RESEARCH ARTICLE

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Grasping reveals visual misjudgements of shape

Abstract There are many conditions in which the visually perceived shape of an object differs from its true shape. We here show that one can reveal such errors by studying grasping. Nine subjects were asked to grasp and lift elliptical cylinders that were placed vertically at eye height. We varied the cylinder's aspect ratios, orientations about the vertical axis and distances from the subject. We found that the subjects' grip orientations deviated systematically from the orientations that would give the mechanically optimal grip. That this is largely due to misjudging the cylinder's shape (rather than to selecting a comfortable posture) follows from the fact that the grip aperture was initially more strongly correlated with the maximal grip aperture (which is related to the expected contact positions) than with the final grip aperture (which is determined by the real contact positions). The correlation with the maximal grip aperture drops from 0.8 to 0.6 in the last 1% of the traversed distance (11% of movement time), showing that the grip aperture was anticipated incorrectly (it is automatically "corrected" at contact). The grip orientation was already strongly correlated with the grip orientation at the time of maximal grip aperture, half way through the movement ($R \geq 0.7$), showing that the suboptimal grip orientations were planned that way. We conclude that subjects plan their grasps using information that is based on the misperceived shape.

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Introduction

When grasping and lifting an object, it is crucial that the fingertips are placed correctly so that one does not fumble (Mamassian 1997). Where the fingertips should be placed depends on the task constraints, but also on the object's shape. If we want to lift a vertically placed cylinder with a precision grip (only thumb and index finger), the grip axis should ideally pass through the cylinder's vertical axis above the centre of gravity. This leaves an infinite number of suitable grasp positions, which are further limited by constraints such as the relative comfort of the grasp (Rosenbaum et al. 2001). If the cylinder's circumference is elliptical rather than circular, suitable grasp positions are also limited by the fact that the grip axis will not be perpendicular to the surface for most grip orientations. The grip axis is only perpendicular to the surface for grasps along the ellipse's principal axes. If a cylinder (circular or elliptical) is not grasped at the ideal grip positions, the amount of friction determines whether the grasp is mechanically stable. If friction is sufficiently large, one can still lift the cylinder. If not, the fingertips will slip while the cylinder will rotate or move away. Thus, it is very important to consider the object's shape when grasping it.

Vision is a rich source of information about the shape of an object, but it does not always lead to a veridical percept (Todd et al. 1995; Brenner and Van Damme 1999; Johnston 1991), so visual errors can influence the way that people grasp objects (Hibbard and Bradshaw 2003; Watt and Bradshaw 2003). Similarly, misperceiving an object's size can influence grasping (Franz et al. 2003), but the evidence is still under debate (Aglioti et al. 1995; Smeets and Brenner 1999). Neurological evidence that perceiving shapes veridically is not crucial for grasping them correctly has been taken as a support for grasping having access to different, veridical, visual information about the object (Goodale et al. 1994; Goodale and Milner 1992). Since different aspects of the visual information do not have to be mutually consistent

(Smeets et al. 2002), any difference between performance on two tasks could be explained by assuming that different aspects of the visual information are used for the two tasks. For example, if grasping is accomplished by moving the fingertips to suitable locations on the target's surface then the distance between these points is irrelevant so that an illusion of size should have no effect (Smeets and Brenner 1999). Matters become more complicated if more than one aspect is relevant for the task. Glover and Dixon (2001) found that the effect of an illusion that altered the perceived orientation of an object, diminished as the hand approached the object. They concluded that different sources of information are used for movement planning and for on-line control. However, if the illusion affects the perceived orientation of the target's surface, but not the perceived locations at which to grasp the surface, the illusion's influence will automatically diminish as the hand approaches the target (Smeets et al. 2002).

We previously examined how an object's shape influences the preshaping of the hand and the selection of grip locations (Cuijpers et al. 2004). Subjects grasped elliptical cylinders that were placed at waist height. We varied the cylinders' aspect ratios, orientations and locations. Based on their shape, the ideal grip locations would be along the ellipses' principal axes. We found that the subjects' grip orientations covaried with the orientations of the principal axes, but they deviated systematically from the ideal grip locations. These suboptimal grip locations were probably planned that way, because the grip aperture and grip orientation were highly correlated to their final values early in the movement. We suspected that the systematic deviations were due partly to a deformation of perceived shape. If so, we could expect an interaction between the distance of the cylinder from the observer and its shape, because the perceived depth (along the line of sight) is a non-linear function of distance (Brenner and Van Damme 1999; Johnston 1991; Todd et al. 1995). However, the systematic deviations did not depend on either the cylinder's aspect ratio or its distance from the observer. The reason for this could be that the perceptual errors were too small in comparison with the influence of other factors such as comfort and the general variability.

The present experiment was designed to investigate the effect of systematic deformations of the perceived shape on grasping. We repeated our former experiment with the cylinders placed at eye height instead of at waist height. We expect the effects of perceptual deformations to be larger for grasping cylinders at eye height than at waist height, because the relevant dimension—the cylinder's elliptical circumference—extends in depth, which is the direction in which the perceptual deformations are usually found to be largest. In addition, the shape and orientation of elliptical cylinders is much harder to determine when they are placed at eye height than when they are placed at waist height. In the latter case, the entire elliptical outline is visible. In the former case, the elliptical outline of the top (and bottom) surface is only partly visible and at grazing angles.

The preceding arguments relate to systematic errors, but uncertainty about the cylinder's shape could also influence the grip orientation, assuming that subjects take the comfort of their grip orientation into account (Rosenbaum et al. 2001; Elsinger and Rosenbaum 2003), because the more uncertain the physically optimal grip orientation is, the more the statistically optimal grip orientation will be biased towards the comfortable grip orientation (Ernst and Banks 2002; Knill 2005). To understand what is physically optimal we need to look at the physical constraints in more detail. When grasping elliptical cylinders with a precision grip, the most stable grip is obtained when the digits are placed along one of the cylinder's principal axes (left column in Fig. 1). In that case, the grip axis passes through the centre of gravity and the grip force is aligned with the surface normals at the points of contact. If the digits are not placed along one of the principle axes, the surface normals will not be aligned with the grip axis. In that case, a stable grip can still be obtained if the fingertips exert equally large forces in opposite directions along the grip axis (middle column in Fig. 1). Friction cancels the tangential component. If there is not enough friction, the tangential component is only partially compensated for so that the fingers will slip towards the minor axis (bottom right graph in Fig. 1). In addition, the cylinder will experience a torque and/or a net force causing it to rotate and/or move away, because the forces acting on the cylinder are no longer aligned with the grip axis (top right graph in Fig. 1).

The above reasoning implies that grasping an elliptical cylinder by its minor axis is a safer choice, because a small error in grip orientation tends to correct itself when grasping the minor axis, whereas a small error tends to augment itself when grasping the major axis. The uncertainty about cylinders' shapes and orientations is expected to be larger at eye height than at waist height. We therefore start by examining whether subjects have a stronger tendency to grasp the cylinder along the minor axis when it is at eye height than when it is at waist height.

