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On the Relation Between Object Shape and Grasping Kinematics

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Cuijpers, Raymond H., Jeroen B. J. Smeets, and Eli Brenner. On the relation between object shape and grasping kinematics. *J Neurophysiol* 91: 2598–2606, 2004. First published January 28, 2004; 10.1152/jn.00644.2003. Despite the many studies on the visual control of grasping, little is known about how and when small variations in shape affect grasping kinematics. In the present study we asked subjects to grasp elliptical cylinders that were placed 30 and 60 cm in front of them. The cylinders' aspect ratio was varied systematically between 0.4 and 1.6, and their orientation was varied in steps of 30°. Subjects picked up all noncircular cylinders with a hand orientation that approximately coincided with one of the principal axes. The probability of selecting a given principal axis was the highest when its orientation was equal to the preferred orientation for picking up a circular cylinder at the same location. The maximum grip aperture was scaled to the length of the selected principal axis, but the maximum grip aperture was also larger when the length of the axis orthogonal to the grip axis was longer than that of the grip axis. The correlation between the grip aperture—or the hand orientation—at a given instant, and its final value, increased monotonically with the traversed distance. The final hand orientation could already be inferred from its value after 30% of the movement distance with a reliability that explains 50% of the variance. For the final grip aperture, this was only so after 80% of the movement distance. The results indicate that the perceived shape of the cylinder is used for selecting appropriate grasping locations before or early in the movement and that the grip aperture and orientation are gradually attuned to these locations during the movement.

INTRODUCTION

To grasp an object, the digits of the hand must somehow be directed toward appropriate positions on the object's surface. It has been well established that the visual system is capable of supplying the necessary information. Yet there is much debate about what information is extracted from the visual input and how it is linked to the control of (grasping) movements (e.g., Desmurget et al. 1998; Jeannerod 1988; Smeets and Brenner 1999). One of the outstanding issues is whether or not the movements of the digits can best be understood as independently controlled grip and transport components. It is well known that for a given object shape and orientation, the maximum grip aperture depends on the object's size, whereas the transport component depends on the location in space (Jeannerod 1981; Paulignan et al. 1991, 1997). The orientation of an object was also found to affect wrist pronation without changing its transport kinematics (Stelmach et al. 1994). These findings suggest independent control of grip and transport components, although other interpretations are possible (Smeets and Brenner 1999). However, when grasping irregular objects, the final grip aperture is determined by the grasping locations on the object's surface (Goodale et al. 1994). As a consequence, we expect that under such circumstances, the maximum grip aperture will be coupled to the orientation of the hand in space. Similarly, the perceived size of an object is no longer a self-evident measure. The relevant measure may be the distance between the perceived (grasping) locations (Smeets and Brenner 1999) in which case, other aspects of the object's (apparent) dimensions may not be important at all (Smeets et al. 2002). We therefore want to determine whether the maximum grip aperture only scales to the length of the grip axis or also to other aspects of the object's dimensions.

The correlation between grip aperture and the object's size has predominantly been studied for the maximum grip aperture. Naturally, such a correlation must exist at other instances of the grasping movement as well. The same applies for the hand orientation. It has been shown that the hand orientation is already adjusted to the object orientation in the first half of the movement (Glover and Dixon 2001; Mamassian 1997). However, it is still unclear how such correlations develop during the course of the movement.

In the present study, we investigate how asymmetrical objects are grasped by systematically varying both their shape and orientation. We let subjects grasp elliptical cylinders with different aspect ratios at various orientations and distances from the subject. In the first part of our paper, we will focus on the points on the surface at which the cylinders are grasped. In the second part, we will focus on how the reach-to-grasp evolves for given pick-up locations.

METHODS

Subjects

Eight right-handed subjects volunteered to participate in our experiment, two of whom were authors (*EB* and *JS*). The other subjects were unaware of the purpose of the experiment. All subjects had normal or corrected-to-normal acuity and binocular vision except *subject JS* who is stereo blind.

Objects

We used seven 10-cm-tall cylinders made out of a white plastic material. One of the cylinders was circular, but the others had an elliptical base. The aspect ratio of the base was varied: the length of one of the principle axes was always 5 cm, whereas the length of the other ranged from 2 to 8 cm in steps of 1 cm (see Fig. 1). The cylinders' masses ranged from 110 to 440 g (the density is 1.40 10^{-3} kg/cm^3).

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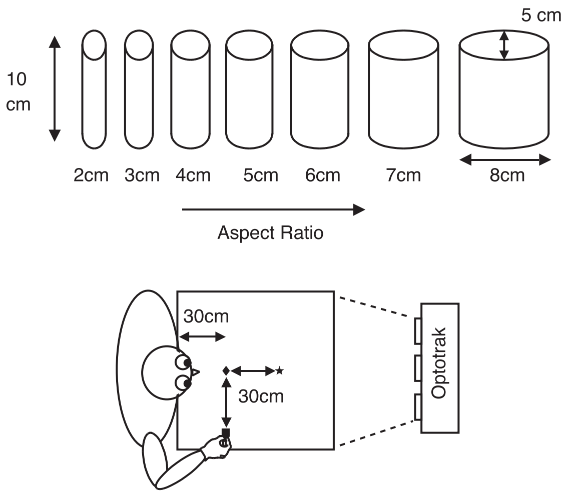

FIG. 1. Schematic drawing of the objects (*top*) and a top view of the experimental setup (*bottom*).

Experimental setup

The subjects were seated behind a table with a white surface in a normally illuminated room. The equipment that would normally be visible just behind the table was shielded from view with white paper. Although this reduced the visual contrast between the cylinders and the background, the visibility was hardly affected. From where the subject was sitting the shapes and contours of the cylinders were clearly visible (due to shading, texture, albedo, etc.). Three markings were visible on the table, indicating the starting position of the hand (30 cm in front and 30 cm to the right of the subject) and the two target locations (30 and 60 cm in front of the subject, see Fig. 1). With this configuration, the directions of movement differ by 45° while the cylinder orientation relative to the line of sight is unaffected. This enables us to distinguish between effects of target orientation and of direction of movement on the final grasp. The fact that this introduced additional differences, such as a difference in distance, was not considered to be a disadvantage because we were interested in aspects of the movement that are independent of such factors. One pair of infrared emitting diodes (IREDs) was attached to the index finger and another to the thumb of each subject. The locations of the IREDs were tracked by an Optotrak 3010 camera system at a sampling frequency of 200 Hz. Each pair of IREDs was attached to a small stalk. The stalks prevented the cylinders from occluding the IREDs when they were grasped. A computer image displayed by a beamer hanging above the table was used in-between trials to accurately position each cylinder in the required orientation.

