Journal of Motor Behavior, Vol. 45, No. 4, 2013

RESEARCH ARTICLE

Gravity Affects the Vertical Curvature in Human Grasping Movements

Rebekka Verheij, Eli Brenner, Jeroen B. J. Smeets
MOVE Research Institute Amsterdam, Faculty of Human Movement Sciences, VU University Amsterdam, the Netherlands.

ABSTRACT. When humans make grasping movements their digits' paths are curved vertically. In a previous study the authors found that this curvature is largely caused by the local constraints at the start and end of the movement. Here the authors examined the contribution of gravity to the part of the curvature that was not explained by the local constraints. Subjects had to grasp a tealight (small cylinder) while sitting on a chair. The authors could rotate the whole setup, including the subject, relative to gravity, whereby the positions of the starting point and of the tealight relative to the subject did not change. They found differences between the paths that are consistent with a direct effect of gravity pulling the arm downward.

Keywords: gravity, motor control, prehension, visuomotor behavior

When humans make grasping movements their digits generally move higher than the line between the digits' 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 (e.g., Jeannerod, 1981). This route is obviously not the shortest one. Assuming that humans move close to optimal according to some optimization principle (e.g., Trommershäuser, Gepshtein, Maloney, Landy, & Banks, 2005; Uno, Kawato, & Suzuki, 1989), analyzing how the circumstances influence such detours in grasping movements may reveal why they are made, and thereby provide fundamental insight into the control of grasping movements.

In a previous study (Verheij, Brenner, & Smeets, 2013) we examined whether the vertical curvature is caused by limitations imposed by the environment. We distinguished between global constraints that act during the whole movement, and local constraints that act only at the very beginning or the very end of the movement. We compared grasping a tealight positioned on a table (that was assumed to constrain the whole movement) with grasping the same object when it was mounted on a rod at the same position without a table (comparable to the setup in Figure 1A). We found that the presence of the table did not affect the height of the digits' paths. The tealight could also be mounted below the rod. By also comparing movements when our subjects' hands started below the rod with ones when their hands started above the rod, we evaluated the role of the local constraints at the start and end. We found that the height of the digits' paths is mainly determined by the local constraints at the start of the movement. The local constraints at the end have some influence as well. However, part of the height of the paths was not related to the local constraints, and is still unexplained. In this study we aim to find out whether gravity influences this part.

Normally gravity pulls the hand downward, not upward. However, this pull may be integrated into the movement plan. We hypothesize that people integrate gravity into the movement plan by launching the hand upward, knowing that gravity will bring it down again to end at the goal position. The advantage of following this strategy is that relying partly on gravity rather than muscle force near the end of the movement may make ending at the goal position more precise, because precision is inversely related to muscle force (Harris & Wolpert, 1998; Jones, Hamilton, & Wolpert, 2002; Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979). This reasoning assumes that a possible decrease in precision during the early phase of the movement, caused by the higher muscle force needed to launch the hand upward, does not outweigh the increase in precision gained at the end of the movement. We base this assumption on the finding that movements are constantly adjusted on the basis of feedback (Oostwoud Wijdenes, Brenner, & Smeets, 2011; Paulignan, Mackenzie, Marteniuk, & Jeannerod, 1991; Saunders & Knill, 2003) and there is much more time to compensate for errors that occur in the early phase of the movement than for ones that occur in a late phase of the movement.

The idea that gravity is integrated into the movement plan of the arm is not new. This idea has been proposed in relation to various experimental studies that measured kinematics of pointing movements under altered levels of gravity (Crevecoeur, Thonnard, & Lefèvre, 2009; Papaxanthis, Pozzo, & McIntyre, 2005) or for various movement directions (Berret et al., 2008; Gaveau & Papaxanthis, 2011; Gentili, Cahouet, & Papaxanthis, 2007; Papaxanthis, Pozzo, & Schieppati, 2003; Pinter, van Soest, Bobbert, & Smeets, 2012). The results of one of the studies of Papaxanthis et al. (2003), in which electromyography was measured, showed that the CNS allows gravitational force to replace muscular force when the movement speed is low. A similar use of gravity has been found in a study of Furuya, Osu, and Kinoshita (2009), where gravity replaced triceps force of expert pianists during arm downswing in keystrokes. Although most of these studies examined pointing movements, similar results may be expected for grasping movements, especially if grasping movements are considered as pointing with multiple fingers (Smeets & Brenner, 1999, 2001).

We tested whether gravity influences the height of the index finger's path by asking subjects to grasp a tealight (small

Correspondence address: Rebekka Verheij, Faculty of Human Movement Sciences, VU University Amsterdam, Van der Boechorststraat 9, 1081 BT Amsterdam, the Netherlands. e-mail: r.verheij@vu.nl

cylinder). To alter the possible effect of gravity we rotated the whole setup, including the subject, relative to gravity (a manipulation known from infant research; Savelsbergh & van der Kamp, 1994). We found that this rotation systematically influenced the height of the index finger's path, corresponding to a direct effect of gravity.