Methods

The methods were very similar to those of our previous study (Cuijpers et al. 2004) so that we could directly compare the results. To compare the data of the two experiments, we also applied the new analyses developed for the present data to the data of the previous study. The main difference between the studies was that the positions of the cylinders relative to the subject were different. This study is part of an ongoing research program that has been approved by the local ethics committee.
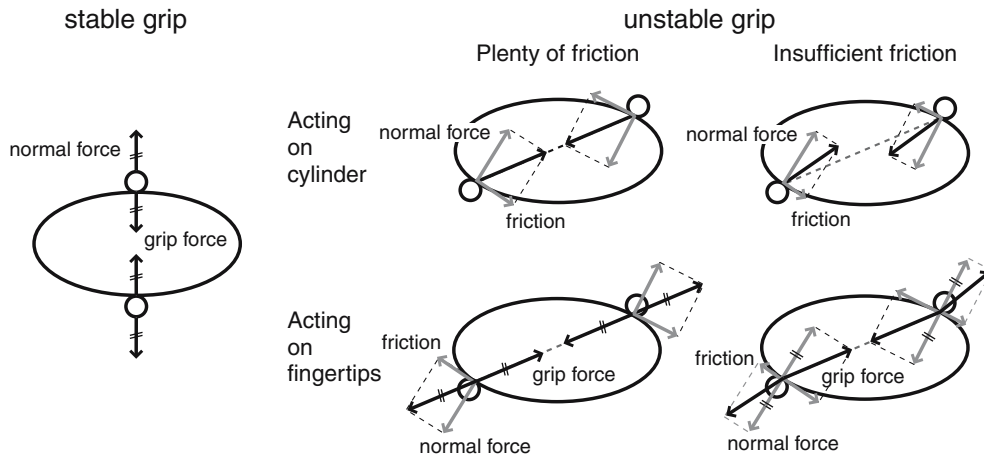
Fig. 1 When grasping an elliptical cylinder, a stable grip is obtained if the grip force is aligned with the surface normals and the grip axis passes through the cylinder's centre of gravity (*left*). For other grip locations, the grip can be stable if friction is large enough (*middle column*). Otherwise, the tangential component of the grip force is not completely compensated for and causes the cylinder to move and the fingers to slip towards the minor axis (*right column*). The *black arrows* indicate the forces acting on the cylinder (*top row*) and fingertips (*bottom row*) and the *grey arrows* indicate normal and tangential components

Subjects

Nine subjects participated in the experiment. They all had normal or corrected-to-normal visual acuity. Stereo acuity was tested to be better than 60″ for all subjects except PA and JS. As we were interested in the effects of visual errors on grasping and expected stereo-blind subjects to make large errors, we deliberately included these subjects. It turned out that these subjects behaved very similarly to the others in most respects. Most subjects were familiar with the task because they had also participated in our previous study (Cuijpers et al. 2004). Except for the authors EB and JS, the subjects were unaware of the specific questions that we wanted to answer. All subjects were right-handed.

Task

The subjects' task was to grasp vertical cylinders and to move them to another location using their thumb and index finger only (precision grip). The subjects were instructed to move at a comfortable pace. No instructions were given concerning the accuracy of the movements. The cylinders were placed at eye height in front of the subject at one of two distances (15 and 45 cm). Whenever the cylinders were placed at the nearer location the subjects had to pick them up and move them to the further location, and vice versa. The cylinder's shape and its orientation about the vertical axis were varied across trials.

Experimental design

We used seven 10 cm tall cylinders with an elliptical circumference. One of the principal axes of the elliptical circumference was always 5 cm whereas the other was varied from 2 to 8 cm in steps of 1 cm (so that one cylinder was circular, see Fig. 2a). The cylinders were made of white plastic (delrin) and their weights ranged from 110 to 440 g (density 1.40 g/cm^3). They were placed on a table with a white surface, either 15 or 45 cm from the edge at which the subject was seated and 5 cm
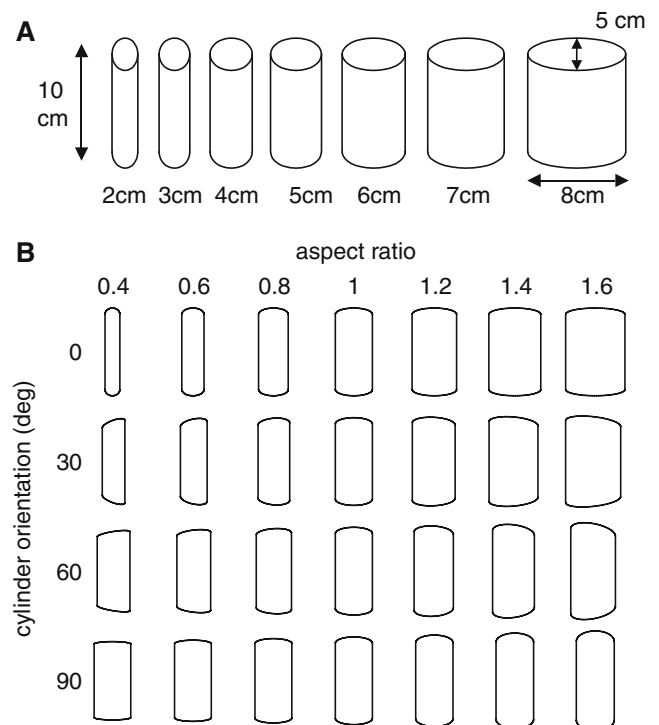

Fig. 2 Schematic drawing of the cylinders used in our experiment (**a**) and their contours when viewed at eye height from a distance of 15 cm (**b**)

from the edge on the subject's right (Fig. 3). This geometry made sure that all subjects could reach the furthest objects and that they could freely move their right arm. The cylinder locations were marked on the table but these marks were invisible when a cylinder was present. The cylinders' orientation was varied from $-60°$ to $90°$ in steps of $30°$, where counterclockwise is defined as positive and where $0°$ corresponds to the orientation in which the cylinder's major axis is aligned with straight ahead. In order to accurately position and orient each cylinder, we used a video projector. In-between trials, an image of an ellipse was projected from above in such a way that when the cylinder was placed correctly the ellipse coincided precisely with the top of the cylinder. The subjects sat behind the table in such a way that their eyes were approximately 5 cm above the table's surface. Thus, subjects could only see the cylinders from the side. Figure 2b shows the cylinder's contours for a viewing distance of 15 cm (the $-30°$ and $-60°$ orientations are mirror symmetric to the $30°$ and $60°$ orientations, respectively). The starting position for each grasp was located 10 cm below the table's surface, and 30 cm to the right of the nearer cylinder location (Fig. 3). The tip of a 5 cm tall stalk, which the subject could hold between her/his thumb and index finger, served as the starting position. The stalk was mounted at the corner of a wooden board (15 cm below the table's surface) which also served as a hand rest between trials.
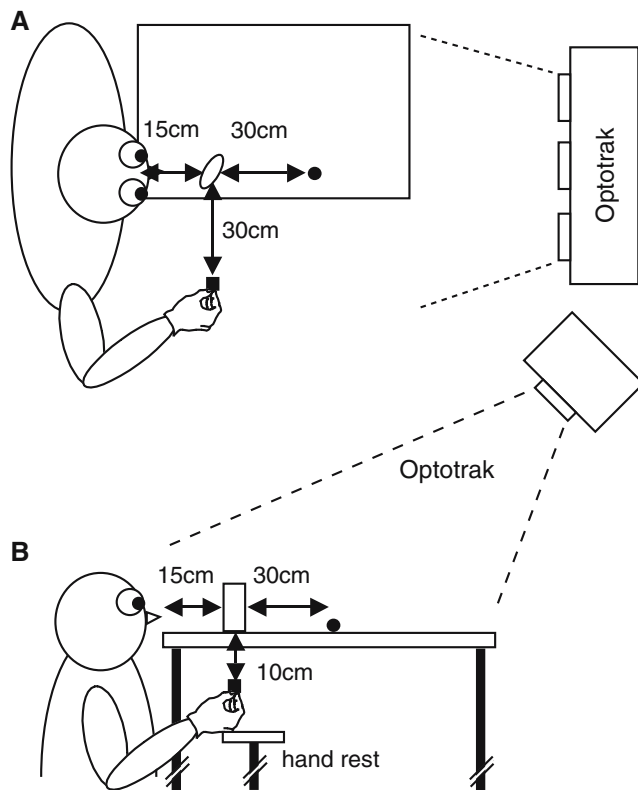

Fig. 3 Schematic drawing of the top (**a**) and side view (**b**) of the experimental set-up

We measured the position of the tips of the thumb and index finger using an Optotrak 3020 camera system. We attached Infrared Emitting Diodes (IRED) to each fingertip by means of two "antennae". Each antenna consisted of a metal stalk (about 5 cm length and 1 mm diameter) and a perspex square ($30 \times 30 \times 1$ mm^3) in the corners of which three IREDs were embedded. The purpose of these antennae was to prevent occlusion of the IREDs by the hand or the cylinder. The antennae were taped to the distal phalanges of the thumb and index finger while taking care that the finger pads remained free. The antennae were bent in such a way that the IREDs were visible for the Optotrak for as wide a range of hand postures as possible. During each trial, the Optotrak recorded the three-dimensional coordinates of all six IREDs with a sample frequency of 250 Hz.