Task

The subjects' task was to pick up the cylinder placed at one of the two locations in front of them and place it at the other location. At the beginning of each grasping movement, they held the fingertips against each other and directly above the indicated starting position with the hand resting on the table. They had to pick up the cylinders by the sides using a precision grip, i.e., using thumb and index finger only. No instructions were given concerning the movement speed and accuracy: the subjects moved in whatever way they felt was comfortable.

Procedure

The projected image of the beamer and the Optotrak system were calibrated before the measurements. Once the subject was seated with his or her belly against the table edge, the IRED stalks were taped to the tips of the thumb and index finger. Care was taken not to cover the finger pads. Subjects were then familiarized with the task by running several practice trials. Once they were clear about the task the real trials began. At the beginning of each trial, the subject moved the hand to the starting position and closed his or her eyes. The experimenter placed one of the seven cylinders at one of the two target locations in one of six orientations (θ). The orientations varied from 0 to 150° in steps of 30° (the orientation is 0° when the major axis is in the sagittal direction and positive is counter-clockwise, see Fig. 2). To position the cylinder accurately, an ellipse of the correct size and orientation was projected onto the table so that when the cylinder was placed correctly the ellipse fitted on its top edge. Once the cylinder was in place, the projected image was extinguished and, on a signal from the experimenter, the subject opened his or her eyes, picked up the cylinder, placed it at the other target location (in an arbitrary orientation) and moved back to the starting position. Typically, the reaction times were $>$0.5 s and the movements toward the cylinder took 1.0 s. Meanwhile the Optotrak recorded the IRED positions. After each movement the subject closed his or her eyes and the next trial was set up. The order of presentation was randomized for each subject.

Data analysis

The positions of the fingertips were determined from the recorded IRED positions by calculating for each stalk the intersection between the line through the IREDs and the inner surface of the corresponding fingertip. The grip aperture was defined as the length of the line segment connecting the fingertips (Fig. 2, - - -). The hand orientation (ϕ) is defined as the angle between the orthogonal projection of this line segment on the horizontal plane and the sagittal direction. The hand position is defined as the mean position of the fingertips. To completely specify the hand orientation, an additional angle of elevation is needed. However, because our task only involves pseudo-horizontal movements and because we only manipulate the horizontal orientation of the cylinders, the relevant angle is the horizontal projection of the hand orientation.

Only the data segment from the start of the movement until the moment of contact was analyzed. This segmentation was based on the minima in tangential hand velocity. For those trials in which the automatic segmentation failed, as was evident from final grasps that did not correspond with the object's location and dimensions, the segmentation was done manually (15% of the trials). Trials in which the markers were occluded during the reach were discarded (7% of the

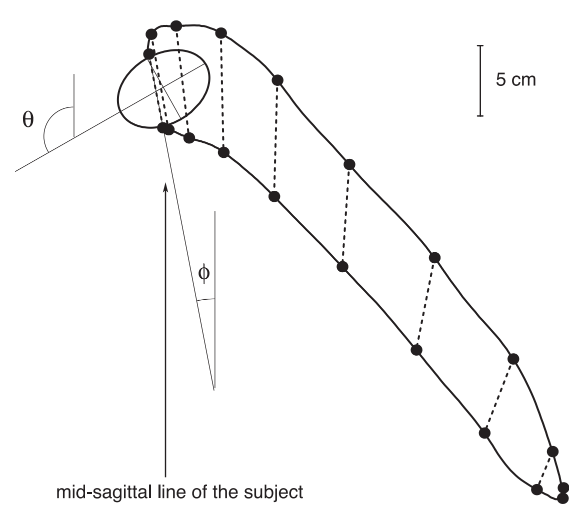

FIG. 2. Example traces of the thumb and index finger (—). The dots denote the fingertip positions at 100-ms intervals. The hand orientation and the grip aperture are indicated by the orientations (ϕ) and the lengths of the lines connecting the digits (- - -). The object orientation is defined as the orientation of its major principle axis (θ). Both angles are given with respect to the sagittal direction and are positive for counter-clockwise rotations.

trails). Conventional numerical differentiation amplifies noise, which is usually resolved by smoothing the data. It is much better to use regularized differential operators: the *n*th-order derivative is calculated by convoluting the data with the *n*th-order derivative of a Gaussian kernel (Koenderink 1984; Nielsen et al. 1997; Witkin 1983). To find the minima in tangential hand velocity, we locate the zero-crossings of the second-order Gaussian derivative of the hand position. The width of our Gaussian kernel was three frames to either side, which corresponds to a smoothing window of 30 ms.

RESULTS

Hand orientation at the time of contact

In general, our subjects picked up the cylinders close to one of their principal axes. The distribution of pick-up orientations relative to the cylinder orientation (ϕ-θ) is illustrated in Fig. 3*A*. This graph shows the number of times that each orientation difference (ϕ-θ) occurred. The number density is obtained by smoothing these occurrences with a Gaussian kernel of unit area and 5° width. The distribution is bimodal with the peaks centered at approximately –3 and 85° (i.e., ~4° off the principle axes). This small systematic misalignment could be due to a mismatch between the calculated and actual grip orientations. The number of times that the cylinders were picked up by their major and minor axes is evident in the area enclosed by the left and right peak, respectively. The probability of choosing the major axis is 0.32 (borders at –45 and 35°) and that of choosing the minor axis is 0.68. The variability of the grasping points when grasping the minor axis is higher than for the major axis. This is evident from the fact that the peak at –85° is wider but not much taller than that at –3°. The ratios between the full width at half-maximum and the peak height are 1.34 and 0.84, respectively (see Fig. 3*A*). This is consistent with the higher accuracy that is required for grasping the major axis compared with the minor axis: the same angular error in grip orientation results in a larger distance from the endpoints of the principal axis when grasping the major axis than when grasping the minor axis. In addition, the misalignment of the surface normals with the grip axis is larger for grasps to the major axis than for grasps to the minor axis (for the same angular error).

