

Why are the digits' paths curved vertically in human grasping movements?

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Abstract When humans grasp an object off a table, their digits generally move higher than the line between their starting positions and the positions at which they end on the target object, so that the digits' paths are curved when viewed from the side. We hypothesized that this curvature is caused by limitations imposed by the environment. We distinguish between local constraints that act only at the very beginning or the very end of the movement, and global constraints that act during the movement. In order to find out whether the table causes this vertical curvature by acting as a global constraint, we compared grasping a target object positioned on a table with the same task without the table. The presence of the table did not affect the vertical curvature. To find out whether constraints at the beginning and end of the movement cause the vertical curvature, we manipulated the constraints locally at those positions by letting the subject start with his digits either above or below the end of a rod and by attaching the target object either to the top or to the bottom of another rod. The local constraints at the start of the movement largely explain the vertically curved shape of the digits' paths.

Keywords Limb movements · Visuomotor behavior · Prehension · Movement control · Human

Introduction

When humans grasp an object off a table, the tips of their digits generally move higher than the starting positions or

the positions at which they end on the target object, so that the tips' paths are curved when viewed from the side (e.g., Jeannerod 1981). This is not explained by theories on grasping (Jeannerod 1981; Haggard and Wing 1997; Rosenbaum et al. 1999; Rosenbaum et al. 2001; Smeets and Brenner 1999). Although its cause is still unknown, we know some variables that influence the curvature. When the distance between the digits' starting positions and the target object increases, maximum height increases and the relative time to maximum height decreases (Jakobson and Goodale 1991; Zoia et al. 2006). Maximum height also increases with increasing target size (Jakobson and Goodale 1991; Zoia et al. 2006) and when an obstacle is placed between the starting position and the target object (Saling et al. 1998).

We have modeled many aspects of grasping successfully by assuming that the movements of the tips of the individual digits matter, rather than the biomechanics of the arm (Smeets and Brenner 1999; Verheij et al. 2012). Following this line of reasoning our hypothesis is that the vertical curvature is determined by the limitations that the environment imposes on the trajectories of the tips of the individual digits. We distinguish between local constraints that act only at the very beginning or the very end of the movement, and global constraints that act during the movement. The grasping model of Verheij et al. (2012) explains the vertical curvature by considering the table as a global constraint. The table is implemented as a surface from which repulsive forces act on the tips of the digits throughout the movement. However, the table may only influence how the movement starts and ends. Local constraints at the start and end correspond to the boundary conditions in minimal jerk models such as the grasping model of Smeets and Brenner (1999). In the view of Smeets and Brenner, endpoints are likely to be particularly

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important because the way in which the digits contact the surface determines the stability and precision of the grip.

We examined the origin of the paths' vertical curvature experimentally by varying the environment between the conditions. We show that local constraints are largely responsible for the height of the digits' paths, and discuss what additional factors might have contributed to the curvature.

Methods

Subjects

Nine naive right-handed subjects took part in the experiment (6 females, 3 males) ranging in age from 24 to 42 years. The experiment was part of a program that was approved by the local ethics committee. Before participating, subjects signed an informed consent form.

Experimental setup and procedure

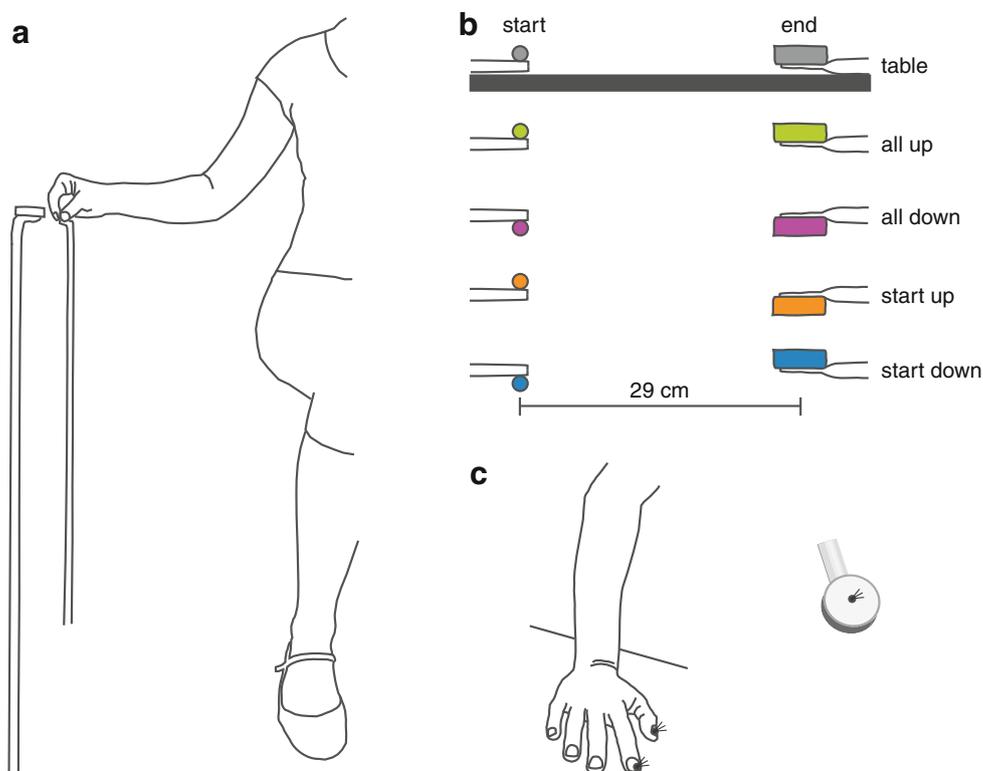
We used a setup in which we could place or remove a table without changing the starting position or the position of the target object and in which we could manipulate the local constraints at the start and end of the movement. The setup consisted of two vertically placed rods that were bent at the