Procedure

Six subjects participated in four sessions and three subjects in three sessions of about half an hour. Usually the sessions for a single subject were held on different days. Each of the 84 configurations (seven shapes, six orientations and two locations) was presented once during each session. The order of the trials was randomised for every session. After the antennae were attached to the distal phalanges of thumb and index finger, the subject held a separate IRED between her/his fingertips. A calibration recording was made in order to determine the relationship between the IREDs on the antennae and the positions on the fingertips indicated by the separate IRED.

Before each trial, the subject had to move his or her hand to the starting location and close his or her eyes. The experimenter projected the outline of an ellipse and placed the corresponding cylinder at the correct location with the correct orientation. When the cylinder was in place, the experimenter extinguished the projected image, gave a signal to the subject, and started the Optotrak recording. The subject opened her/his eyes, grasped the cylinder with a precision grip, placed it at the other location, moved back to the starting position and closed her/his eyes again. The same procedure was repeated for all 84 trials.

Data analysis

Primary analysis

After converting the positions of the IREDs on the antennae into positions of the fingertips, we determined the beginning of the movement and the moment that the cylinder was reached. To determine the movement onset, we first determined when each fingertip's distance from the starting location exceeded 1 cm and then traced the movement back in time until the tangential velocity reached a (local) minimum. The overall movement onset

was the moment that the first fingertip started moving. Similarly, the first minimum in tangential velocity after the first of the fingertips was within 0.5 cm of the cylinder's surface was considered as the end of the movement. Calculating the tangential velocity involves taking a derivative. This was achieved by convolving the data with the derivative of a Gaussian kernel (see Nielsen et al. 1997; Witkin 1983). The width of the kernel was three frames to either side, corresponding to a smoothing window of about 30 ms. The advantage of this method is that it does not amplify noise. The dependent variables that we analysed were the grip aperture and grip orientation. The grip aperture is defined as the Euclidean distance between the fingertips. The grip orientation ϕ is defined as the horizontal orientation of the grip axis. That is, the orientation of the orthogonal projection of the vector from the tip of the thumb to the tip of the index finger on the horizontal plane. We define the orientation θ of the elliptical cylinders as the orientation of their major axes. An orientation of $0°$ is parallel to the subject's mid-sagittal line and positive angles are defined as counter-clockwise.

Fitting straight lines to grip orientation data

The relation between the grip orientation ϕ and the cylinder orientation θ was approximately linear, both for grasping the major and the minor axis (see Fig. 6). To quantify this relationship, we used the following procedure: suppose that the grip orientations for grasps to the major axis can be modelled as $\phi = (1 + a)\,\theta_{\mathrm{major}} + b$, then

$$(\phi - \theta) = a\theta_{\mathrm{major}} + b. \tag{1}$$

Similarly, we can derive

$$(\phi - \theta) = a\theta_{\mathrm{minor}} + b, \tag{2}$$

for grasps to the minor axis. Since $\theta_{\mathrm{minor}} = \theta_{\mathrm{major}} \pm 90°$, we can express grasps to the minor axis in terms of the orientation of the major axis:

$$(\phi - \theta) = a\theta_{\mathrm{major}} + b \pm (1 + a)90°. \tag{3}$$

For given values of the slope a and offset b, we determined the squared differences between each point and the nearest line specified by Eq. 1 or Eq. 3. We obtained the parameters a and b by minimising the total sum of these residual squares.

Determining correlation coefficients

For both the grip aperture and grip orientation we calculated the correlation coefficients between different stages of the movement. We analysed the data separately for each subject and then took the average across subjects. First, the data had to be cast in a format that is comparable across all the different grasps. To do so, we normalised the movements using the normalised traversed distance. The advantage of using the normalised

traversed distance—instead of, for instance, the relative timing—is that the beginning and end of the movement can be determined much more accurately spatially than temporally (because the velocity is approximately zero). The traversed distance is defined as the Euclidean distance between the starting position and the midpoint between the fingertip positions. It is normalised by dividing it by the total traversed distance. The calculated normalised traversed distances of the individual measurements generally do not coincide between any two movements. The grip aperture and orientation were therefore re-sampled for 100 normalised traversed distances (from 0 to 100%) using linear interpolation between the nearest values.

Figure 4 illustrates the relationship between the traversed distance and the time from movement onset. Since both the total traversed distance and the movement time vary from trial to trial, we averaged the normalised time from movement onset for each of 100 values of the normalised traversed distance, where the normalised time is the ratio of the time from movement onset to the movement time. We did this separately for the two distances of the cylinders from the subject. The results are shown in Fig. 4 for the cylinder distances of 15 cm (solid line) and 45 cm (dashed line). The traversed distances and times from movement onset are expressed in millimetres and seconds, respectively. These values were obtained by multiplying the normalised traversed distances and the normalised times by the means of the total traversed distance and the movement time, respectively. From Fig. 4, it is clear that the movement is very slow at the beginning and the end. The maximum grip aperture occurs at approximately 95% of the traversed distance (see Results). This corresponds to 76% (77%) of the movement time for a distance of 15 cm
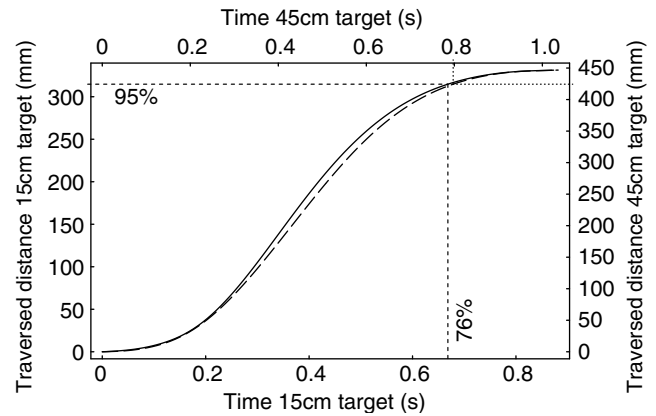

Fig. 4 The traversed distance as a function of the time from movement onset is very similar for each distance of the target. The *solid and dashed curves* indicate the means of all trials for cylinders at 15 cm (*lower-left axes*) and, respectively, 45 cm (*upper-right axes*) from the subject. At the time of maximum grip aperture, the traversed distance is approximately 95% of the total distance. This corresponds to about 76% of the movement time for a distance of 15 cm of the cylinder from the subject and 77% for a cylinder distance of 45 cm (*dotted lines*)

(45 cm) from the subject (Fig. 4). The similarity of the two curves shows that the grasping kinematics are similar for the two cylinder distances after normalisation.

Having normalised our data, we proceeded to calculate correlation coefficients (R). For each of the 100 normalised traversed distances, we determined the correlation between the parameter values at that distance and values at the time that the grip aperture was maximal (as determined separately for each movement trajectory). The correlation coefficients were calculated in this way for each subject individually and then averaged across subjects. To test whether the correlation coefficient is significantly different from zero we use the statistic $t_R = R/s_R$, where $s_R = \sqrt{(1 - R^2)/(n - 2)}$ is the standard error of the correlation coefficient with $n-2$ degrees of freedom. Under the null-hypothesis that $R = 0$, this statistic follows a Student's t distribution (Zar 1996).

Error convention

Data values and their associated errors are indicated as mean ± standard error, unless stated otherwise.

Results

Final grip orientation

First, we need to verify that subjects try to grasp the cylinders by their principal axes. The probability distribution of the grip orientations (ϕ) relative to the orientations of the cylinder's major axis (θ) is shown by the solid curve in Fig. 5. The data from all aspect ratios except 1 and both distances of the cylinder from the subject are included. The distribution was smoothed using a Gaussian kernel of unit area and a half width of 2.5°. The distribution is bimodal with peaks centred at −5° and 83°. These values are close to the expected orientations of 0° and 90° for grasping the major and minor axis, respectively. The areas under the peaks are not equal. If we separate the peaks at the minima between them (at 39° and 133°), we find probabilities of 39 and 61% for choosing the major and minor axis, respectively. For comparison, we also included the results that we obtained in our previous study when the cylinders were placed at waist height (Cuijpers et al. 2004; dashed curve). The peaks in that study appear at very similar locations (−3° and 85°) but they are taller and narrower. The probability of choosing the more stable minor axis was larger in the previous study (68%). Thus, subjects did not have the stronger tendency to choose the more stable minor axis for targets at eye height that we would expect if subjects compensate for the increased uncertainty about the cylinder's shape.

