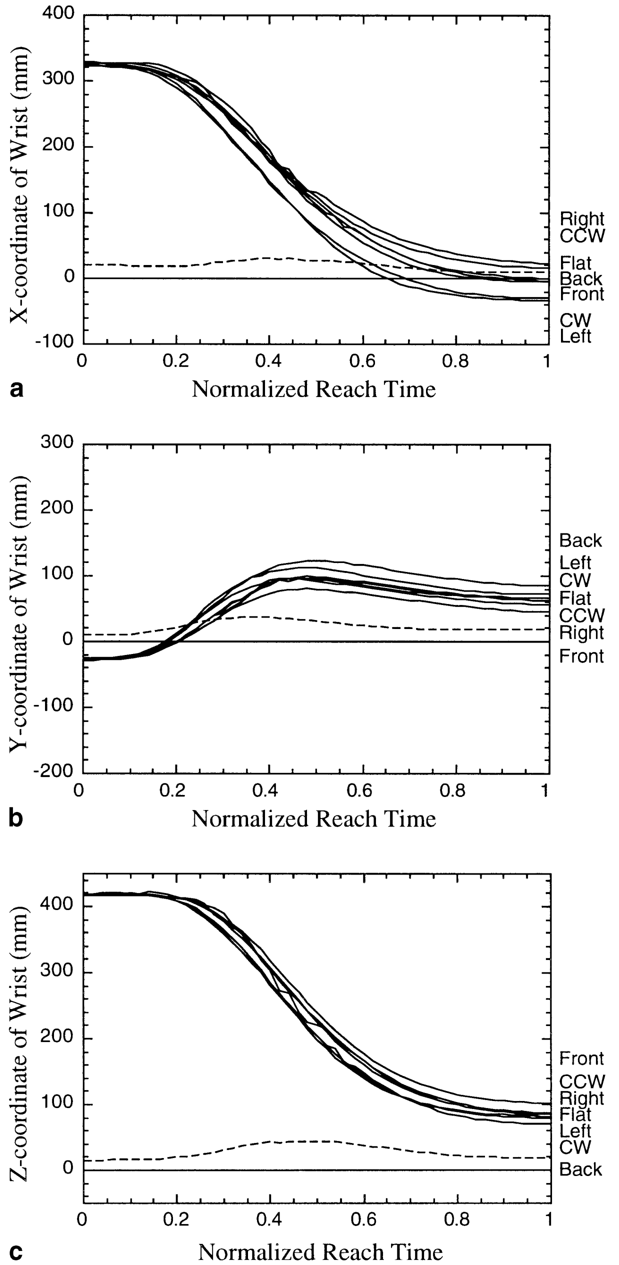

Fig. 4a–c The mean position of the center of rotation of the wrist was computed for the seven object orientations. The coordinate system is defined in Fig. 2. Labels on the *right* indicate the order of the curves when the hand grasped the object. *Dashed curves* represent the means of the SDs

to peak wrist velocity nor the time to peak hand aperture were significantly influenced by the orientation of the object: $F_{6,71}$=0.075, P>0.1 and $F_{6,71}$=0.50, P>0.1, respectively (the hand aperture was taken as the distance between the thumb and index fingers; identical results were obtained if the hand aperture was defined instead as the distance between the thumb and middle fingers: $F_{6,71}$=0.58, P>0.1; the hand aperture is studied more fully in a later section of this paper). The reach duration, time to peak velocity and time to peak aperture are summarized in Fig. 3.

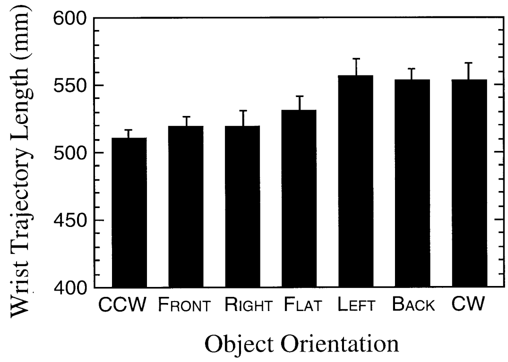

Fig. 5 The trajectory length was measured by integrating the wrist positions from the start to the end of the reach