top so that the final part was horizontal (Fig. 1a). One of the rods had a slender (4.4 mm wide, 8.4 mm high) end whose top or bottom functioned as the starting position for the digits. We will refer to this slender end as the 'start-beam'. The other rod had a flat end (18.2 mm wide, 6.8 mm high) to which the target object, a tealight (cylinder with diameter 4.0 cm and height 1.5 cm), was attached via a magnet. We will refer to this flat end as the 'end-plate'. The size of the end-plate was small enough to not restrict movements of the digits near the tealight. The distance between the starting position and the center of the tealight was 29 cm.

To determine whether the height of the paths arises from considering the table's surface as a global constraint, we placed or removed a table, while keeping the local constraints at the starting position and at the position of the target object exactly the same. In condition 'table', the table (111 cm × 50 cm) was placed directly under the rods. Subjects started with their hand above the start-beam, and the tealight was placed on top of the end-plate. The top of the start-beam was 10 mm above the table, almost as if it were an object on the table. Before movement onset, the index finger and thumb touched each other and the start-beam. We compared this condition with a condition in which the table was removed ('all up', Fig. 1b).

To determine whether the local constraints at the start and end of the movement are responsible for the height of

Fig. 1 The experimental setup. **a** Overview. **b** Side view of the five conditions (dimensions are not to scale). **c** Marker placement. Markers are represented by black dots



the digits' paths, we used the same two rods (without the table) and varied the constraints at the start and end of the movement. The constraints at the start of the movement were manipulated by starting with the hand either above or below the start-beam. The orientation of the hand was similar in both cases. The constraints at the end of the movement were manipulated by placing the tealight either above or below the end-plate. We compared all possible combinations of starting position and position of the tealight, resulting in four conditions: 'all up', 'all down', 'start up' and 'start down' (Fig. 1b).

For all five conditions ('table', 'all up', 'all down', 'start up' and 'start down'), the subject sat on a stool, 30 cm to the side of the starting position (Fig. 1a), so that the rods would never be an obstacle for the wrist or the arm. Before movement onset, the index finger and thumb touched each other and the start-beam. When a verbal 'go' signal was given, subjects grasped the tealight. Subjects were instructed to move at a natural speed, grasp the tealight using their index finger and thumb and to lift the tealight in the conditions 'table', 'all up' and 'start down' or to move the tealight downward in the conditions 'all down' and 'start up'.

Because the conditions we use to test the two hypotheses overlap ('all up' is used for both tests), we chose to combine them in one experiment. The conditions 'table', 'all up' and 'all down' were run in the first part of the experiment. Each condition was presented in two blocks of ten trials, which leads to a total of 6 blocks, or 60 trials per subject. The 6 blocks were run in such an order that three subjects started with 'table', three with 'all up' and three with 'all down'. Likewise, the number of subjects was the same for every condition in the following blocks. The sequence of the blocks (for example, how many times condition 'table' was succeeded by 'all up') was counter-balanced. The exact order of the blocks in the first part of the experiment is shown for each subject in Appendix 1. The conditions 'start up' and 'start down' were run in the second part of the experiment. Each condition was presented in two blocks of ten trials, which leads to a total of 4 blocks, or 40 trials per subject. The conditions 'start up' and 'start down' were alternated. Five subjects started with 'start up' (followed by 'start down', 'start up' and 'start down') and four subjects started with 'start down' (followed by 'start up', 'start down' and 'start up').