The distribution of grip orientations depends on the cylinder's orientation, aspect ratio and location. The systematic pattern is most clearly expressed by plotting
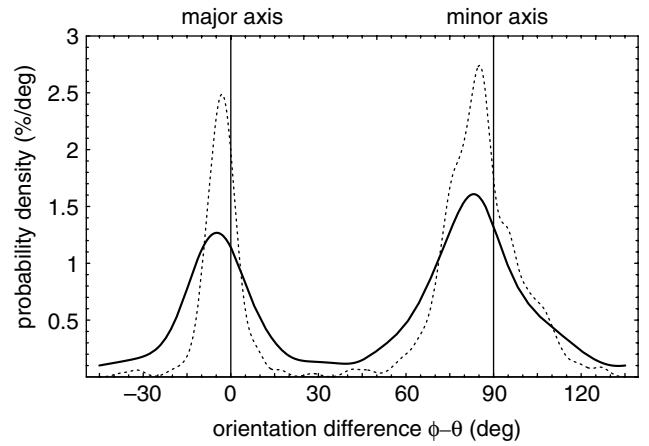

Fig. 5 Smoothed probability distribution of the grip orientations relative to that of the cylinder's major axis, both for cylinders at eye height (*thick, solid line*) and waist height (*thin, dashed line*). The distributions include all data apart from that of the circular cylinder

the difference between the final grip orientation and the orientation of the cylinder's major axis ($\phi-\theta$) as a function of the cylinder's orientation (θ). Some typical examples are shown in Fig. 6. This figure shows the results for all grasps that subjects JD and JM made to all non-circular cylinders when they were placed at distances of 15 and 45 cm. If the cylinders had all been grasped along their major axes ($\phi = \theta$), the points would fall on the dashed horizontal line at 0°. Similarly, if all grasps had been along the minor axis, the points would fall on the dotted horizontal lines at ±90°. Figure 6 shows that the actual grip orientations scatter along three lines, but they have a clear negative slope. The negative slope indicates that a change of the cylinder's orientation gives rise to a slightly smaller change in grip orientation. To quantify these slopes, we fit straight lines to the data using the procedure described in Methods (Eqs. 1, 3).

We determined the slopes separately for each subject, aspect ratio and target distance. In Fig. 7a, the resulting values for the slope (parameter a in Eqs. 1, 3) are shown as a function of the aspect ratio, averaged across subjects. This is shown separately for the two target distances. If subjects had followed the orientation of the cylinder perfectly the slope would be zero. If they had not followed it at all the slope would have been −1.

The slopes that we obtained are significantly more negative for aspect ratios close to 1 than they are for the smallest and largest aspect ratios. An ANOVA applied to the slopes of all elliptical cylinders with distance, aspect ratio and subject as factors, revealed a main effect of aspect ratio [$F(5,40) = 34.52$, $P < 0.001$]. The way the slopes depend on the aspect ratio does not differ between the two cylinder distances (there is a main effect of distance $F(1,8) = 21.21$, $P = 0.002$, but no interaction with aspect ratio [$F(5,40) = 0.466$, $P = 0.799$]. The mean difference between the slopes at a distance of 45 cm and at a distance of 15 cm is 0.090 ± 0.016. No such difference

Fig. 6 Grip orientations relative to the major axis ($\phi-\theta$) shown as a function of the orientation of the major axis (θ). The *solid lines* indicate linear fits (see the text for details). The fitted equation of the centre line is indicated in the *lower left corner* (Eq. 2). The other lines are offset by $\pm(1+a)90°$ (see Eq. 3). The *dashed lines* indicate grasps along the major axis, and the *dotted lines* indicate grasps along the minor axis. The data shown here are for subject JM (*left column*) and subject JD (*right column*) when the cylinders were placed at a distance of 15 cm (*top row*) and 45 cm (*bottom row*). The data include all aspect ratios except 1
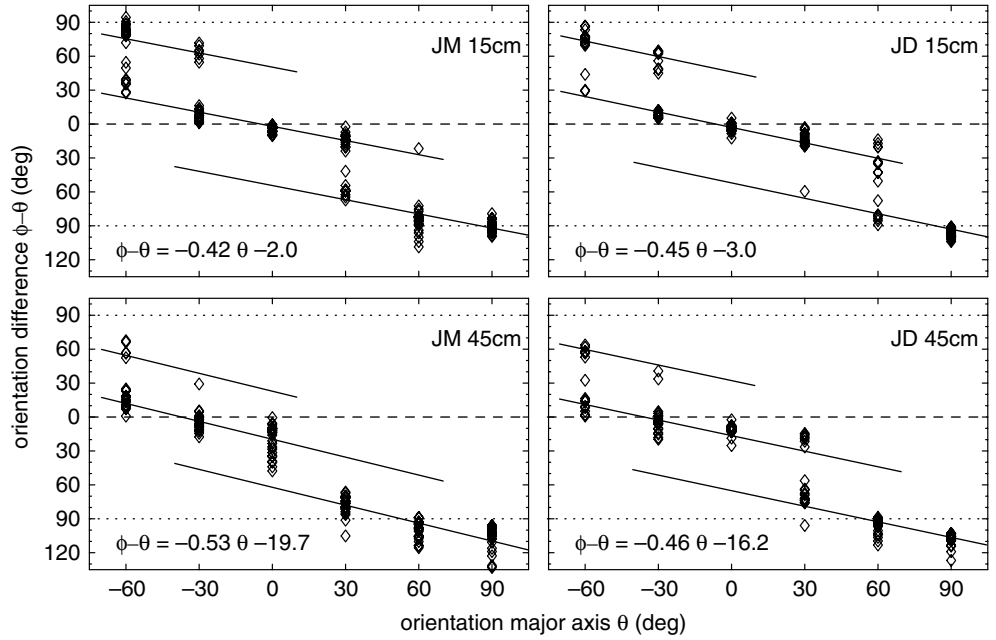
was observed in our earlier study when the cylinders were placed at waist height (Cuijpers et al. 2004, Fig. 4a). The slopes are also significantly [$t(197) = 7.290$ and $P < 0.001$] more negative for cylinders placed at eye height (-0.40 ± 0.015) than for cylinders placed at waist height (-0.24 ± 0.014).

The vertical offsets (parameter b in Eqs. 1, 3) are the orientation difference values of the centre lines in Fig. 6 for $\theta = 0$. The offsets b are shown for each aspect ratio and cylinder distance in Fig. 7b. The values of the offsets b depend on the cylinder's distance from the subject [$F(1,8) = 267.6$, $P < 0.001$]. There is also a significant interaction between the effect of distance and that of aspect ratio [$F(5,40) = 6.76$, $P < 0.001$]: the absolute difference between the offsets for the distances of 15 and 45 cm is larger for aspect ratios 0.8 and 1.2 than for the other aspect ratios. There is no main effect of the aspect ratio [$F(5,40) = 1.205$, $P = 0.324$].

From the residuals of the fits, we can estimate the remaining variability of the grip orientation. We find a standard deviation of $8.5 \pm 0.2°$ averaged across subjects and conditions. If we apply the same analysis to the data from our previous study, we find $5.7 \pm 0.3°$. Thus, the variability is larger for cylinders at eye height than at waist height [$F(107,95) = 2.24$, $P < 0.001$] probably because the perceived orientation is less reliable.