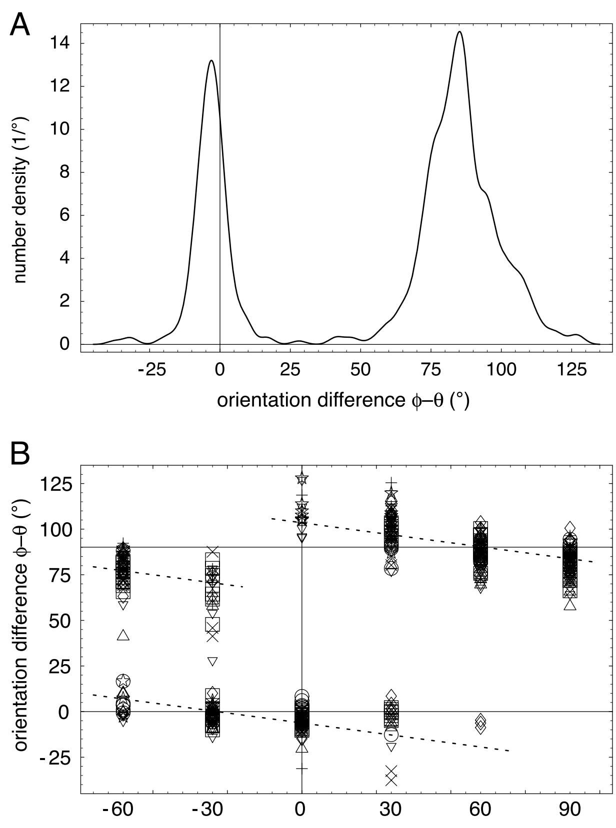

FIG. 3. *A*: distribution of grasping orientations relative to the cylinder's major axis. The graph is a smoothed histogram of the difference in orientation between the hand (ϕ) and the major axis of the cylinder (θ). *B*: effect of the cylinder orientation on the distribution of grasping orientations. The orientation difference (ϕ-θ) at the time of contact is shown as a function of the orientation of the major axis (θ) for the same dataset. Each point is an individual trial with different symbols for each subject. The dashed lines are linear fits to the data (see text for details).

It turns out that the locations of the peaks of the bimodal distribution depend slightly on the orientation of the cylinders. Rather than plotting many smoothed densities, we show this by plotting raw grasping orientation differences as a function of cylinder orientation. Figure 3*B* shows the difference between the orientation of the hand at the time of contact and the orientation of the cylinder's major axis (ϕ-θ) as a function of the orientation of the cylinder's major axis. The bimodal distribution for each orientation of the major axis now appears vertically for each cylinder orientation (the number density follows from the spatial density of the data points). The entire dataset is shown except the data for the circular cylinder, which cannot be included because circular cylinders do not have a major axis. If the subjects had grasped the cylinders exactly at their major and minor principal axes, all the data would fall on the horizontal lines with 0 and 90° offsets, respectively. Clearly, the data points are scattered near these lines, but they do show a negative trend. Note that if the hand orientations were uncorrelated to the orientations of the cylinder's major axis, a negative trend with a slope of –1 would occur.

To examine potential effects of aspect ratio and cylinder distance in the data shown in Fig. 3*B*, we performed a separate linear regression to the data of each subject for each aspect ratio and distance. Extra care is needed when fitting these data because there is a periodicity of the cylinder orientation of 180°. One can see from Fig. 3*B* that the data are, in fact, divided into two groups: the first group appears to be scattered near a line through the origin and the second near a line through the point (90°, 90°) that wraps around to the other side (this point corresponds to grasping the minor axis in a 0° orientation). The easiest way to proceed would be to split the data in an upper and lower half, unwrap the upper half and then apply the linear regressions. However, this involves a rather arbitrary choice of segmenting the data. Although a choice of, say 45°, may be plausible for the entire dataset, it may not be valid for a particular subset. We therefore simultaneously fitted the lines $y = ax + b$ and $y = a(x \pm 90) + b + 90$ where y is the orientation difference and x is the orientation of the major axis. The fit was calculated by determining the residual squares for each point and for each equation. For each point, the least of these two residual squares was used to compute the total sum. The desired values of the parameters a and b are those for which the total residual sum of squares is minimal. Using the same slopes (a) and offsets (b) in the equations in the preceding

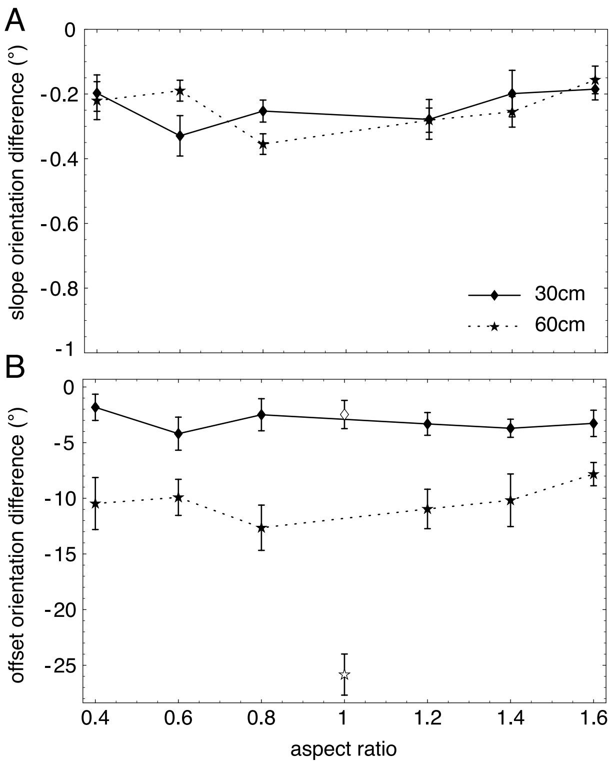

FIG. 4. Slopes (*A*) and offsets (*B*) of the relationship between the orientation difference (ϕ-θ) and the orientation of the cylinder (θ) are shown as a function of the aspect ratio. These values were obtained from linear fits for each distance to the data shown in Fig. 3. The data points are the means of 8 subjects (with the SE). The open symbols indicate the mean hand orientations (ϕ) at which the circular cylinder was grasped.

text is equal to assuming that there is no essential difference between picking up the cylinders at the major and minor axis.