Reach trajectory

Depending on the orientation of the object, the wrist needed to be positioned at a specific location at the moment of object seizure. For instance, the wrist had to be placed slightly to the right of the object when the object was slanted to the right. To determine when the wrist started to move in one direction rather than another, we computed the instantaneous position of the center of rotation of the wrist (see Materials and methods section above), normalized the reach duration to 1, and resampled the wrist trajectory into 50 intervals (Fig. 4). An analysis of variance was then performed for each of these 50 intervals to detect a difference in wrist position across the different object's orientations. Fixing arbitrarily the type I error to 0.01, the hand trajectory was significantly affected by the object's orientation after 26% of the reach duration along the x-direction and 60% along the y-direction; the Z-coordinate of the wrist position was only affected at the 0.05 level after 84% of the reach (see Fig. 2 for the orientation of the coordinate system).

As a result of the effect of object's orientation on wrist position, the distance traveled by the hand to approach the object was also dependent on object orientation, being for instance shorter when the object was slanted to the right than to the left (Fig. 5). This effect of object orientation over trajectory length was significant: $F_{6,50}$=3.21, P<0.01.

In summary, although the object was rotated about its center of gravity, so that the object can be said to be always at the same location, the trajectory of the hand was different from one object's orientation to another. The fact that this effect can be seen as early as around the first quarter of the reach duration suggests that the visual information for the object's orientation was taken into account at the very beginning of the prehension movement.

Hand rotation

We then analyzed the accuracy and kinematics of hand orientation in the experiment described in the previous section. The orientation of the hand is mainly possible thanks to the three degrees of freedom provided by the

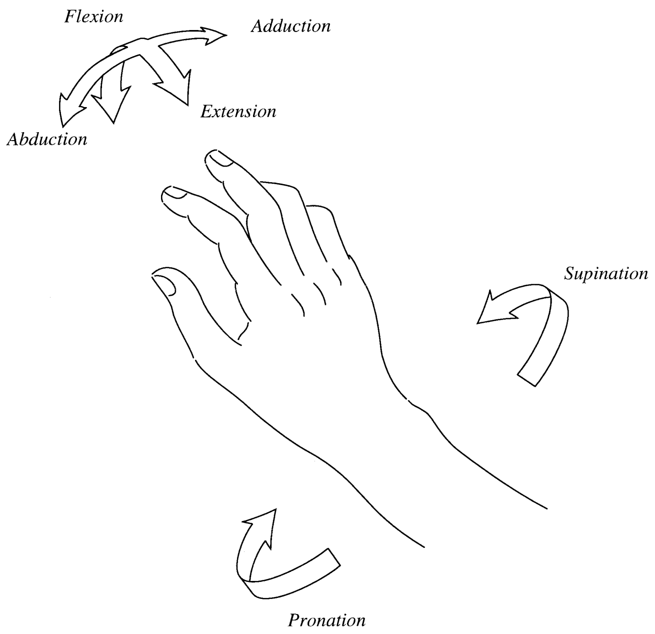

Fig. 6 The rotation of the hand has three degrees of freedom, two at the wrist joint and one at the radio-ulnar joint

wrist (Fig. 6). The spherical joint globally referred to as the wrist is actually composed of the wrist itself and the forearm. At the forearm level, the relative motion of the radius and ulna bones produces a pronation of the hand if the palm is turned downward, or a supination if the palm is turned upward. At the wrist level, the complex shapes and arrangement of eight small bones provide the remaining two degrees of freedom for the hand orientation. The first degree of freedom can be described as an extension or flexion of the wrist, which produces an elevation or a depression of the hand, respectively. The second degree of freedom can be described as an abduction or adduction of the wrist, which corresponds to a movement of the hand away from or towards, respectively, the body midline, when the arm is resting along the body, the palm facing forward. It is important to realize that the orthogonal decomposition into extension and abduction angles is rather arbitrary, since neither the wrist bone surfaces nor the wrist muscles provide any obvious ground to describe these two degrees of freedom (Berger and Garcia-Elias 1991).

In this section, we shall first analyze the accuracy with which the hand and object orientations match each other just before the hand touches the object. For this purpose, we define the *fingertip plane* as the plane passing through the tips of the thumb and index and middle fingers. In anticipation of the grip, this plane should match the plane of the slab-shaped object, because the grip forces have to be applied perpendicularly to the axes of the finger bones (Westling and Johansson 1984). We then analyze the kinematics of the hand orientation by computing the temporal variation of the extension, abduction, and supination angles across the different object's orientations. Finally, we evaluate the coupling between the wrist and the forearm during the prehension.