Comfortable posture

When grasping a circular cylinder the grip orientation is not constrained by its shape because all grip orientations are equally good in terms of the mechanical stability of the grip. However, subjects prefer one particular grip orientation, say ϕ_0, for each location of the cylinder. This could be because the bio-mechanical cost of
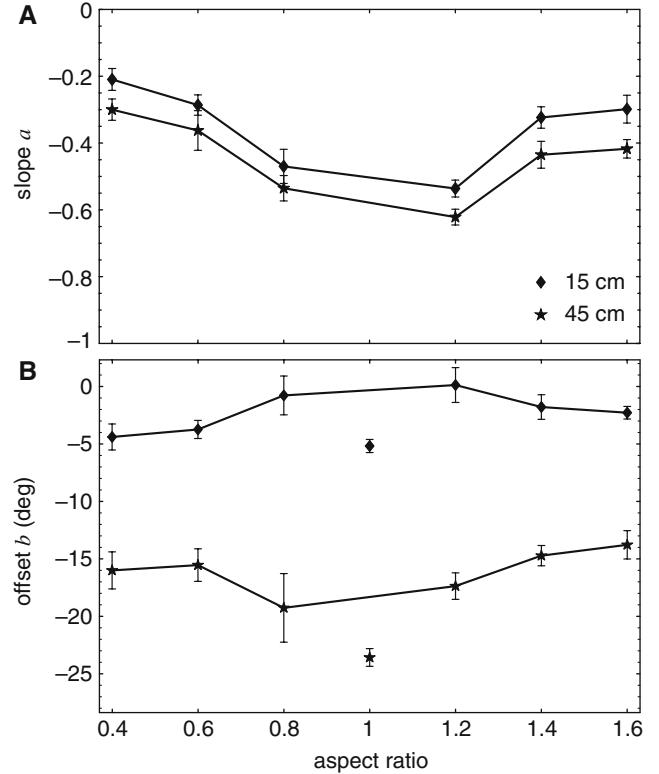

Fig. 7 The slope a (**a**) and offset b (**b**) of linear fits of deviations in grip orientation versus cylinder orientation (see the text for details) as a function of the cylinder's aspect ratio. Symbols show averages and *error bars* show standard errors across subjects. *Diamonds* 15 cm distance and *stars* 45 cm distance

grasping differs for different orientations, making some grip orientations more comfortable than others. Can this also explain the slopes and offset-values of the elliptical cylinders? If so, then the grip orientation should

correspond with one of the cylinder's axes when that axis is oriented at an angle ϕ_0. In Fig. 6, we see that this is the case for angles of 0° and −30° for the distances of 15 and 45 cm. These subjects grasped circular cylinders with grip orientations of −3° and −33° at these distances.

A more quantitative approach to this question is by assuming that the grip orientation (ϕ) at the time of contact is a weighted average of the cylinder's orientation (θ) and the most comfortable grip orientation (ϕ_0). Thus, $\phi = w\theta + (1-w)\phi_0$ for some weight w or, alternatively,

$$\phi - \theta = (w-1)\theta + (1-w)\phi_0. \qquad (4)$$

This is equivalent to Eq. 1, which we used to obtain the slopes and offsets in Fig. 7. The slope is $a = w-1$ and the offset is $b = -(w-1)\phi_0$. Thus, if the grip orientation is a weighted average of the most comfortable orientation and the real cylinder orientation, the offset will be linearly related to the slope:

$$b = -a\phi_0. \qquad (5)$$

Figure 8 shows the offset (b) as a function of the slope for each aspect ratio (a) and each distance of the cylinder (averaged across subjects). The relationships are approximately linear: the solid lines indicate the linear fits $b = (-13.0 \pm 2.2)\,a - (6.6 \pm 0.8)$ for 15 cm and $b = (10 \pm 5)\,a - (10.9 \pm 2.3)$ for 45 cm. The dashed lines show the predicted relationships given by Eq. 5 for each distance of the cylinder. Equation 5 is clearly not supported by our data: the linear fits do not even pass near the origin or near ϕ_0 (when $a = -1$) for cylinders at 15 cm. Thus, a simple weighted average of the cylinder's orientation and the most comfortable grip orientation cannot account for the deviations from the principle axes.

Maximum grip aperture

The maximum grip aperture is a well-known indicator for the anticipated size of rectangular and circular
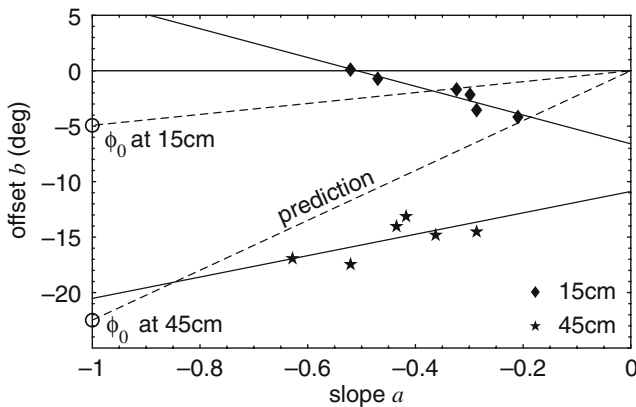
objects (Paulignan et al. 1997). Typically, a linear relationship is found between maximum grip aperture and object size with a gain of about 0.7−0.8 (Smeets and Brenner 1999). For our elliptical cylinders the 'object size' depends on the grip orientation at the time of contact. We can nevertheless estimate the gain of the relationship between the maximum grip aperture and object size by linear regression of the maximum grip aperture to the grip aperture at the time of contact. We find gains varying from 0.2 to 0.5 for different subjects (averaged across subjects the gain is 0.36 ± 0.03 and the average R is 0.53 ± 0.05). These values are exceptionally small compared to the range that is theoretically predicted and experimentally observed (Smeets and Brenner 1999). If we apply the same analysis to the data from our previous study, we find that the gains for grasping cylinders at waist height range between 0.5 and 0.8 (the average gain is 0.66 ± 0.03 and the average R is 0.80 ± 0.02). Thus, placing the cylinders at eye height reduces the gain of the scaling of grip aperture with object size considerably.

To investigate this further, we plot the maximum grip aperture as a function of the cylinder's aspect ratio (Fig. 9). Because one of the cylinder's principal axes has a fixed length of 5 cm and the other's length varies from 2 to 8 cm, we distinguish between grasps to the variable axis (bold squares) and grasps to the 5 cm axis (bold triangles). By grasps to the variable axis, we mean grasps whose end grip orientations lie within 45° of the orientation of the variable axis. The same applies to the 5 cm axis. Grasps to the circular cylinder are indicated by the bold circle. As expected, the maximum grip aperture for grasps to the 5 cm axis hardly depends on the aspect ratio. For grasps to the variable axis, the maximum grip aperture clearly depends on the aspect ratio. If we fit a straight line, we find a gain of -0.01 ± 0.03 for the

Fig. 8 Offset b as a function of the slope a for target distances of 15 cm (*diamonds*) and 45 cm (*stars*). The *circles* show the mean grip orientations ϕ_0 when grasping the circular cylinder. Linear fits (*solid lines*, see the text for details) and the model predictions assuming a linear weighting of comfort and grasp stability (*dashed lines*) are indicated. Symbols show averages across subjects
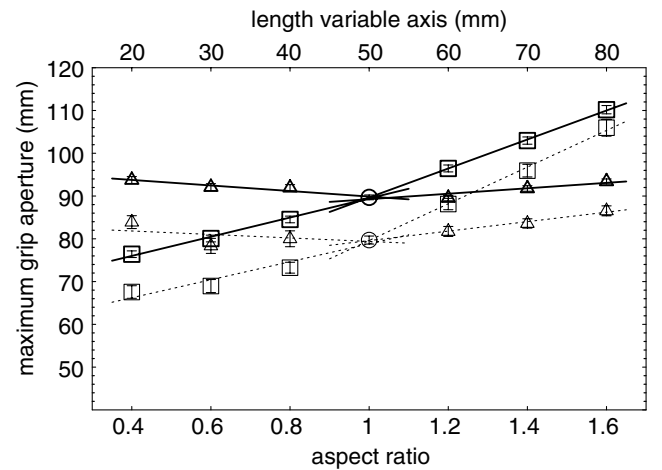

Fig. 9 Maximum grip aperture as a function of the aspect ratio for cylinders placed either at eye height (*thick symbols*) or at waist height (*thin symbols*). Each symbol is the average across subjects and conditions, the *error bars* indicate the standard error. *Squares* cylinders grasped by their variable axis. *Triangles* cylinders grasped by their 5 cm axis. *Circles* grasps to the circular cylinder

grasps to the 5 cm axis, which is not significantly different from zero ($P = 0.68$). For grasps to the variable axis, we obtain a gain of 0.57 ± 0.03, which is significantly larger than zero ($P < 0.001$). This value lies above the range of $0.2-0.5$ obtained when correlating with the final grip aperture, but it is still smaller than other experimentally observed values (Smeets and Brenner 1999). Comparing the two preceding analyses, we see that the maximum grip aperture scales better with the length of the nearest principal axis than with the final grip aperture [if we compare the mean gains of the two analyses, which we generated based on the pooled data of all subjects, we obtain: $t(2605) = 4.372$, $P < 0.001$].