Movements were recorded at 100 Hz with an Optotrak 3020 motion recording system (Northern Digital, Waterloo, ON, Canada). Since our hypothesis only considers the kinematics of the end-effectors, in accordance with evidence that the motion of the end-effectors is largely independent of the underlying joint movements (Morasso 1981; Flash 1987; Wolpert et al. 1994; Schillings et al. 1996; Marteniuk et al. 2000; Smeets and Brenner 2001; Tresilian

and Stelmach 1997), we do not examine hand posture or orientation but only the trajectories of the tips of the thumb and of the index finger. Single infrared emitting diodes (IREDS) were attached to the subject at the nail of the thumb and at the nail of the index finger. An additional marker was attached to the top surface of the tealight (Fig. 1c).

Data analysis

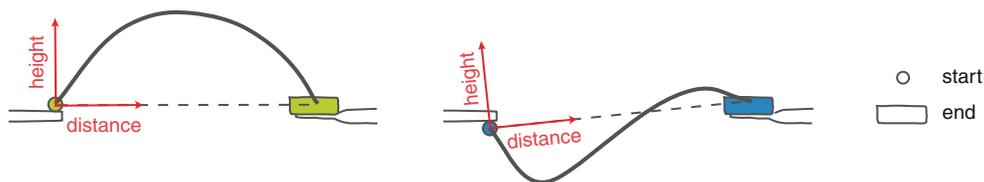
We defined the start of the grasping movement as the first moment at which the velocity of the tip of the thumb and the tip of the index finger both exceeded 100 mm/s. The end of the grasping movement was defined as the moment at which the displacement of the tealight exceeded 0.1 mm in the vertical direction. We rejected the trial if there were more than two consecutive missing samples between the start and end of the grasping movement for either the thumb or the index finger. This resulted in the rejection of 18 (out of 900) trials. Isolated or pairs of missing marker samples were reconstructed using linear interpolation.

Starting and ending a bit above or below the rods means that the starting and end positions of the digits are not identical for all conditions. We therefore rotated and translated the coordinate system of each trial and each marker of the digits, such that we can examine the height of the curve as a function of the distance from the starting to the end position of the digit (Fig. 2). This rotation and translation allowed us to directly compare the curves across conditions.

To be able to statistically analyze whether considering the table's surface as a global constraint causes the height of the digits' paths, we calculated the maximum height for each trial of condition 'table' and condition 'all up'. We calculated the mean maximum value per subject, condition and digit. For each digit, the effect of the presence of the table on these mean maximum values was then tested using a one-way repeated measures analysis of variance (ANOVA). We also examined whether the table has an effect on the shape of the vertical movement path by comparing how the height varies with the distance in the conditions 'table' and 'all up'. We resampled the height-component of each trial such that each step corresponds to 1 % of the distance from the starting to the end position. We calculated the mean of these resampled height-components per subject, condition and digit. Next, we averaged these mean paths across the subjects to get an overview of the average behavior.

To evaluate how the constraints at the start and end of the movement influence the height of the digits' paths, we examined how the height varies with the distance in the conditions without a table. We did so in the same way as we did to examine the effect of the table throughout the

Fig. 2 The coordinate system's origin and orientation for two example trials (dimensions are not to scale)



movement. To analyze the data of these four conditions quantitatively, we used a mathematical approach which will be explained in the result section.

The experiment was inspired by the difference between two models (Verheij et al. 2012; Smeets and Brenner 1999). In order to interpret the results qualitatively in terms of the constraints and objectives that form the basis of these models, we simulated our experiment with both models.

Results

The effect of the table on the height of the digits' paths was negligible (Fig. 3a). There was no significant difference in the maximum height between conditions 'table' and 'all up' for either of the digits (thumb: $F(1,8) = 0.337$, $p = 0.578$; index finger: $F(1,8) = 0.005$, $p = 0.945$). The shape of the movement paths was similar as well (Fig. 3b). Thus, the vertical curvature is not the result of considering the table as a global constraint. Given the lack of effect of the table, we will concentrate in the rest of the paper on the local constraints: the analysis of the four conditions without a table.