Materials and methods

Design

The analysis described in this section is complementary to the one performed in the previous section. The data are therefore taken from the experiment already detailed.

Data processing

The orientation of the fingertip plane has three degrees of freedom, which can be described in a coordinate system tied to the table. Only one degree of freedom, the slant of the fingertip plane, will be reported here. Slant is defined as the angle between the normals to the table and fingertip plane, and corresponds to Gibson's "geographical" slant (Gibson and Cornsweet 1952) in contrast to the more familiar "local" slant, which is defined relative to the observ-

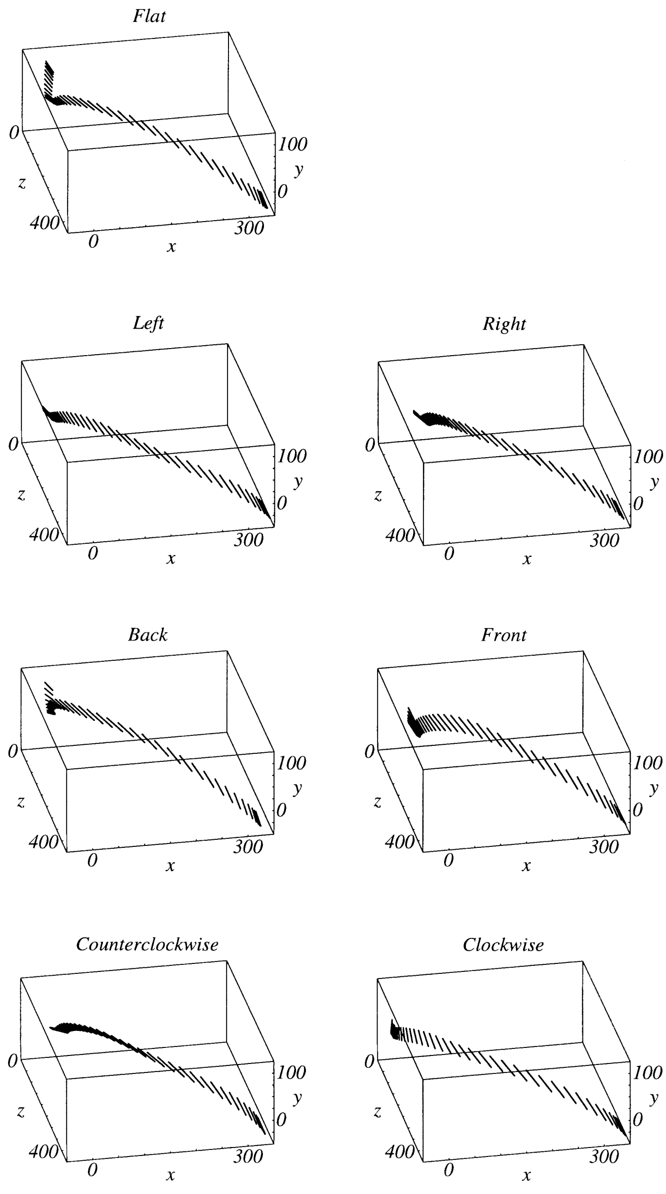

Fig. 7 The progressive rotation of the hand toward the orientation of the object, for the seven experimental conditions (sampled every 25 ms). The orientation is symbolized by a segment whose tail is located at the center of rotation of the wrist (the tail is at the bottom of the segment). The coordinate system is defined in Fig. 2

er (e.g., Mamassian and Kersten 1996). Since the markers were not precisely positioned at the tips of the fingers, the plane passing through the three markers will only be an approximation of the fingertip plane. We shall therefore report here only the orientation of the fingertip plane relative to the baseline provided by the *flat* experimental condition. If the hand is correctly oriented relative to the object, the fingertip plane for the *back*, *front*, *left*, or *right* object orientations should all have a slant equal to 20°.