It is conceivable that when a cylinder is grasped by its minor axis, the protruding parts of the orthogonal major axis act as obstacles. In that case, one would expect larger maximum grip apertures. We examined this possibility by separately fitting straight lines for aspect ratios ≤ 1 and aspect ratios ≥ 1 (see Fig. 9). For grasps to the 5 cm axis, we find a gain of -0.13 ± 0.03 for aspect ratios ≤ 1 and a gain of 0.13 ± 0.03 for aspect ratios ≥ 1 [the difference is 0.26 ± 0.04; $t(2092) = 6.44$, $P < 0.001$]. Similarly for the variable axis, we find gains of 0.45 ± 0.03 and 0.68 ± 0.03 for aspect ratios ≤ 1 and ≥ 1, respectively [the difference is 0.23 ± 0.05; $t(1854) = 5.04$, $P < 0.001$]. So only grasps towards the variable axis of cylinders with aspect ratios ≥ 1 (i.e. when the variable axis is the major axis) show a normal gain of increase in maximum grip aperture with object size. When grasping the minor axis, the orthogonal major axis probably acts as an obstacle, so that the scaling of the maximum grip aperture is a trade-off between a scaling according to the two axes.

For comparison, the results of our previous study (Cuijpers et al. 2004) are indicated by the thin symbols in Fig. 9. It is immediately clear that the present results (bold symbols) are very similar to our earlier results (thin symbols) except for a vertical shift of 9.4 ± 0.7 mm. Since the same cylinders were used in both experiments (and most of the subjects participated in both experiments), this shift is most likely due to an increased uncertainty about the cylinder's spatial properties. The gains are only significantly different for grasps to the variable axis when the aspect ratio is ≥ 1, where there is a difference in gains between grasping cylinders at eye height and grasping cylinders at waist height of -0.18 ± 0.08 [$t(981) = 2.37$, $P = 0.018$]. Grasping cylinders with a large aspect ratio by their variable axis also requires the largest grip openings, so it is possible that the lower gain for grasps to cylinders at eye height is because the maximum grip aperture approaches the largest possible grip aperture of the subjects.

Time course of prehension

The average movement time of all 2,772 trials is 0.96 ± 0.20 s (mean $\pm$ standard deviation, in this paragraph). We conducted a multi-way ANOVA with subject, aspect ratio, cylinder orientation and cylinder distance as factors. We found a main effect of subject [$F(8,2016) = 284$, $P < 0.001$]. The individual averages differ significantly, ranging from 0.83 ± 0.01 to 1.03 ± 0.02 s for eight of the subjects, but the subject JM had an average movement time of 1.23 ± 0.02 s. Movements to the nearer cylinder location are faster (by 0.15 ± 0.01 s) than to the further cylinder location [$F(1,2016) = 826$, $P < 0.001$]. There was also a main effect of aspect ratio [$F(6,2016) = 17.2$, $P < 0.001$]. Post-hoc testing with Tukey–Kramer's test revealed that the movement times are significantly longer for the three smallest aspect ratios (0.4, 0.6 and 0.8) than for the other aspect ratios (1, 1.2, 1.4 and 1.6). These differences in movement times of the individual comparisons are about 0.05 ± 0.02 s. There was no main effect of cylinder orientation [$F(5,2016) = 1.59$, $P = 0.16$]. Several interactions are also significant: the effect of aspect ratio is largest for a cylinder orientation of $-60°$ and a cylinder distance of 45 cm from the subject [aspect ratio $\times$ orientation, $F(30,2016) = 2.43$, $P < 0.001$; aspect ratio $\times$ orientation $\times$ distance, $F(30,2016) = 1.58$, $P = 0.023$]. The effects of distance and aspect ratio on the movement time also differ slightly between subjects, but these effects on the movement times are relatively small so we will not discuss them here.

Figure 10 shows some examples of the grip aperture (top row) and grip orientation (bottom row) as a function of the traversed distance. Each line is a representative trial for the condition in question. The grip aperture at the time of contact depends on the aspect ratio of the cylinder and the orientation in which it is grasped. In the upper panels of Fig. 10 the grip aperture is shown for different aspect ratios, for the cylinder at 15 cm from the subject with an orientation of 90° (so the cylinders were grasped by their minor axis, see Fig. 6). As is to be expected, the grip aperture is already larger for larger grasps well before reaching the maximum grip aperture. In the lower panels of Fig. 10, the grip orientation is shown for different orientations of the cylinder's major axis. The cylinder was 15 cm from the subject and its aspect ratio was 1.6. Again, the lines separate well before the cylinder is reached, despite the fact that the range of grip orientations is much smaller than the range of cylinder orientations.

To quantify the time course of prehension, we calculated the correlation coefficients as a function of the normalised traversed distance for both the grip aperture and the grip orientation (see Data analysis for details). We saw that the maximum grip aperture was more strongly correlated with the cylinder's shape than with the grip aperture at the time of contact. Assuming that this is because subjects misjudged the cylinder's orientation and/or shape, it makes sense to determine how the planned movement evolves by correlating parameter values at various times with respect to their values at the moment of maximum grip aperture (instead of at contact). We will do so for both grip aperture and grip orientation.

Fig. 10 Grip aperture (*top row*) and grip orientation (*bottom row*) as a function of the traversed distance for subject JM (*left column*) and JD (*right column*) when the cylinder was placed 15 cm from the subject. The different lines in each graph of the grip aperture data correspond to the different aspect ratios of cylinders. The orientation of the cylinder's major axis was 90°. The different lines in each graph of the grip orientation data correspond to the different orientations of the cylinder's major axis. The cylinder's aspect ratio was 1.6
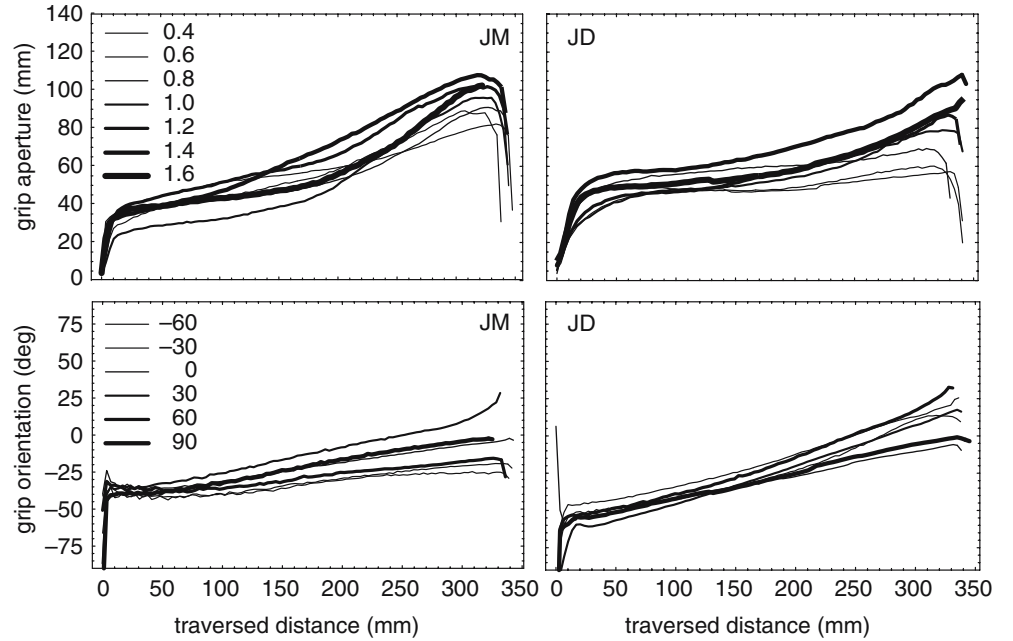
In Fig. 11a, the mean correlation coefficient between grip orientation and its value at the moment of peak grip aperture ($R_{\mathrm{orientation}}$) is plotted as a function of the traversed distance. The results of the present experiment using cylinders at eye height are indicated by the solid curve. The value of $R_{\mathrm{orientation}}$ increases almost linearly, and reaches a value of 0.9 at about 70% of the traversed distance (54% of the movement time, or about 0.47 and 0.56 s for a cylinder distance of 15 and 45 cm, respectively), after which it levels off to a value close to $R_{\mathrm{orientation}} = 1$. Note that a high correlation does not imply that the cylinders are grasped by their principal axes. In fact, the final grip orientations are considerably biased (Fig. 7). The mean correlation coefficient is significantly different from zero after 5% of the traversed distance [from this point on the statistic t_R exceeds $t_{0.975}(304) = 1.968$]. This corresponds to 16% of the movement time (about 0.14 and 0.17 s for a cylinder distance of 15 and 45 cm, respectively). The grey area denotes the range between the minimum and maximum values of the individual correlation coefficients for grasps to cylinders at eye height.