The slopes (*A*) and offsets (*B*) of the linear regressions are shown in Fig. 4 as a function of the aspect ratio. The circular cylinder has no meaningful orientation, but the mean hand orientation was plotted as an offset (*B*, ◇, ☆). This makes sense because if the hand orientation is independent of the orientation of an object, we would obtain a slope of –1 and an offset equal to the mean hand orientation.

For the noncircular cylinders the average slope is -0.24 ± 0.02, indicating that the subjects' hand orientation follows that of the cylinder with a gain of $\sim 1–0.24 = 76\%$. An ANOVA indicates that the slopes are independent of the aspect ratio [$F(5,79) = 1.786$, $P = 0.13$] and of the target distance [$F(1,79) = 0.075$, $P = 0.78$] and that there is no interaction [$F(5,79) = 1.465$, $P = 0.21$]. The size of the offsets depends on the target distance [$F(1,79) = 60.00$, $P < 0.0001$], but it is independent of the aspect ratio [$F(5,79) = 0.269$, $P = 0.93$] and there is no significant interaction [$F(5,79) = 0.608$, $P = 0.69$]. For a distance of 30 cm, the average offset is $–3.1 \pm 0.5°$. For a distance of 60 cm, it is $-10.5 \pm 1.9°$. The mean orientations with which the circular cylinder is grasped are $–2.4 \pm 2.6°$ and $-25.8 \pm 3.2°$ for cylinders at 30 and 60 cm, respectively. Comparing these mean orientations to the mean offsets of the noncircular cylinders, we observe a large difference for a distance of 60 cm [$t(54) = –6.831$, $P < 0.0001$] but not for 30 cm [$t(49) = 0.462$, $P = 0.65$]. At 30 cm, the hand orientations for grasping the circular and noncircular cylinders are equal when the orientation of one of the principal axes is 0.9°. Apparently, this is the preferred cylinder orientation when grasping noncircular cylinders. At 60 cm, the preferred hand orientation for grasping the circular cylinder was –25.8° rather than –2.4°. We can estimate what we expect to happen for noncircular cylinders at 60 cm by shifting all hand and cylinder orientations for a distance of 30 cm by the difference between these two orientations (–23.4°). The resulting estimate of the offset is $-0.24*23.4–3.1 = –8.7°$, which is close to the fitted value of $-10.5°$. Thus it is quite likely that for both distances the offsets of the noncircular cylinders are largely determined by the preferred orientation for grasping as revealed by the way that subjects grasped circular cylinders.

In summary, our subjects choose one of the principal axes of the noncircular cylinders as the pick-up axis and grasped the cylinder by this axis with a systematic bias. But which of the two axes is chosen? To gain some insight, we define the probability that a cylinder is picked up by its major axis as the proportions of trials in which it is picked up within 45° of the major axis. In Fig. 5, the probability of choosing the major axis is plotted as a function of its orientation for each target distance. For a distance of 30 cm (◆), the probability is closest to unity for an orientation of 0° (when the major axis is in the sagittal direction). The probability gradually drops off to either side, becoming zero at an orientation of $\pm 90°$. A similar pattern is visible for a target distance of 60 cm (★) except that the distribution is shifted by about –30° (counter-clockwise).

We already found that the preferred orientation for grasping a circular cylinder is about –3° for a distance of 30 cm and about –26° for 60 cm (Fig. 4*B*, ◇ and ☆). These values agree quite well with the orientations for which the probabilities of grasping noncircular cylinders by their major axis are at their maximum (see Fig. 5). The preferred hand orientation for grasping circular cylinders probably depends on the relative comfort of the hand at each posture. Thus the comparable shift in probability distribution is probably also a consequence of the relative comfort of the hand as is the change in offsets for the noncircular cylinders.

Maximum grip aperture

For noncircular objects, the final grip aperture depends on the orientation of the hand at the time of contact. The question is whether the maximum grip aperture depends only on the

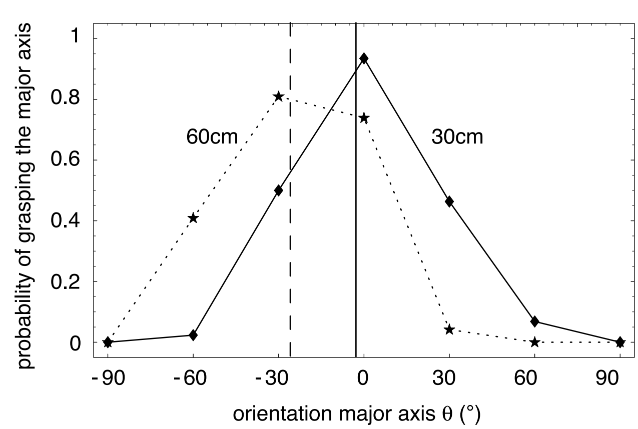

FIG. 5. Probability that a noncircular cylinder is picked up by its major axis as a function of its orientation. The preferred orientations for picking up the circular cylinder are shown for a distance of 30 cm (—) and 60 cm (- - -).

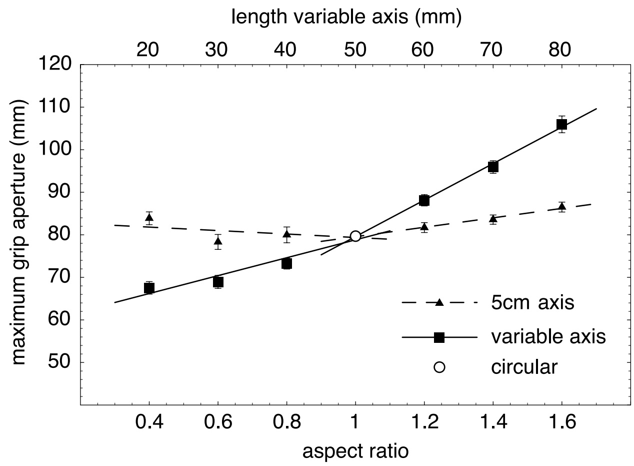

FIG. 6. Maximum grip aperture as a function of the aspect ratio when grasping along the 5 cm-axis (▲) or the variable axis (■). ○, the maximum grip aperture for the circular cylinder. Each symbol is the average value across all subjects, orientations and target distances. The error bars indicate the SEs. The lines are linear fits for aspect ratios ≤1 and ≥1 for each axis.

dimensions in the direction of the final grip. To study the relationship among grip aperture, target dimensions, and hand orientation, we plot the maximum grip aperture as a function of aspect ratio (Fig. 6). The corresponding length of the variable axis is indicated on the upper horizontal axis. The ▲ correspond to picking up the cylinders at orientations closest to their 5-cm axes and the ■ to picking them up at orientations closest to their variable axis. The maximum grip aperture for the circular cylinder (aspect ratio 1) is indicated as a separate point (○) because it does not have principal axes and, consequently, it belongs to both (or neither) of the other data groups.