The analysis of the coupling between the wrist and the forearm relied on a piece-wise linear approximation of the joint angles variations. First, the local minima of the hand velocity were collected along the supination dimension, and then along the extension/abduction dimension (the extension and abduction angles were combined to form a two-dimensional vector representing the orientation of the wrist; see Fig. 7). To decrease the effects of muscle tremor and measurement errors (which were magnified by differentiations and referential transformations), the angle amplitude was beforehand smoothed by a discrete-time low-pass filter of cutoff frequency 10 Hz. Two successive linear segments were then merged if the angle speed difference between the two segments did not exceed 40°/s. These values were chosen on pragmatic grounds, after screening all trials individually. To estimate the goodness of fit for the piece-wise linear approximation, a linearity index was needed (Mathew and Cook 1990). For this purpose, we computed for each segment the *covered angle* as the integration of the angle variation between two temporal samples (every 5 ms). We also computed the *straight angle* as the angle difference between the end and the beginning of the segment. Then, the *linearity index* is just the ratio of the straight angle to the covered angle; it varies between zero (highly sinuous segment) and 1 (perfectly straight segment).

Results

Orientation of the fingertip plane

The examination of the orientation of the fingertip plane revealed a consistent bias. Just before grasping the object, the fingertip plane was regressed to the orientation of the supporting table (Fig. 8). This effect was significant at the 0.01 level for the right and front orientation conditions (t_{11}=3.71, P<0.01; and t_{11}=5.12, P<0.01, respectively) and at the 0.05 level for the back condition t_{11}=2.35,P=0.019); it failed to reach significance for the left condition (t_6=0.50, P>0.1).

It is likely that the misorientation of the hand at the seizure of the object was due to a lack of time to complete the orientation movement. When time was no longer a critical constraint, such as when the subject was instructed to match the object's orientation with the help of another hand-held object, no such slant underestimation was found (Mamassian et al. 1995).

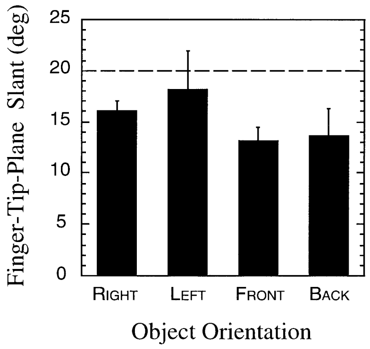

Fig. 8 The plot shows the orientation of the fingertip plane just before the hand touches the object, for the right, left, front, and back conditions

Rotation of the wrist

Depending on the object's orientation, either the extension, the abduction, or the supination angle was primarily affected. For instance, the hand was more supinated when the object was slanted to the right and, conversely,