The large size of the grey area indicates that there are considerable individual differences. In particular, the lower boundary is due to one subject (DG) whose correlation coefficients are much lower than those of all other subjects. This is caused by the fact that she only opens her hand after about half of the distance has been traversed. Since the grip orientation is obviously very sensitive to noise for small grip apertures, the correlation coefficient is close to zero until the subject opens her hand. If we compare the results of the present study with the reanalysed data from our previous study (Cuijpers et al. 2004, dashed line in Fig. 11a), we see that the correlation coefficient increases much more slowly early in the movement in this study, and then starts catching

up after about 25% of the traversed distance (31% of the movement time). In the second half of the movement the correlations are more similar, but still smaller in the present experiment. This difference in comparison with the previous study indicates that subjects adjusted their movement more frequently for movements at eye height. This could have its origin in the different postures of the arm in the two studies, or in the difference in perceptual uncertainty.

Applying the same procedure to the grip aperture, we obtain Fig. 11b. The mean correlation coefficient (R_{aperture}) quickly rises to a value of 0.4 after which it increases approximately linearly to its maximum value of 0.97 at a traversed distance of 95% (77% of the movement time, or about 0.67 and 0.80 s for a cylinder distance of 15 and 45 cm, respectively). Note that the grip aperture does not have to reach its maximum at the same traversed distance for each grasping movement, so that the maximum value of R_{aperture} does not have to be 1. The fact that the maximum value of R_{aperture} is so close to 1 indicates that the grip aperture does reach its maximum at approximately the same traversed distance on most trials. The mean correlation coefficient is significantly different from zero after 2% of the distance has been traversed [from that point on t_R exceeds $t_{0.975}(306) = 1.9678$]. This corresponds to 11% of the movement time (or about 0.09 and 0.12 s for a cylinder distance 15 and 45 cm, respectively).

The correlation coefficient for grasps to cylinders at eye height (solid line) is clearly very similar to that for grasps to cylinders at waist height (dashed line) until 99% of the distance has been traversed (88% of the movement time, about 0.77 and 0.91 s for a cylinder distance of 15 and 45 cm, respectively). In the last 1% of the total traversed distance the correlation coefficient drops to a value of 0.6 for grasps at eye height while it
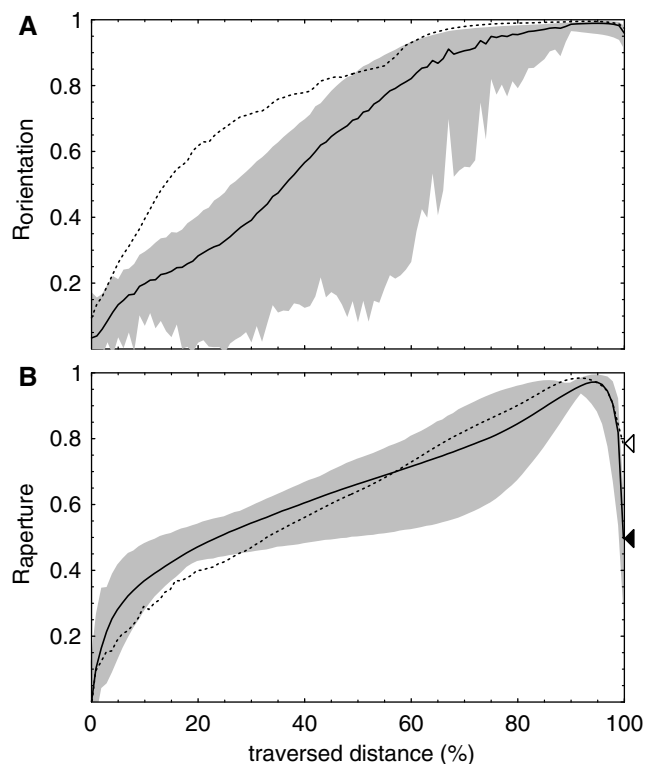
Fig. 11 a Correlation coefficient ($R_{orientation}$) of the correlation between the grip orientation at each traversed distance and the grip orientation at the moment of maximal grip aperture (*solid line*). **b** Correlation coefficient ($R_{aperture}$) of the correlation between the grip aperture at each traversed distance and the *maximum* grip aperture (*solid line*). The *triangles* indicate the correlations at the time of contact. **a, b** The *grey areas* denote the ranges of individual correlation coefficients. Data for cylinders at waist height are shown for comparison (*dashed lines*)

only drops to 0.8 for grasps at waist height. This means that at the end of the movement, there is an unexplained variance of $1 - 0.6^2 = 64\%$ compared to 36% for grasps at waist height. There was no such difference between the studies for the grip orientation. Apparently, the final grip aperture was anticipated incorrectly in the present experiment, so that the digits are either stopped "prematurely" by the cylinder or have to continue further than anticipated.

Discussion

For the perceived shape of the cylinders, the errors that we expect to see are compressions or expansions of depth extents (Brenner and Van Damme 1999; Johnston 1991; Todd et al. 1995). The visual information about the shape and orientation of the cylinders is primarily contained in the contours of the top and bottom edges, stereopsis and motion parallax. It has been shown that stereopsis and motion parallax are fairly weak cues for perceiving the shape of smoothly shaded cylinders in the absence of contour information and haptic feedback (Bülthoff and Mallot 1998). However, in our study, the

cylinders' contours are clearly visible providing both monocular and binocular information about shape. Since contour information is less salient at eye height than at waist height (because the top surface is no longer visible), the shape of cylinders at eye height is not only more likely to be subject to deformations but is also likely to be less reliable. Subjects also received haptic feedback, which allowed them to fine tune their performance in subsequent trials. It is unclear to what extent each source of information about the cylinder's shape and orientation is responsible for the grip formation, but we do know that these attributes were sufficiently clear for subjects to adjust their grips to the cylinders' dimensions.

Ideally, our elliptical cylinders should be grasped along one of their principal axes because then the mechanical stability is highest. Indeed, we observed that the distribution of grip orientations relative to the cylinder's orientation has two peaks which are centred on the orientations of the major and minor axes. These peaks are broader than those observed for grasps to cylinders at waist height (Cuijpers et al. 2004). The broadening of the peaks is largely explained by the fact that the distributions are less well aligned for the different cylinder orientations. We found that the distributions shift linearly as a function of the cylinder orientation (Fig. 6). This linear shift corresponds to the grip orientation having a gain of less than 1 with respect to the cylinder orientation (slope less than zero in Fig. 7). The gains are smallest for the aspect ratios closest to 1. We also found gains smaller than 1 in our previous experiment using cylinders at waist height, but the gains were smaller in the present study. In addition, the gains are now clearly modulated by the aspect ratio, which they were not in our earlier study (Fig. 4a in Cuijpers et al. 2004). The residuals were also larger, showing that by placing the cylinders at eye height we succeeded in making judgments of the perceived cylinder orientation less reliable.