The behavior for the index finger is quite consistent across trials within a subject ($SD \approx 0.9$ cm, Fig. 4). The different subjects showed similar effects of the manipulations (different panels in Fig. 4). The paths for the thumb (not shown) are similar to those of the index finger. The average of all the subjects' paths is depicted in Fig. 5 for both digits. There are clear effects of the local constraints on the curvature. The most salient effect is the difference

between conditions with a different starting position. Subjects started with an upward curve if the starting position was above the start-beam and with a downward curve if the starting position was below the start-beam, irrespective of the constraints at the end. Note that this is an important finding since from the moment the digits are no longer under the start-beam the trajectories could theoretically converge. However, we find a large difference. Moreover, we find the greatest difference at a considerable distance from the start-beam. Furthermore, the similarity at the beginning of the movement between conditions with the same starting position is remarkable. Together, these three observations indicate that the local constraints at the start influence the height of the paths considerably, especially at the beginning of the movement. When the starting position is the same but the position of the tealight varies, the curves differ, especially at the end of the movement. This difference, which is much smaller than the difference between conditions with different starting positions, indicates that the local constraints at the end influence the curvature as well.

Pairs of conditions in which the local constraints in one condition are the mirror image of the local constraints in the other condition (conditions 'all up' and 'all down' and conditions 'start up' and 'start down') do not yield symmetric outcomes. The amplitude of the upward curves in condition 'all up' is larger than the amplitude of the downward curves in condition 'all down'. Likewise, the amplitude of the upward curves in condition 'start up' is larger than the amplitude of the downward curves in condition 'start down'. Since we see no reason to assume that

Fig. 3 The effect of the table on the height of the digits' paths. **a** The maximum height for the thumb and the index finger, per condition, averaged across the subjects (with the associated standard errors). **b** The height as a function of the distance, per digit and condition, averaged over subjects

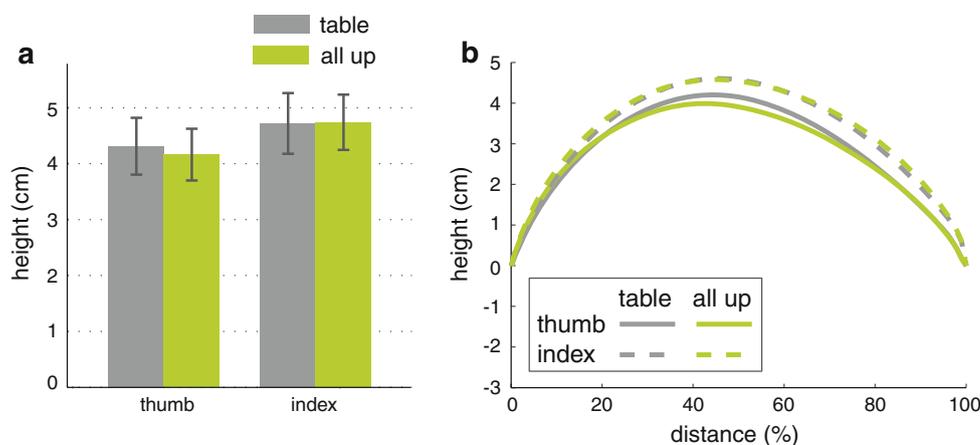


Fig. 4 The average paths of the index finger per subject and condition. The *error bars* indicate the associated standard deviations at one-third and two-third of the distance