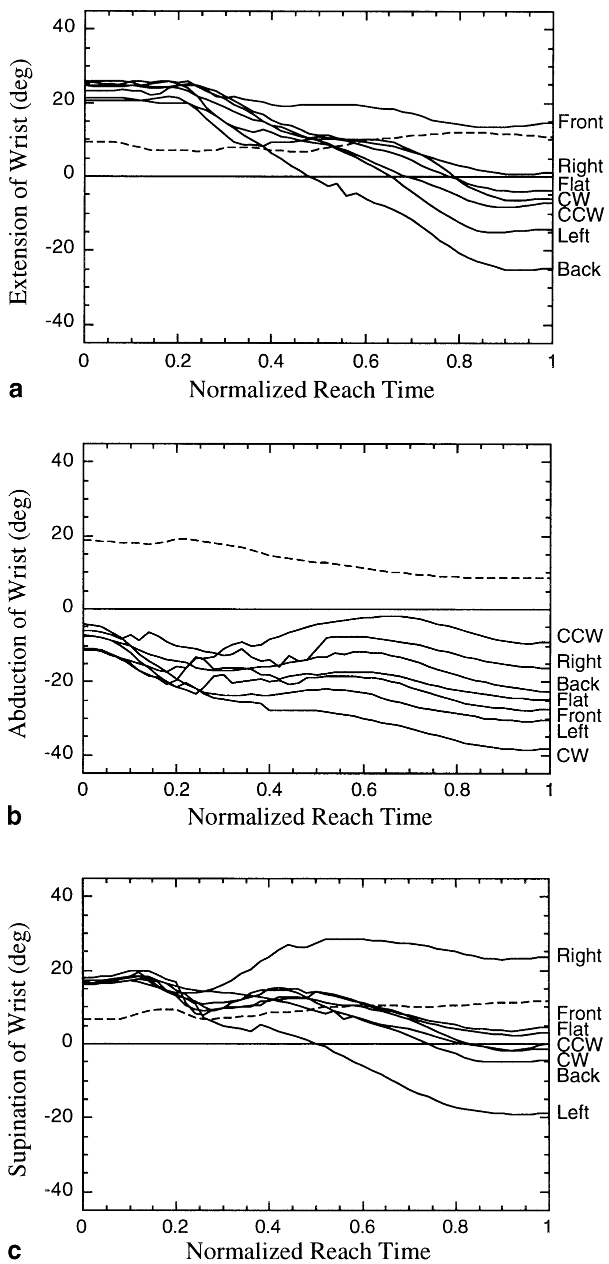

Fig. 9a–c The progressive orientation of the hand was dependent on the orientation of the object: **a** extension of the wrist; **b** abduction of the wrist; **c** supination of the forearm. The order of the curves at the grasping time is indicated on the *right* of the plot. *Dashed curves* represent the means of the SDs

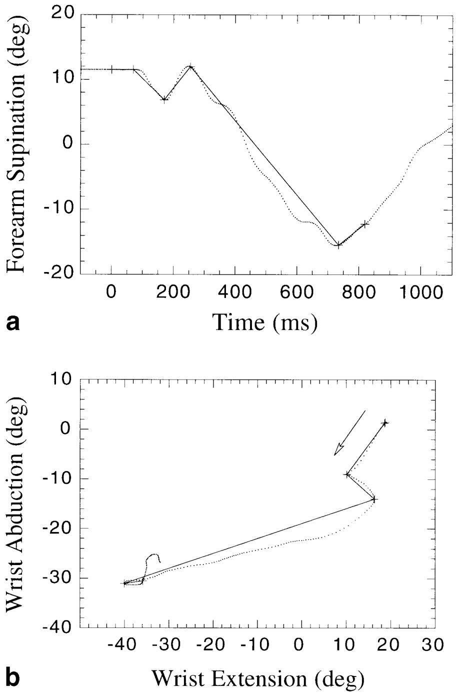

Fig. 10a, b The kinematics of hand rotation can be studied by looking at the temporal variation of the supination angle (**a**), and of the combined extension and abduction angles (**b**). Each *dot* represents the computed angles every 5 ms. Superimposed on the graphs are the piece-wise linear approximations of the rotation movement for this particular trial. The *arrow* indicates the direction of movement

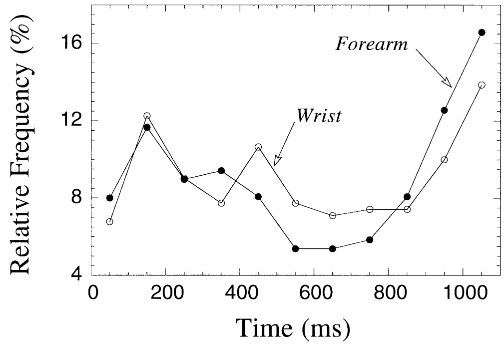

Fig. 11 By collecting the boundaries of the piece-wise linear approximations, two distributions are obtained for the supination angle (*Forearm*), and the extension/abduction angle (*Wrist*). The time occurrence of these boundaries are plotted in bins of 100 ms long, origin and end of the reach excluded

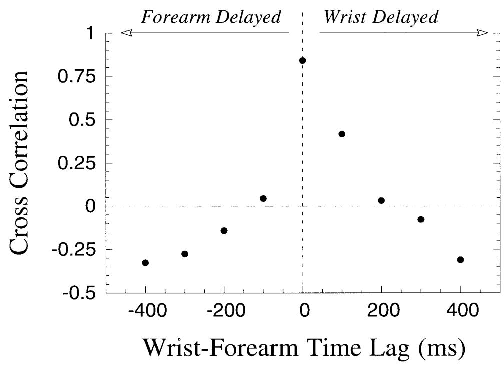

Fig. 12 A cross-correlation between the two distributions displayed in Fig. 11 is informative on the synchronization of the wrist and the forearm. Positive correlations were found for the 0-ms and 100-ms time lags between the wrist and the forearm

more pronated when it was slanted to the left. To determine when the hand started to rotate in one direction rather than another, we computed the instantaneous extension, abduction, and supination angles, normalized the reach duration to 1, and resampled the wrist orientation angles into 50 intervals (Fig. 9). The first significant departures from the mean as computed from an analysis of variance with a type I error fixed to 0.01 were observed after 38% of the reach duration for the extension, 48% for the abduction, and 36% for the supination.