The question that remains is whether our results are due to an increased perceptual uncertainty or to systematic changes in the perceived orientation. In the first case, the observed slopes and offsets need to be explained by some 'cue'-weighting scheme of object properties (available visually) and bio-mechanical constraints (available from prior experience). If the weights differ according to the reliability of each cue (Ernst and Banks 2002; Knill 2005), changed perceptual uncertainty could potentially explain our results. By interpreting the grip orientation at the time of contact as the weighted average of a comfortable grip orientation and a mechanically stable grip orientation, we can predict the interdependence between the slopes and offsets (Eq. 5). This equation holds independent of whether the weights depend on the reliabilities of each cue or not. Quantitatively, our results are not even close to Eq. 5. It is conceivable that a linear weighted average is too simple a model, but Fig. 8 does not suggest that second and higher order terms will improve the fit. Thus, we think

that the mismatch is due to a misperception of the object's shape causing a systematic change in the perceived orientation. One possibility is a linear scaling in depth, but such a scaling leaves the perceived orientation of cylinders that have a 0° or 90° orientation unaffected. The non-zero offsets in Fig. 7b show that this is not the case. A linear scaling also leaves the major and minor axes perpendicular to each other (for all cylinder orientations). We found that grasps to the major and minor axis typically differ by between 36° and 72° (90° multiplied by the slope + 1, with slopes ranging from −0.6 to −0.2; this is the deviation of the vertical distances between fit lines in Fig. 6 from 90°). Thus, a linear scaling in depth cannot be the whole story either.

Evidence for a perceptual origin of the grasping error is that the maximum grip apertures correlate better with the length of the nearest principal axis than with the final grip aperture. If the planned grip orientation were the weighted average of a comfortable orientation and a mechanically stable orientation, we would expect the maximum grip aperture to scale with the length of the planned grip axis, i.e. the final grip aperture. However, this is not the case, so apparently a different grip was planned. This is confirmed by our analysis of the time course of the grip aperture (Fig. 11b). The correlation coefficient for grasps at eye height drops in the last 1% of the movement relative to that for grasps at waist height. Thus, the final grip aperture was anticipated incorrectly.

For the maximum grip aperture, we find a nearly identical pattern to that for grasps at waist height (Fig. 9), but the grip aperture is 9.4 mm larger. This is what one would expect if subjects are less certain about the spatial properties of the cylinders (Smeets and Brenner 1999). We prefer this interpretation to assuming that the cylinders are perceived to be larger, because a consistent error of about 1 cm seems very unlikely considering that subjects receive haptic feedback when they grasp the cylinders. In contrast, it is likely that subject feel less certain about the cylinder's spatial properties when the visually perceived shape often turns out to be incorrect (as will become evident from the haptic feedback). This additional uncertainty does not affect the gain of the maximum grip aperture when expressed as a function of the length of the nearest principal axis (in line with theoretical predictions, Smeets and Brenner 1999). Therefore, it cannot explain the decrease in gain when the maximum grip aperture is expressed as a function of the final grip aperture. Although we found that subjects considered their uncertainty about the cylinder's shape, because they had a considerably larger maximum grip aperture for targets at eye height than for targets at waist height, they did not appear to compensate for this uncertainty by grasping the minor axis more often (Fig. 5).

From the preceding arguments, we conclude that grasps are planned to locations that deviate systematically from the ideal grip locations, because subjects incorrectly estimate the cylinder's orientation and shape.

Thus, grasping is influenced by perceptual deformations of shape. The grip orientation is not automatically corrected upon touching the cylinder's surface, so the correlation with the final grip orientation is quite high during the movement (because the object is grasped with the planned orientation of the digits). On the other hand, the grip aperture does correct itself upon contact, so that the (maximum) grip aperture does not correlate well with the final grip aperture (because it was anticipated incorrectly). The correlation coefficient is smaller for grasps to cylinders at eye height than at waist height because visual deformations are larger at eye height. Since the visual shape of an object depends on its distance from the observer, the systematic deviations should also depend on the object's distance, which was also the case. However, a simple compression in perceived depth is not enough to explain the results.

The fact that the planned grip locations deviate systematically from the ideal grip locations seems to be similar to Glover and Dixon's (2001) finding for a pictorial illusion of object orientation. In their study, the effect of the illusion diminished as the hand approached the target. However, in our studies the deviations of the grip orientation did not diminish and the grip aperture was corrected automatically by the contact itself. Apparently, visual information did not provide an error signal for the on-line control of the movement. We see no reason to doubt that planning and on-line control use the same source of information, rather than two different sources as Glover and Dixon (2001) suggested. This raises the question whether the effects of pictorial illusions are fundamentally different from visual deformations of shape. We do not think so: to explain the effects of the orientation illusion, it is sufficient to assume that the planned grip orientation and grip locations do not have to be mutually consistent (Smeets et al. 2002).

Conclusions

We have shown that subjects plan their movements towards suboptimal grip locations. They do so in a systematic way. The systematic deviations cannot be explained by assuming that the final grip orientation is a simple function of the most comfortable grip orientation and the optimal grip orientation. Therefore, we conclude that the grasping is influenced by visual misjudgements of shape.

References

Aglioti S, DeSouza JFX, Goodale MA (1995) Size-contrast illusions deceive the eye but not the hand. Curr Biol 5:679–685

Brenner E, Damme WJM van (1999) Perceived distance, shape and size. Vision Res 39:975–986

Bülthoff HH, Mallot HA (1998) Integration of depth modules: stereo and shading. J Opt Soc Am A 5(10):1749–1758

Cuijpers RH, Smeets JBJ, Brenner E (2004) On the relation between object shape and grasping kinematics. J Neurophysiol 91:2598–2606

Elsinger CL, Rosenbaum DA (2003) End posture selection in manual positioning: evidence for feedforward modeling based on a movement choice method. Exp Brain Res 152:499–509

Ernst MO, Banks MS (2002) Humans integrate visual and haptic information in a statistically optimal fashion. Nature 415:429–433

Franz VH, Bülthoff HH, Fahle M (2003) Grasp effects of the Ebbinghaus illusion: obstacle avoidance is not the explanation. Exp Brain Res 149:470–477

Glover S, Dixon P (2001) Motor adaptation to an optical illusion. Exp Brain Res 137:254–258

Goodale MA, Milner AD (1992) Separate visual pathways for perception and action. Trends Neurosci 15:20–25

Goodale MA, Meenan JP, Bülthoff HH, Nicolle DA, Murphy KJ, Racicot CI (1994) Separate neural pathways for the visual analysis of object shape in perception and prehension. Curr Biol 4:604–610

Hibbard PB, Bradshaw MF (2003) Reaching for virtual objects: binocular disparity and the control of prehension. Exp Brain Res 148:196–201

Johnston EB (1991) Systematic distortions of shape from stereopsis. Vision Res 31:1351–1360

Knill DC (2005) Reaching for visual cues to depth: the brain combines depth cues differently for motor control and perception. J Vis 5:103–115

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

Nielsen M, Florack L, Deriche R (1997) Regularization, scale-space, and edge detection filters. J Math Imaging Vis 7:291–307

Paulignan Y, MacKenzie C, Marteniuk R, Jeannerod M (1997) Influence of object position and size on human prehension movements. Exp Brain Res 114:226–234

Rosenbaum DA, Meulenbroek RJ, Vaughan J, Jansen C (2001) Posture-based motion planning: applications to grasping. Psychol Rev 108:709–734

Smeets JBJ, Brenner E (1999) A new view on grasping. Motor Control 3:237–271

Smeets JBJ, Brenner E, De Grave DJ, Cuijpers RH (2002) Illusions in action: consequences of inconsistent processing of spatial attributes. Exp Brain Res 147:135–144

Todd JT, Tittle JS, Norman JF (1995) Distortions of three-dimensional space in the perceptual analysis of motion and stereo. Perception 24:75–86

Watt SJ, Bradshaw MF (2003) The visual control of reaching and grasping: binocular disparity and motion parallax. J Exp Psychol: Hum Percept Perform 29:404–415

Witkin AP (1983) Scale-space filtering. Proc Int Joint Conf Artif Intell 2:1019–1022

Zar JH (1996) Biostatistical analysis. Prentice-Hall, Englewood Cliffs