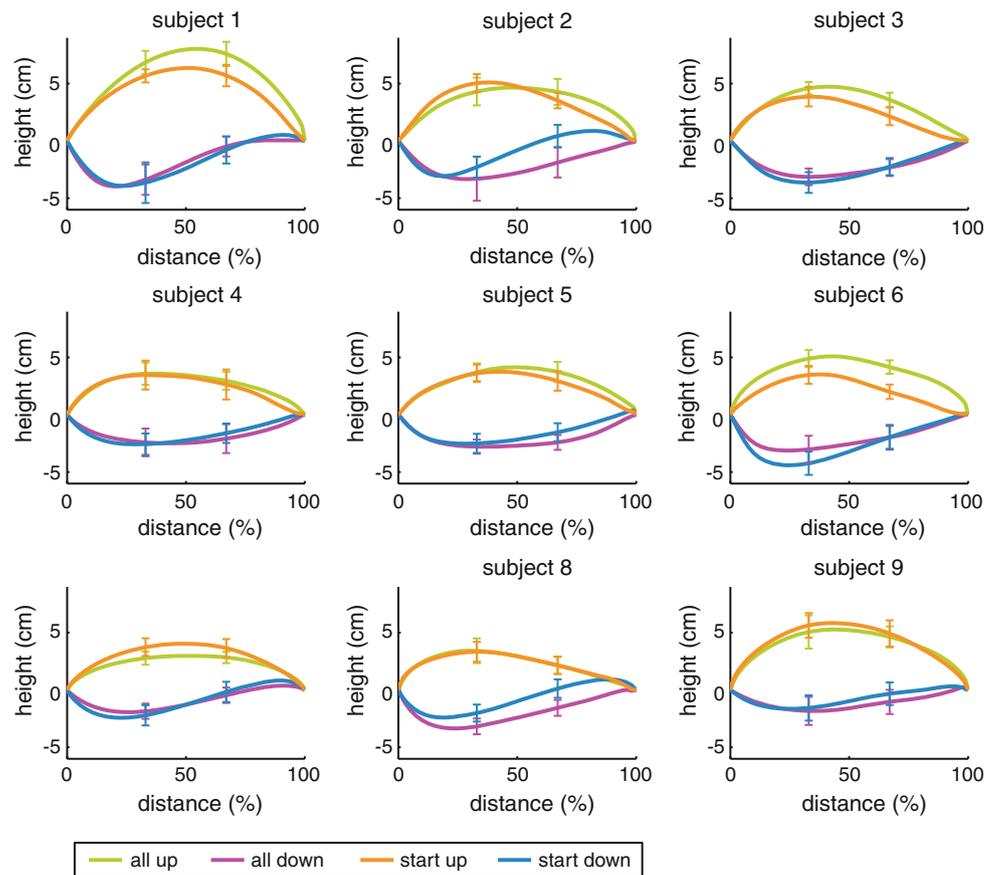
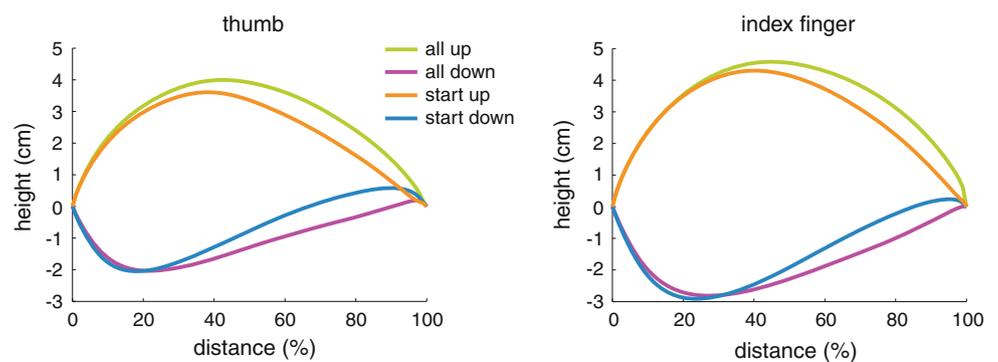


Fig. 5 The height as a function of the distance, per digit and condition, averaged across subjects



the effects of the local constraints at the start and end of the movement differ for the ‘above’ and ‘below’ positions, other than in polarity, the above mentioned observation indicates that there must also be a general tendency to make upward curves that is not related to these local constraints.

Based on the above reasoning, we examined mathematically whether the height of the path could be caused by a combination of three components: one caused by the local constraints at the start of the movement (CS), one caused by the local constraints at the end of the movement (CE) and a general tendency to curve upward (GT). In our analysis, we assume that CS is equal but opposite in sign

when the starting position is below the start-beam compared to when it is above the start-beam. Likewise, we assume that CE is equal but opposite in sign when the tealight is below the end-plate compared to when it is above the end-plate. We assume that GT is the same in all conditions.

Considering the height of the path as the sum of CS, CE and GT, we obtain a system of four equations with three unknowns (Table 1). Therefore, we can determine the contribution of each component in two ways. To determine GT, for example, we can sum the profiles of condition ‘all up’ and condition ‘all down’ or we can sum the profiles of condition ‘start up’ and condition ‘start down’. Both sums

Table 1 The height of the path considered as the sum of the components

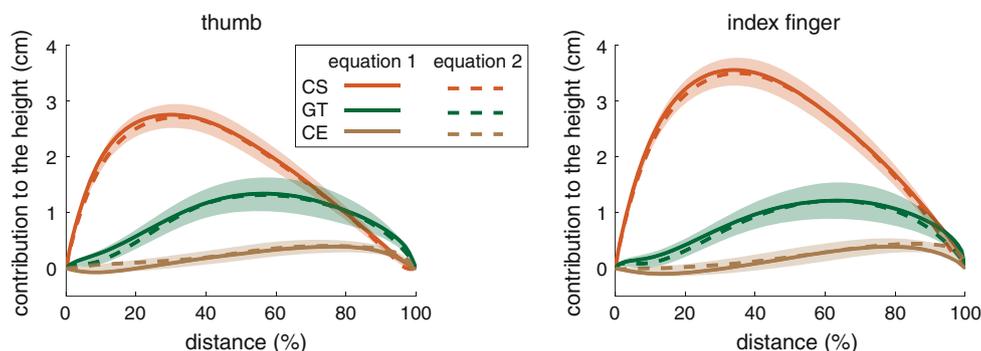
| Condition | Sum of the components |
|------------|-----------------------|
| All up | GT + CS + CE |
| All down | GT - CS - CE |
| Start up | GT + CS - CE |
| Start down | GT - CS + CE |