The variation of the supination, extension and abduction angles tended to be fairly constant within some temporal intervals (Fig. 10). This property, which suggests that the hand changes direction in a discrete manner, can be quantified by computing linear approximations to the joint angle variations. The piece-wise linear approximations fitted for the trial displayed in Fig. 10 are traced over the plots. Over all segments per trial and all trials per subject, the mean linearity index reached 0.89 for the supination angle (SD 0.22) and 0.91 for the extension/abduction angle (SD 0.11). Obviously, higher linearity indices could have been obtained had we segmented each prehension movement into a larger number of segments. In our analysis, the mean number of segments per reach was 3.98 for the supination angle (SD 1.76), and 5.54 for the extension/abduction angle (SD 1.51).

The piece-wise decompositions of the supination and extension/abduction angle variations are convenient entities to study further the hand orientation kinematics. In particular, we can look at the time occurrence of the boundary between two successive linear segments and compare these time occurrences between the forearm and the wrist. Figure 11 shows the distribution of these boundaries for both the supination and the extension/abduction angles, when all the trials of the experiment were pooled. The amount of synchronization between the forearm and the wrist can then be estimated by computing the cross-correlation between the two distributions of segment boundaries, including temporal shifts of 100 ms of one distribution relative to the other to detect a potential time lag of one joint relative to the other. We found two positive cross-correlations (R>0.4) for the 0-ms and 100-ms time lags between the wrist and radio-ulnar joints (Fig. 12). In other words, the movements of the wrist were occuring on the average after those of the forearm, with a delay of duration between 0 and 100 ms. This time lag of the most distal joint may result from the different inertial moments of the segments in movement (Lacquaniti and Soechting 1982).

Hand opening

We investigated the effect of object orientation on hand preshaping in a second experiment. Previous work has shown that the maximum aperture of the hand during its displacement was proportional to the size of the target object and independent of its distance to the subject (Jeannerod 1981; von Hofsten and Rönnqvist 1988). Thus the hand opens appropriately to the physical size of the object rather than its retinal size, a phenomenon known as size constancy. Like the distance separating the object and the observer, the orientation of the object also affects its apparent size as projected on the retina (Fig. 13). We asked whether size constancy generalizes to the case where the retinal image is affected by the orientation of the object.

Furthermore, we touched upon the issue of the use of visual information during prehension. Previous studies have reported an increase in hand aperture when vision of the hand is prevented during reaching (Jakobson and Goodale 1991), but a decrease in hand aperture when reaching is executed monocularly (Servos et al. 1992). In the present experiment, we compared two experimental conditions, one visually "rich," where the object was textured and seen binocularly, and another one visually "poor," where the object had a uniform color and was seen monocularly.

Materials and methods

Subjects

Five subjects participated in this experiment, aged between 22 and 27 years old. All subjects were right-handed, and naive to the purposes of the experiment. None of them participated in the first experiment.

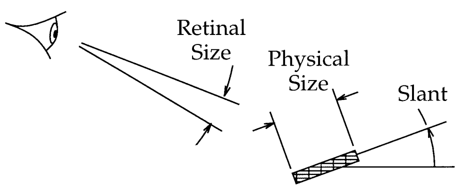

Fig. 13 The geometrical relations between the physical size of an object, its orientation, and its retinal size

Table 1 The different object sizes (in millimeters) were computed so that the objects subtended one of three possible visual angles and were rotated by one of three possible orientations. In addition, one object (of size 30 mm) was seen at all three orientations. Negative slant corresponded to an object slanted backward

Visual angle (deg)	Object slant (deg)		
	–20	0	20
0.75	30	16	12
1.41	57	30	22
1.90	76	40	30

Apparatus

The apparatus was identical to the one used in the first experiment, except that only the three markers placed at the tips of the thumb and index and middle fingers were used.

Stimulus

The objects used in this experiment were again rectangular polyhedra, of sizes $a \times 40 \times 8$ mm, where a varied between 12 and 76 mm.

Design

The physical size of an object was selected from Table 1. This table was obtained by crossing two factors, *object orientation* and *object retinal size*. The three object orientations were identical to the "flat", "back", and "front" conditions of the first experiment. The three object retinal sizes corresponded to the angles subtended by an object of physical size a=30 mm under all three object orientations.