Method

Subjects

Eight naive right-handed subjects took part in the experiment (2 women, 6 men; ranging in age from 20 to 43 years old). 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

The setup consisted of a chair and two vertically placed rods. The rods were bent at the top so that the final part was horizontal (Figure 1A). One of the rods had a slender (4.4 mm wide, 8.4 mm high) end that indicated the starting position. 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 using a magnet. We refer to this end as the endplate. The size of the endplate was small enough not to restrict movements of the digits near the tealight. The distance between the starting position and the center of the tealight was 29 cm. The subject sat on a chair, 30 cm to the side of the starting position, so that the rods would never be an obstacle for the wrist or the arm.

In the natural orientation, gravity works orthogonal to the main direction of movement. In order to test whether the height of the index finger's path is related to gravity we tilted the whole setup, including the subject, 70° backward so that the component of gravity that is orthogonal to the main direction of movement decreased to 34% of the normal value. The positions of the start beam and the tealight were the same relative to the subject in both the natural and the tilted conditions.

In a previous study (Verheij et al., 2013) using a similar setup in the natural configuration, we manipulated the local constraints at the start by having the starting position either directly above the start beam or directly below it, and we manipulated the local constraints at the end by placing the target object either directly above or directly below the endplate. The bent rods were placed so that the start beam and endplate only limited the very beginning and very end of the movements, and there were no other objects nearby that could constrain the movements. Almost symmetric influences of starting and ending above and below the rods showed that local constraints at the start and end of the movement are largely responsible for the height of the digits' paths when making grasping movements. However, the influences were not completely symmetrical, so the paths are not only determined by these local constraints. The small part of the digits' paths that cannot be attributed to the local constraints might be related to gravity, and will be the focus of the present article.

As in the previous study, we varied the starting position together with the position of the tealight (both either above or below the far end of a rod) to be able to identify the part of the

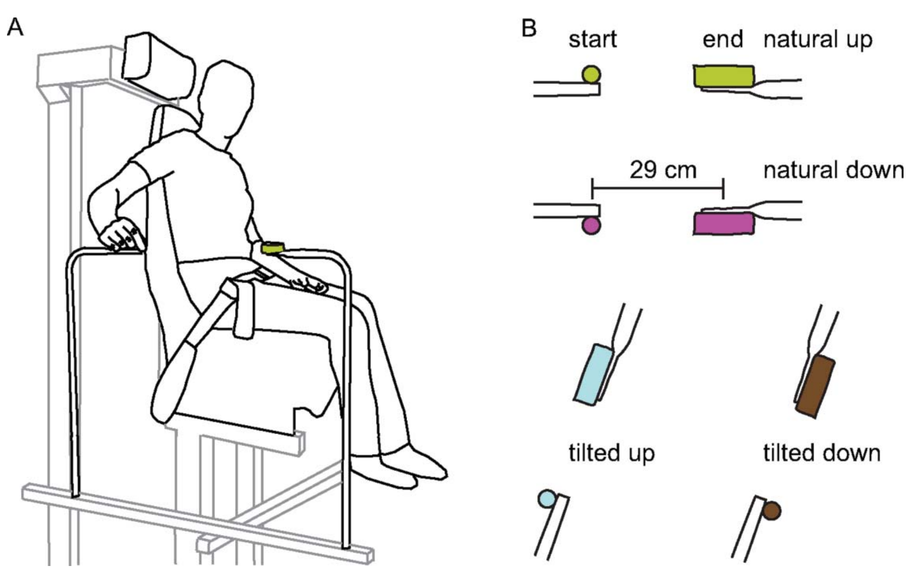

FIGURE 1. The experimental setup. (**A**) Overview of a subject in the 'natural up' condition. (**B**) The four conditions (dimensions are not to scale). (Color figure available online).

height of the index finger's path that is not caused by the local constraints, and is therefore possibly influenced by gravity. There were therefore two combinations of local constraints for each of the two orientations of the setup (Figure 1B). Subjects 1–4 started in the natural orientation and subjects 5–8 started in the tilted orientation. The subjects performed 20 trials for each of the two pairs of local constraints in the initial orientation. The order of the two pairs of local constraints was randomized. Next the setup, including the subject, was rotated to the other orientation. Again 20 trials were performed for each of the two pairs of local constraints, in randomized order. Thus, altogether there were 80 trials per subject, equally divided over four conditions.

In all conditions the index finger and thumb of the right hand touched each other and the start beam before movement onset. When a verbal "go" signal was given subjects reached and grasped the tealight. Subjects were instructed to move at a natural speed, to grasp the tealight using their index finger and thumb, and to lift the tealight in the conditions in which the tealight was above the endplate or to move the tealight downward in the conditions in which the tealight was below the endplate. To check whether subjects understood this instruction they made one movement in the 'natural up' condition and one movement in the 'natural down' condition before the start of the experiment. There were no further practice trials.