GT general tendency to curve upward, CS local constraints at the start, CE local constraints at the end

Table 2 Equations to obtain the contribution of the three components CS, CE and GT

| Component | Equation 1 | Equation 2 |
|-----------|-------------------------------|-------------------------------|
| GT | (‘All up’ + ‘all down’)/2 | (‘Start up’ + ‘start down’)/2 |
| CS | (‘All up’ - ‘start down’)/2 | (‘Start up’ - ‘all down’)/2 |
| CE | (‘Start down’ - ‘all down’)/2 | (‘All up’ - ‘start up’)/2 |

give 2GT, so dividing the resulting profile by two gives GT. In Table 2, equations to obtain all three components are given. For the calculations, we used the mean profiles per subject, condition and digit. If a sum of the components GT, CS and CE indeed describes the height of the path, the two equations for each component should yield similar profiles. This is exactly what we found (Fig. 6). The component CS is (much) larger than the other two (except close to the end) and has its peak at around 30 % of the distance. The component CE is very small. The component GT is intermediate and has its peak at around 60 % of the distance.

**Fig. 6** Contributions of the constraints at the start (CS), constraints at the end (CE) and a general tendency to curve upward (GT) to the height of the digits' paths, averaged across the subjects. In Table 2,

Model comparison

How do the components CS and CE result from the local constraints? To answer this question, we chose to use the two grasping models that inspired us to do our experiments: the simple 2-D model of Smeets and Brenner (1999) and the more complex 3-D model of Verheij et al. (2012).

In its published form, the model of Smeets and Brenner (1999) does not give a prediction for the height of the digits' paths, but using the same equation as for the horizontal plane, we can expand this model to the third dimension. The local constraints at the start (to obtain CS) and end (to obtain CE) can be implemented in a similar way to the constraints on object contact that are already in the model: by giving the digits a non-zero vertical acceleration at the start and end of the movement (see Appendix 2).

In the original model of Verheij et al. (2012), the height of the digits' paths is mainly caused by the digits being repelled by the table throughout the movement, with some additional influence of avoiding contacting the target at a position other than the goal position. Because we found experimentally that the table had no effect, we revised the model to eliminate the effect of the table on grasping kinematics. In the revised model, the part of the vertical curvature that we attribute to CE arises solely from avoiding contact with the target at a position other than the goal position. We implemented CS by considering the start-beam as an obstacle (see Appendix 3).

For the simulations of both models, the dimensions were equal to the dimensions in our experiment. In the experiment, subjects were free to select the grip orientation with which they grasped the tealight. The average orientation across the four conditions and across all subjects was 11°, where 0° is a final grip orthogonal to the direction from the starting position to the tealight's center. For the simulations, we selected the goal positions that correspond to this orientation.

two equations are given to calculate each component. The outcome of the two equations is similar for all components. The shaded area indicates the standard error, averaged over the two equations

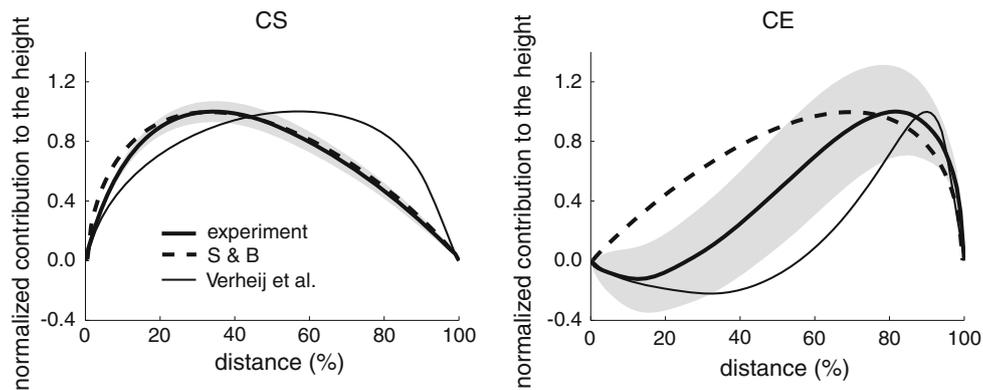


Fig. 7 Normalized contributions of the constraints at the start (CS) and the constraints at the end (CE) to the height of the index finger. For both CS and CE, the contribution can be calculated using equation 1 or 2 (Table 2), which give identical results for the model simulations. The *line* representing the experimentally found

contribution is the average of the contribution calculated using equation 1 and the contribution calculated using equation 2. The *shaded area* indicates the normalized standard error, averaged over the two equations. Details of the models are provided in the text and in Appendices 2 and 3