These nine experimental conditions (three orientations times three retinal sizes), were run under two viewing conditions, in alternate blocks of trials. In a visually "rich" viewing condition, the object was textured and seen binocularly. The texture consisted of black disks uniformly positioned on a white background. In the visually "poor" viewing condition, the object was uniformly white and seen monocularly. Four repeated trials were run for each experimental condition and each viewing condition. In contrast to the previous experiment, subjects were asked to grasp the object using the more conventional precision grip where the thumb comes in opposition to the other fingers.

Data processing

The hand aperture was evaluated from the distance between the thumb and the index tips. The actual pinch size was obtained after correction for the fingers' thickness, since the markers were attached next to the nails of the fingers.

Results

Hand aperture

The fingers extended as the hand left the resting dome and extended again as the hand approached the target object. As a consequence, the distance between the thumb and the index fingers exhibited two peaks, the second of which is referred to as the peak hand aperture.

The size and orientation of the objects were so chosen that only three retinal sizes could be discriminated by the subjects. If the peak hand aperture was solely based on retinal size, then different combinations of physical size and object orientation should produce the same pinch size as long as the retinal size was identical. An analysis of variance rejected this hypothesis. The interaction between the two independent variables – object orientation and retinal size – was highly significant: $F_{4,343}$=376, P<0.001. Instead of being based on retinal size, the peak hand aperture was linearly related to the object's physical size (Fig. 14). The slope of the linear fit was 0.76 (Pearson's correlation, R=0.92) for the rich condition and 0.64 (R=0.83) for the poor condition. In summary, our

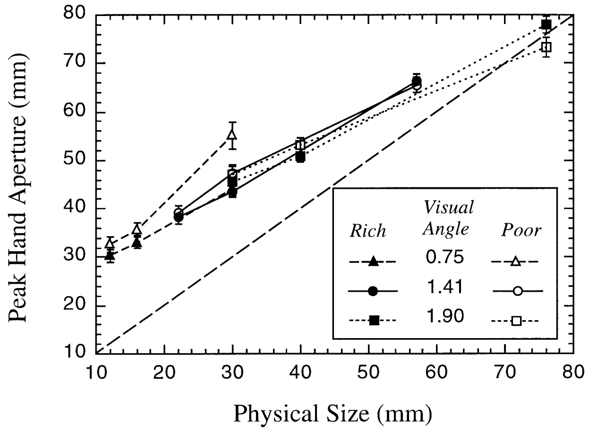

Fig. 14 The peak hand aperture is plotted against the physical size of the object, grouped according to the orientation of the latter. *Filled symbols* or *open symbols* show the aperture when the visual information about the object orientation was "rich" or "poor", respectively

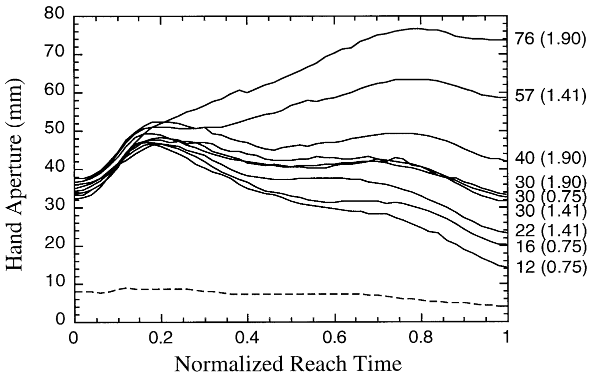

Fig. 15 The mean hand apertures were computed as the distance separating the thumb and index fingers for the nine experimental conditions. Labels on the *right* indicate the physical size of the object and (*in parentheses*) the visual angle subtended by the object. The *dashed curve* represents the mean of the SDs

results complement the phenomenon of size constancy from object proximity in that the present subjects displayed size constancy from object orientation.

To determine when the hand started to open more or less widely as a function of the object's size, we computed the instantaneous hand aperture, normalized the reach duration to 1, and resampled the hand aperture into 50 intervals (Fig. 15). This computation was made for the "natural" viewing condition, where the subjects reached for a textured object seen binocularly. The first significant departure from the mean as computed from an analysis of variance with a type I error fixed to 0.01 was observed after 26% of the reach duration.