It is conceivable that when the cylinders are grasped by their short axis, the protruding parts of the orthogonal major axis act as obstacles, giving rise to larger grip apertures. We therefore fit separate lines for aspect ratios ≤1 and ≥1 (see Fig. 6). For grasps along the 5 cm axis, we find slopes of -0.08 ± 0.06 (aspect ratio ≤1) and 0.22 ± 0.05 (aspect ratio ≥1). For grasps along the variable axis, we obtain 0.42 ± 0.05 (aspect ratio ≤1) and 0.86 ± 0.06 (aspect ratio ≥1). This shows that the maximal grip aperture depends on which axis is grasped and that the size of the other, orthogonal axis does matter. For the reason mentioned in the preceding text, we expect an increased maximum grip aperture when the orthogonal axis is longer than the axis that is grasped. When grasping the 5 cm axis, the orthogonal axis is longer than the grip axis for aspect ratios >1. And indeed, the increase in grip aperture with object size is significantly larger for aspect ratios ≥1 than for aspect ratios ≤1 [the slope difference is 0.30 ± 0.08; $t(455) = 3.96$; $P < 0.0001$]. Similarly, when grasping the variable axis, the orthogonal axis is longer for aspect ratios <1. In this case, the increase in maximum grip aperture with object size is significantly reduced [the slope difference is 0.44 ± 0.08; $t(444) = 5.31$; $P < 0.0001$].

Time course of grasping

The cylinder's shape and its orientation are reflected in the way that the cylinder is picked up. The hand orientation is adjusted to one of the principal axes and the maximum grip aperture to the length of the grasped axis. The maximum grip aperture correlates well with the final grip aperture. This is not surprising because the grip aperture reaches its maximum at the very end of the grasping movement (see Fig. 7). Although the maximum grip aperture occurs at ~70% of the movement time, this takes place at >95% of the total distance. We are interested in determining how early in the movement the final grasp can be predicted: do the hand orientation and grip aperture start to adjust at the movement onset or only later as the hand approaches the object? To address this question, we examined the correlations between the hand's orientation at different times during the movement and the final hand orientation. By definition, the correlation will be close to 100% at the end of the movement. To be able to compare different stimulus conditions, we select points in relation to the normalized traversed distance. Spatial (rather than temporal) parameters have been used before for such normalization (e.g., Haggard and Richardson 1996; Haggard and Wing 1998). The advantage of doing so is that corresponding points are easier to define. The normalized traversed distance is defined as the distance between the starting position and the average position of the tips of the index finger and thumb divided by the distance between the starting position and the position of the center of the target.

In Fig. 7, *top*, the hand orientation is shown as a function of the traversed distance. This is shown for two subjects (*JD* and

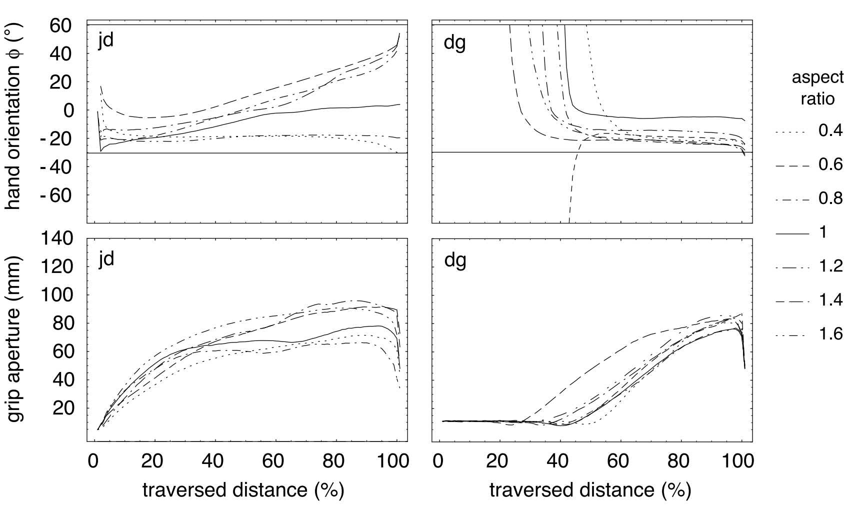

FIG. 7. Example traces of the hand orientation (*top*) and grip aperture (*bottom*) vs. the traversed distance for *subjects JD* (*left*) and *DG* (*right*). The different traces in each graph correspond to the different aspect ratios. The cylinders were placed at a distance of 30 cm and had an orientation of –30°.

DG) for a distance of 30 cm and an orientation of −30°. The lines correspond to the different aspect ratios of the cylinders. For *subject JD*, the hand orientation changes gradually from the very beginning of the movement to its final value. It can be seen that for noncircular cylinders, the final hand orientations approach the orientations of one of the principal axes (60 or –30°). For most subjects, the pattern was very similar. *Subject DG* (*right*), however, only opened her hand after traversing about half the total distance, so the hand orientation is undefined in the first half of the movement. As soon as her hand opens, its orientation is close to one of the target's principle axes.

In Fig. 7, *bottom*, the grip aperture is shown for the same trials. For *subject JD* (*left*), the grip aperture gradually increases until ~90% of the distance has been traversed, after which he closes his fingers on the target cylinder. The same applies for most other subjects. For *subject DG* (*right*), who only opens her hand after about half of the distance has been traversed, the pattern is similar but only from the moment that she starts to open her hand.