For both models and experimental data, the normalized components CS and CE for the index finger are depicted in Fig. 7. The profiles for the thumb are similar. For the expanded model of Smeets and Brenner, the shape of the predicted CS is strikingly similar to the shape of the experimentally observed component. The correspondence is remarkable since we did not tune any parameter value of the expanded model to our experimental outcome (Appendix 2). The prediction for the shape of CE is less similar to the experimentally found shape. This difference in shape can be put into perspective by considering the relatively large confidence interval for CE. The most salient difference is the downward curve followed by an upward curve in the experimental profile compared to only an upward curve in the model prediction.

The revised model of Verheij et al. (2012) does predict a downward curve followed by an upward curve for CE. Note that the exact shape depends on the parameter values. We used the same set of parameter values as in the paper in which the original model was introduced (Verheij et al. 2012), so a better fit of CE could be achieved if we tune the model parameters to the experimental profile. The prediction of CS is not in line with the experimental profile, the largest difference being the location of the peak.

Discussion

In this study, we aimed to find out why grasping movements are curved vertically when humans grasp an object off a table. Inspired by the grasping models of Verheij et al. (2012) and of Smeets and Brenner (1999), we experimentally tested two possible explanations: curving vertically to avoid contacting the table throughout the movement and

doing so as a consequence of local constraints at the start and end of the movement.

The clearest result is that the maximum height of the movement paths was not influenced by the presence of a table. This means that considering the table as an obstacle throughout the movement, as implemented in the model of Verheij et al. (2012), is wrong. This model therefore needs to be revised if it is to give valid predictions for the height of the digits' paths.

Using a mathematical approach, we found evidence that the local constraints at the start and end of the movement and a general tendency to curve upward, that is independent of the local constraints, are responsible for the height of the digits' paths. Our analysis suggests that there is no interaction between these three components, because mathematically the data could be described very well without including any interactions.

We labeled the contribution of the local constraints at the start of the movement, the contribution of the local constraints at the end of the movement and the contribution of the general tendency to the height of the path, CS, CE and GT, respectively. We examined whether we can understand the shape of the components CS and CE based on model predictions on the influence of the constraints at the start and end of the movements of the individual digits. We found that the shape of CS matches strikingly well with a modeled non-zero vertical acceleration at the start of the movement. The shape did not match with modeling the start-beam as an obstacle in the manner proposed in Verheij et al. (2012). We propose that CS is independent of the surface area of the object that is constraining the movement. This matches with our finding that the presence of a table did not influence grasping kinematics. Based on the modeling results for CE, we propose that this

component is caused by avoiding contact with the target object at positions other than the goal position. Further experimental research is needed to test this.

We do not know what causes the general tendency to curve upward. Since gravity did not change between the conditions, we cannot rule out an influence of gravity on the general tendency. Humans might take gravity into account in movement planning (Papaxanthis et al. 1998; Papaxanthis et al. 2003; Pinter et al. 2012) by ‘launching’ their hand upward, knowing that gravity will bring it down again to end on the goal position. Relying partly on gravity rather than muscle force near the end of the movement may make ending on the goal position more precise, if precision is inversely related to muscle force (Schmidt et al. 1979; Harris and Wolpert 1998; Jones et al. 2002). The general tendency might also be influenced by the familiarity of the target object. The target object we used was familiar to all subjects. Certain grasping kinematics, the scaling of the maximum grip aperture with object size and the relative position of the maximum grip aperture, differ slightly between familiar and unfamiliar objects with the same dimensions (Borchers and Himmelbach 2012). The general tendency might also be the effect of human anatomy, a strategy to obtain a better viewing angle (Baker et al. 1999; Ustinova et al. 2010) or of some other aspect of the task that is independent of the local constraints imposed by objects in the environment. Although further experimental research is needed to examine the possible influence of all these factors on the general tendency, we found that together they are responsible for only a minor part of the height of the digits’ paths.

In sum, we found that the height of the digits’ paths is not the effect of a strategy to avoid contacting the table throughout the movement, but of the local constraints at the start and end of the movement together with a general tendency to curve upward. The local constraints at the start are most influential.

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Appendix 1

In this design, each condition was presented first to 3 subjects, second to 3 subjects, third to 3 subjects and so on. The order of the conditions was also counterbalanced as far as possible. For example, condition ‘table’ followed condition ‘all up’ 7 times and followed condition ‘all down’ 8 times. Each subject performed each condition twice, once in the first 3 blocks and once in the second 3, with no condition being repeated in the third and fourth block (Table 3).