Quality of the visual information

The comparison between the visually rich and poor conditions revealed a slight increase in peak hand aperture when the visual information for object size was impoverished; this effect, however, failed to reach significance under a paired *t*-test: t_8=1.53, P>0.1. Even though the objects were always at the same location, this knowledge alone was not sufficient to infer the size of a given object. We can thus conclude that, at least in the impoverished condition, subjects used alternative depth cues other than stereopsis and texture to estimate the object orientation. For instance, the observers could have been using motion parallax from small head movements, linear perspective, or the ratio of height to thickness of the object. Further experiments should determine the weight of each of these cues for a manual prehension task.

General discussion

In this paper, we have investigated how the visual information to assess the orientation of an object was used during the manual prehension of that object. Subjects were asked to reach for and grasp a polyhedron object whose orientation was varied between trials. Their prehension movements were divided into three components for the purpose of the analysis, namely, the transportation, orientation, and opening of the hand.

Even though the object remained at the same location, varying its orientation incited subjects to place their wrist at different locations just before object seizure. In effect, the trajectory of the wrist was longer or shorter depending on the object's orientation, even though the reach duration remained approximately constant as imposed by the experimenter. The first noticeable deviation of one trajectory relative to another was observed less than 300 ms after the onset of the movement.

Probably the most drastic effect of varying the orientation of the object was a rotation of the wrist and forearm to enable a stable grip. The first noticeable deviation of one hand orientation relative to another was observed about 400 ms after the onset of the movement. The gradual wrist and forearm rotations were well fitted by piecewise linear approximations. The analysis of these linear fits revealed that the wrist rotations were slightly delayed relative to the forearm. Lastly, the precision of the hand rotation was examined with the help of the fingertip plane, a virtual plane passing through the tip of the thumb and index and middle fingers. The analysis of the orientation of this fingertip plane just before object seizure revealed a bias toward the orientation of the table supporting the object.

Finally, we demonstrated that the peak hand aperture was linearly related to the physical size of the object, even though the estimation of this physical size was hindered by the object's orientation. In other words, subjects displayed size constancy from object orientation. The first noticeable deviation of one hand opening relative to another was observed as early as 300 ms after the onset of the movement. No difference in hand opening was noticed when the prehension was performed toward untextured objects under monocular viewing.

In summary, the object orientation affected not only the rotation of the hand, but also its transportation and opening. These results show that whatever mechanisms were responsible for the hand transportation and opening, these mechanisms had access to the amplitude of the object's orientation, which could be obtained only visually. Therefore, it seems that a common representation of the extrapersonal space is made available to the different motor commands.

The notion of a common visual representation is certainly plausible from a biological point of view. The evaluation of recent anatomical and physiological studies suggests the existence of two pathways within the parietal cortex of the primate (Mountcastle 1995). A first medial system seems to be mainly concerned with the transportation of the hand towards a target (Caminiti et al. 1996). Cells selective to the arm displacement have been identified in the posteromedial part of the primary motor cortex (Georgopoulos et al. 1982), the caudal part of the ventral premotor cortex (area F4; Weinrich and Wise 1982; Gentilucci et al. 1988; Caminiti et al., 1991), and the dorsal part of area 5 within the superior parietal lobule (Johnson et al. 1996). In contrast, a second system, more lateral, seems primarily devoted to the preshaping of the hand in anticipation of the grasp (Jeannerod et al. 1995). Cells that respond during hand manipulation have been reported in the lateral part of the primary motor cortex (see Godschalk et al. 1984), in the rostral part of the ventral premotor cortex (area F5; Kurata and Tanji 1986; Rizzolatti et al. 1988), and in the anterior intraparietal and lateral intraparietal areas (AIP and LIP) within the intraparietal sulcus (IPS; Taira et al. 1990; Sakata et al. 1995).

The quest for the visual inputs to these frontal and parietal areas is currently a matter of intense investigations (Caminiti et al. 1996). In the primate brain, the posterior parietal cortex at the pinnacle of the dorsal stream has long been regarded as a critical region for the visuomotor coordination (Hyvärinen 1982; Andersen 1987). Lesions to the intraparietal sulcus and the neighboring superior parietal lobule (SPL) produce a general deficit of the transportation, rotation, and preshaping of the hand (Perenin and Vighetto 1988). Interestingly, in an area that projects to the IPS (area PO; Colby et al. 1988), some neurons have their receptive fields defined relative to the head, independently of the position of the eyes in their orbit (Galletti et al. 1993). Such a property is of primary importance if a representation of extrapersonal space is to be built. In this representation, the location, orientation, and shape of objects should all be estimated to achieve a coherent description of the world in which the action is to take place.

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