On average, the movement time is 1.0 ± 0.1 s. It differs considerably between subjects: 0.81 ± 0.01 s for the fastest and 1.55 ± 0.02 s for the slowest subject. The average movement time is affected significantly by the target distance [0.99 ± 0.01 s for the nearer and 1.09 ± 0.01 s for the further distance; $F(1,480) = 120.0$, $P < 0.001$]. Despite the differences in movement time between subjects, this influence of distance is always ~0.10 s and, consequently, there is no significant interaction between the factors subject and target distance. The only other significant effect is the interaction between aspect ratio and cylinder orientation [$F(30,380) = 1.98$, $P = 0.0018$]. This reflects the fact that the principal axis closest to the preferred orientation is grasped quicker than the other one. Given that the cylinders are placed either 30.0 or 42.4 cm from the starting position, the above-mentioned movement times imply an average speed of 30.3 and 38.9 cm/s for the nearer and further target distance, respectively. The associated peak tangential velocities are 84 and 104 cm/s, respectively.

In Fig. 8*A*, we show the difference between the mean hand orientations when the elliptical cylinders are grasped at the minor and major axes as a function of the target distance. Because the cylinder orientation varied, we have to calculate the difference in hand orientation before averaging. The mean difference in hand orientation was obtained by averaging these differences across all subjects, target distances, aspect ratios (excluding 1), and cylinder orientations. The result is shown in Fig. 8*A* as a function of the traversed distance (—). The SE was determined from the variability in the differences in hand orientation for each subject individually and then averaged across subjects. The SE obtained in this way is a measure of the accuracy of the average subject, ignoring individual differences (- - -). The difference in hand orientation is almost a straight line, although it curves upward at the end. It runs from zero toward its final value of 71 ± 7°. The fact that the final difference is not 90° reflects the fact that the gain of hand orientation to cylinder orientation is only 76% (see description of Fig. 4*A*). From the SE, one can estimate the 95% confidence interval [multiply by $t_{0.975}(190) = 1.97$]. We find that after 15% of the traversed distance, the hand orientations for grasping the minor and major axis are significantly different. *Subject*

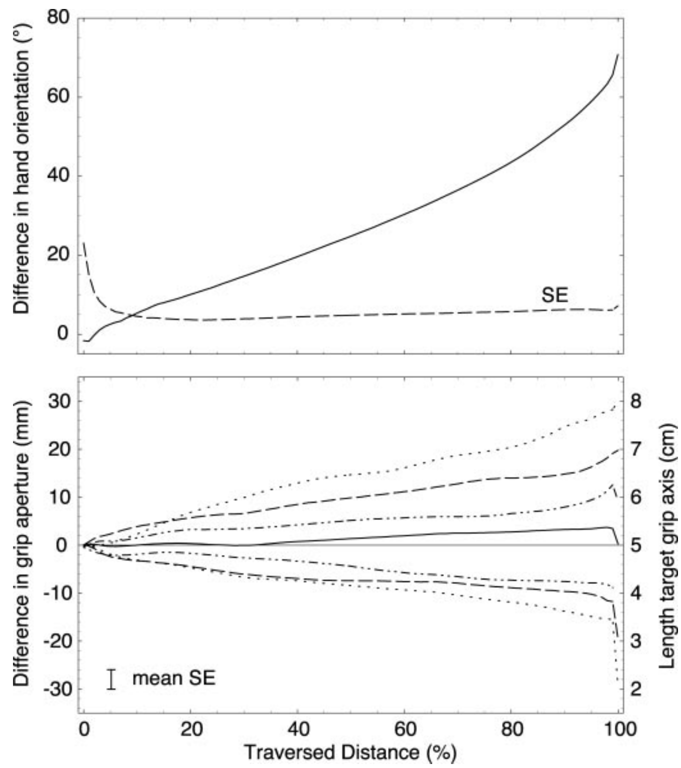

FIG. 8. Time course of the effect of cylinder shape and orientation on the grip formation. *A*: difference in hand orientation between grasping the minor and major axis. —, the mean difference as a function of the traversed distance; - - -, the SE. *B*: difference between the mean grip apertures for grasping the elliptical cylinders and the circular cylinder. Each line is the mean of all traces with a final grip aperture that lies within 5 mm of the corresponding target axis length.

DG was excluded because she kept her fingers together during the first half of the movement, which results in undefined hand orientations. A major drawback of analyzing the data in this way is that one needs at least two grasps at the major axis and two at the minor axis for each subject and cylinder orientation. This is only the case in 17 out of 42 possibilities (7 subjects × 6 orientations), so all other grasps are not considered in Fig. 8*A*. Another problem is that one cannot analyze the grip aperture in the same way because the final grip aperture also depends on the aspect ratio. Instead, we determined the mean grip aperture as a function of the traversed distance for each length of the target axis (Fig. 8*B*). The length of the principle axis varies from 2 to 8 cm in steps of 1 cm, so the final grip aperture will vary correspondingly. We therefore averaged all the traces for which the final grip aperture falls within ±5 mm of each of the axis lengths. We obtain Fig. 8*B* by subtracting the values for the circular cylinder from those for the elliptical cylinders. Each line runs from zero toward its final value, which is equal to the mean final grip aperture minus 50 mm. The average SE associated with each line is 2 mm. All lines are almost straight except at the very end and they diverge after 15% of the traversed distance. The disadvantage of this method of analysis is that the final grip aperture is not necessarily distributed within ±5 mm of the corresponding axis length because subjects do not always grasp exactly along the principal axes, which undermines a meaningful error analysis.

The problems mentioned in the preceding text can be overcome by analyzing the correlations between the values of the grip aperture at a given percentage of the traversed distance and its final value. This method of analysis can also be applied to the hand orientation. Therefore we determined the linear correlation coefficients for 100 distances (0–99%). To obtain these values, the data were resampled using linear interpolation between the nearest data points. All trials for a given target distance were included in this analysis (7 aspect ratios × 6 orientations).