Appendix 2

The model presented by Smeets and Brenner (1999) is a 2-D minimum-jerk model (Flash and Hogan 1985). It models grasping movements by simulating two single-digit pointing movements and combining the outcomes. For each digit and each coordinate of the movement, the following polynomial equation with six constants gives the minimum-jerk trajectory:

$$z(t) = c_0 + c_1t + c_2t^2 + c_3t^3 + c_4t^4 + c_5t^5 \tag{1}$$

The values of the constants follow from six boundary conditions: the initial and final position, velocity and acceleration. To acquire a perpendicular approach to the target surface, a non-zero final deceleration is chosen perpendicular to the surface. The final deceleration is scaled by the squared movement time resulting in the so-called approach parameter, a_p . The larger this parameter, the more perpendicular the simulated digit’s path approaches the target surface. The movement time (MT) does not affect the digits’ paths and can thus be chosen independently.

We expanded the model of Smeets and Brenner by adding a polynomial equation for the vertical movement, making it a 3-D minimum-jerk model. We chose the following boundary conditions for this extra polynomial equation.

Table 3 The order of the blocks ‘table’, ‘all up’ and ‘all down’ per subject

| Subject | Order of the blocks | | | | | | |
|---------|---------------------|----------|----------|----------|----------|----------|--|
| 1 | Table | All up | All down | All up | All down | Table | |
| 2 | All up | All down | Table | All down | All up | Table | |
| 3 | All down | All up | Table | All down | Table | All up | |
| 4 | All up | Table | All down | All up | All down | Table | |
| 5 | Table | All down | All up | Table | All up | All down | |
| 6 | All down | Table | All up | Table | All down | All up | |
| 7 | Table | All up | All down | All up | Table | All down | |
| 8 | All up | All down | Table | All down | Table | All up | |
| 9 | All down | Table | All up | Table | All up | All down | |

$$z(0) = 0 \quad z(MT) = 0 \quad v(0) = 0 \quad v(MT) = 0$$

$$a(0) = \frac{a_{cs}}{MT^2} \quad a(MT) = \frac{a_{ce}}{MT^2}$$

The strength of the effect of the local constraints at the start is set by the parameter a_{cs} , which is positive when simulating movements in which the starting position was above the start-beam and negative when simulating movements in which the starting position was below the start-beam. The strength of the effect of the local constraints at the end is set by the parameter a_{ce} , which is positive when simulating movements in which the tealight was above the end-plate and negative when simulating movements in which the tealight was below the end-plate. Like a_p , the parameters a_{cs} and a_{ce} have the dimension of length. The boundary conditions that we chose result in the following values for the constants of Eq. 1:

$$c_0 = 0 \quad c_1 = 0 \quad c_2 = \frac{a_{cs}}{2MT^2} \quad c_3 = \frac{-3a_{cs} + a_{ce}}{2MT^3}$$

$$c_4 = \frac{3a_{cs} - 2a_{ce}}{2MT^4} \quad c_5 = \frac{-a_{cs} + a_{ce}}{2MT^5}$$

In the simulation of our experiment, we used a magnitude of 1.5 m for the parameter values of a_p , a_{cs} and a_{ce} . We did not tune the parameter values to our experimental results; 1.5 m was the value used in the paper of Smeets and Brenner (1999) as a typical value for a_p .

Appendix 3

In the original model of Verheij et al. (2012), the tips of the index finger and the thumb are modeled as point masses moving in a force field. We refer to these point masses as ‘tips’. The force field is the sum of multiple forces. Each force represents one or two objectives. The implemented objectives for each tip are the following: arrive at the preselected goal position, avoid collisions with positions other than the goal position, limit the distance to the other tip, arrive at approximately the same time as the other tip and move smoothly. The table is considered as an obstacle throughout the movement; hence, there is a repulsive force from the table on which the target object is placed. To a large extent, the repulsive force from the table causes the height of the digits’ paths. Avoiding collisions with positions on the surface of the target object other than the goal position causes the remainder of the vertical curvature.

In the revised model, the table has no influence on grasping kinematics. Instead, we considered the start-beam as an obstacle. The length of the start-beam is 4.5 cm, and its width is 4.4 mm. In the simulation, the tips started 0.1 mm above the start-beam, 0.1 mm from each other laterally and 1 cm from the end of the rod. The simulation

ended when the tip representing the thumb was at a distance of 0.1 mm from its goal position. We used the same set of parameter values as in the paper in which the original model was introduced (Verheij et al. 2012), with the one difference that the parameter R_t (indicating the repulsiveness of the table) was zero.

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