In Fig. 9, *top,* the correlation coefficient of the hand orientation is shown as a function of the traversed distance. This is shown for the same subjects as in Fig. 7 as well as for the mean of all eight subjects. The — correspond to a target distance of 30 cm and the - - - to a target distance of 60 cm. For *subject JD* (*left*), the correlation coefficient rapidly increases to a high value as the traversed distance progresses. For both distances, the correlation coefficient exceeds 70% (50% of the variance explained) after 34% of the total distance has been traversed. For *subject DG* (*middle*), the correlation is lower, especially in the first half of the movement. As mentioned before, *subject DG* kept her fingers against each other in the first half of the movement. As a result, the correlation is poor until 60% of the distance has been traversed. For the other subjects, the observed pattern is most similar to that of *subject JD.* In Fig. 9, *top right,* the mean of the correlation coefficients of all subjects is shown as function of the traversed distance. The mean correlation coefficient follows the same pattern as for *subject JD.* The mean correlation exceeds 70% after 37% of the total distance has been traversed.

In Fig. 9, *bottom,* the same graphs are shown for the correlation coefficients of the grip aperture. For *subject JD* (*left*) the correlation quickly rises to a level of ∼80% and remains approximately at that level until the grip aperture reaches its maximum (when the traversed distance is ∼95%, see Fig. 7). For *subject DG,* the results are different: the correlation is very variable for the first 40% of the movement because the grip aperture is ∼0 (see Fig. 7). From ∼60% of the movement, the correlation coefficient gradually increases to ∼90% near the maximum grip aperture. The other subjects' behavior was similar to that of *subject JD,* but usually with lower values of the correlation coefficient. The mean of all subjects therefore lies in-between the curves for *subjects JD* and *DG* (Fig. 9, *bottom right*). On average, there is no significant difference in correlation between the target distances of 30 and 60 cm.

To address the question of how early in the movement the grip aperture and hand orientation are affected by the different cylinder shapes and orientations, we can evaluate when the correlation coefficient becomes significantly different from zero. We use the statistic $t = R/s_R$, where $s_R = \sqrt{(1 - R^2)/(n - 2)}$ is the SE of the correlation coefficient with $n - 2$ df (Zar 1996). At a 95% confidence level, the correlation coefficient is significantly different from zero whenever this t statistic exceeds $t_{0.975}(82) = 1.99$. The SE is typically $s_R = 0.1$, so that the correlation coefficient is significant whenever R exceeds 0.2. For the hand orientation, we find that the correlation coefficient becomes significant after between 0 and 14% of the traversed distance, depending on the subject and the target distance. *Subject DG* is an exception for whom the correlation coefficient is not significantly different from zero until 57% of the traversed distance. The mean correlation coefficient is significant (using the mean number of trials per subject minus 2 for the degrees of freedom because we want to analyze the average subject) after 4% of the traversed distance (irrespective of the target distance). For the maximum grip aperture, the individual correlation coefficient is significant after between 0 and 81% of the traversed distance, where the highest values are again for *subject DG.* The mean correlation coefficient is significant after 14 and 7% of the traversed distance for a target distance of 30 and 60 cm, respectively. Both the grip aperture

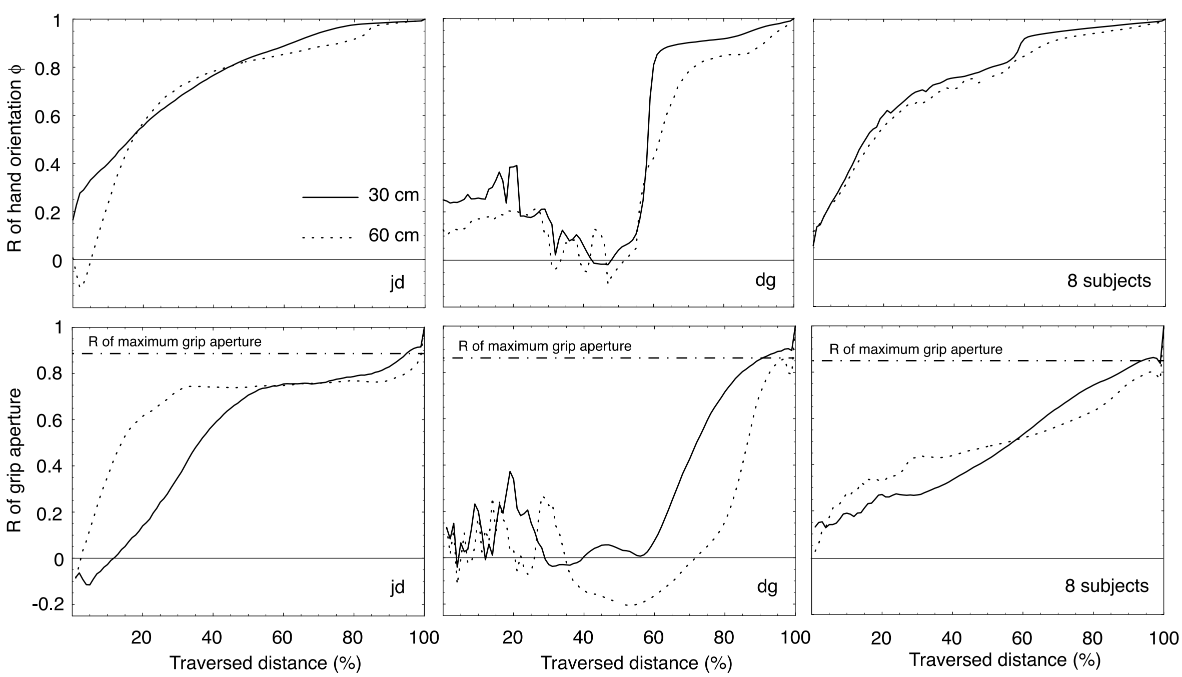

FIG. 9. Correlation coefficient (R) as a function of the traversed distance for the hand orientation (*top*) and grip aperture (*bottom*). The results for *subjects JD* and *DG* and the mean of all subjects are shown in the *left, middle,* and *right columns,* respectively. - · -, the correlation coefficients at the maximum grip aperture.

and the hand orientation appear to be affected by manipulations of the cylinder's orientation and shape from the beginning of the movement.

DISCUSSION

Selection of pick-up locations

When analyzing the orientation of the hand at the time of contact, we found that its final orientation is closely matched with the orientation of one of the cylinder's principal axes. The probability with which each of the principal axes of noncircular cylinders is chosen depends on their orientation and the distance from the subject. Note that the only stable way to grasp an elliptical cylinder is along the principle axes. For any other grip axis, the surface normals are not aligned with the grip axis, and the fingers will slip along the surface in the direction of the short principle axis. If friction is sufficiently high, the applied grip force generates a torque causing the cylinder to rotate. In 68% of the trials, subjects chose the minor axis (Fig. 3*A*). This makes sense because an error in aligning the grip axis with the minor axis results in a smaller misalignment of the surface normals than an error in aligning the grip axis with the major axis.

The average gain of orienting the grip axis to match changes in orientation of the cylinder was only 76%, with an offset of –3.1° for a distance of 30 cm and –10.5° for a distance of 60 cm. Thus there is a systematic bias which increases the further the cylinder's orientation departs from 13 and 44°, respectively. For the latter values (obtained from the linear fit), the cylinder orientations equal the hand orientations ($\phi - \theta = 0$). Although departures from the precision grip or a mismatch between the calculated and actual fingertip positions could have introduced a bias, one would expect such a bias to be similar in all conditions, which is not the case. Thus the subjects grasp the cylinders at unstable locations on the cylinder's surface, and they have to rely on friction and/or have to readjust their grip to be able to pick up the cylinders. The instability will be most severe for the largest and smallest aspect ratios, so one would expect more accurate grasps in these cases. This would mean that the gain should be closer to 100%. This is not what we find: the gain is independent of the aspect ratio (Fig. 4*A*).

When grasping the circular cylinder, the subjects are free to choose a convenient hand orientation. We found that the preferred hand orientation is about $-3°$ for a target distance of 30 cm and –26° for a distance of 60 cm (Fig. 4*B*). It was reported earlier that the movement direction largely determines the orientation of the hand at the time of contact (Bennis and Roby-Brami 2002; Roby-Brami et al. 2000). In our experiment, the movement direction changes from 90 to 45°, so we find a gain of 51% in adjusting grasp orientation to movement direction, which is close to the 57% obtained from the study by Bennis and Roby-Brami (2002).

The misalignment between the hand orientation and the orientations of the principal axes may have several causes. First of all, subjects may avoid uncomfortable grasps. Indeed, the observed range of hand orientations is only $\sim$130°. The preferred hand orientations for grasping circular cylinders at 30 and 60 cm is only partially explained by the change in movement direction, so at least part of the difference may be due to the comfort of posture. Thus subjects may tolerate less stable grasps to increase the comfort of their grasp. Another cause for the observed systematic alignment errors is that the grasping locations on the cylinder's surface may be incorrectly specified: the alignment errors may be due to misjudging the cylinder's shape.

Influence of the cylinders' shape

The fact that subjects grasp the cylinders at one of their principal axes implies that they judge the shape and orientation of the cylinders to select suitable grasping locations. It is known that the visual perception of shape is distorted in the depth dimension (for an overview, see Todd et al. 1995). Such a depth scaling affects the perceived orientation of our cylinders, so the planned grasping locations on the cylinder's surface may not be correct in the first place. The difference between the scaling of width and depth can be $\sim$50% (Bingham et al. 2000; Brenner et al. 1999; Johnston 1991), but these large distortions were found for isolated objects at eye height. In the present study, subjects could see the cylinders obliquely from above, on a well-illuminated surface, so we expect the errors in perceived orientation to be small.

Time course of grasping

During the movement, the hand orientation and the grip aperture change gradually to their final values. We used the traversed radial distance instead of time as the parameter for comparing different velocity profiles and movement times. The reliability with which the instantaneous value lets us predict the final hand orientation and grip aperture was estimated by calculating the correlation between these grasp parameters and their final values. For the hand orientation, we found that the correlation increases monotonically and exceeds 70 after 35% of the distance has been traversed. Note that the correlation coefficient is unaffected by systematic alignment errors, so that a high correlation does not mean that subjects make no systematic errors (which they do). The final grip aperture can only be predicted with the same reliability after $\sim$80% of the distance has been traversed. One of the reasons for this is that at 99% of the traversed distance the correlation coefficient of the grip aperture is still only 0.8. The remaining 36% of the variance is only eliminated when subjects close their fingers on the target cylinder. At that time, the hand is already in the final orientation. The difference is easily understood if one assumes that subjects reached for incorrect locations: errors in anticipating the grip aperture are automatically corrected at contact, whereas errors in the planned orientation are not corrected.

The correlation coefficients of both the grip aperture and the hand orientation increase gradually during the movement without any apparent transitions. Because the starting position is the same in all conditions, the correlation coefficients are zero at the start of the movement. The correlation coefficients are significantly different from zero after 4% of the traversed distance for the hand orientation and after 14% for the grip aperture. Therefore it appears that the preshaping of the hand starts immediately at the movement onset rather than at some point during the movement. Similar results were found when grasping rectangular disks in different orientations (Mamassian 1997). This is especially interesting in terms of the planning and control of the movement (for an overview, see Desmurget et al. 1998). Glover and Dixon (2001, 2002) argued that illusions of object size and orientation should primarily affect the planning of the movement whereas the on-line control corrects these errors by using different sources of information (such as the distance from the digits to the object's surface). Our results suggest that systematic errors in the final grasping locations arise when the movement is planned. These errors are not corrected with on-line control. Apparently, no "error signal" occurs during the movement even though the final grip frequently needs to be readjusted after the digits touched the surface. One explanation could be that the different sources of information for planning and on-line control result in the same errors. Another explanation is that both planning and control use the same sources of information (Smeets et al. 2002).

The present results fit into our new view on grasping (Smeets and Brenner 1999). The basis for this view is that the nervous system disentangles the information in a visual scene into more or less separate components (e.g., color, shape, position, etc.). The separation also holds for physically linked properties such as the distance between points on the surface of an object and the locations of these points relative to the observer. One of the consequences of such a separation is that an illusion of size will only affect a grasping movement if size information is actually used (Smeets et al. 2002). Thus if a grasp is accomplished by guiding the fingertips to appropriate locations on the target's surface, information about the perceived dimensions of the target will be irrelevant for the movement and size illusions will have no effect on grasping. Our results show that the formation of the grip mainly depends on the selection of target locations for the fingertips on the cylinders' surfaces. This selection depends on the perceived shape because the locations on the surface of an object for which a stable grip is obtained depends on its shape. Consequently, a distorted perception of a cylinder's shape will influence the movement from the start, and this will not be corrected while the movement is executed unless vision of the approaching hand provides new information. The systematic errors that we observed are consistent with the grasps having been planned incorrectly.

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