Movements were recorded at 100 Hz with an Optotrak 3020 motion recording system (Northern Digital, Waterloo, Ontario, Canada). A single infrared emitting diode was attached at the nail of the subject's index finger.

Data Analysis

We defined the start of the grasping movement as the first moment at which the velocity of the index finger exceeded 0.1 m/s (a value frequently used in grasping studies; e.g., Hesse, Nakagawa, & Deubel, 2010; Schot, Brenner, & Smeets, 2010; van de Kamp & Zaal, 2007; Verheij et al., 2013). The end of the grasping movement was defined as the first moment, after the start of the movement, at which the velocity of the index finger dropped below 0.1 m/s. We rejected the trial if there was a missing sample between the start and end of the grasping movement (18 trials). Furthermore, three trials were rejected because subjects did not make a single smooth movement, but made several submovements. This resulted in the rejection of 21 (of 640) trials.

The starting and end position of the index finger's path differed systematically between the four conditions because subjects started and ended either a bit above or below the rods and of course because the setup was either in the natural or the tilted orientation. We therefore examined the distance between the index finger and a straight line connecting the starting and end position; we will refer to this measure as 'height' (Figure 2). The 'height' provides information about

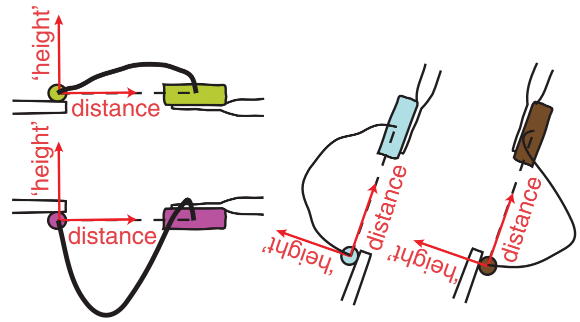

FIGURE 2. An illustration of our measure 'height' for four example trials (dimensions are not to scale). (Color figure available online).

the detour made by the index finger (positive is away from the feet). The larger the absolute value of the 'height', the larger the detour made by the index finger. This measure also allows us to directly compare the paths' curvatures across conditions. When we mention 'height' in the remainder of this article we refer to this measure (orthogonal to the main movement direction) rather than to the direction opposite gravity (although they almost coincide in the natural orientation).

We resampled each trajectory such that each step corresponds to 1% of the path length, and then calculated the means of the resampled trajectories per subject and condition. We plotted the mean resampled height component as a function of the percentage of path length per subject and condition, together with the associated standard deviations, to get an overview of how the index finger moved.

To be able to statistically evaluate whether the 'height' of the path is influenced by gravity, we first calculated the maximum 'height' for each trial of condition 'natural up' and 'tilted up' and the minimum 'height' for each trial of condition 'natural down' and 'tilted down'. Next, we determined the means of these extreme values per subject and condition. We used these means to test the effect of gravity with a two-way repeated measures analysis of variance with factors: orientation and constraints.

To evaluate changes in performance with practice, we also plotted the mean resampled 'height' component as a function of percentage of path length for the first five trials and for the last five trials of each condition. To evaluate whether practice influenced the 'height' of the path systematically, we determined the means of the extreme values within such phases of five trials. The resulting mean values per subject, condition and phase of five trials were used in a three-way repeated measures analysis of variance (ANOVA) with factors orientation, constraints, and phase. For subject 5, one trial was excluded from the last phase of trials of condition 'natural down' (for the reasons given above). For subject 4, one trial was excluded from the last phase of condition 'natural down', three trials were excluded from the first phase of condition 'tilted down', and one trial was excluded from the last phase of condition 'tilted down'.

If gravity influences the 'height' of the index finger's path, calculating the component of the 'height' of the path that is not related to the local constraints at the start and end of the movement is useful to examine how gravity affects the 'height'. In our previous study (Verheij et al., 2013) we labeled this component GT and developed a method to isolate it. In this method we considered the 'height' of the index finger's path as composed 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 one possibly caused by gravity GT. We assumed 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 assumed that CE is equal but opposite in sign when the tealight is below the endplate compared to when it is above the endplate. We also assumed that GT is the same in condition 'natural up' and condition 'natural down'. Using experimental data we mathematically validated this split into three components as well as our assumptions.

For each condition we expressed the measured profile of the 'height' of the index finger's path as the sum of the three components with their associated signs. When we consider the equation for the 'natural up' condition ('height' of the index finger's path = GT + CS + CE) and the equation for the 'natural down' condition ('height' of the index finger's path = GT – CS – CE) it is apparent that averaging the 'height' of the index finger's path in conditions 'natural up' and 'natural down' gives GT. In this study we assume that the same holds for the conditions tilted up and tilted down, because the local constraints are the same as in conditions 'natural up' and 'natural down'. We calculated GT for the two orientations by using the mean of the resampled profiles per subject and condition. To be able to observe how gravity affects GT, we compared the shape of GT for the two orientations for each subject.

Rotating the setup from the natural to the tilted orientation means that in order to minimize muscle force near the end of the movement increasing the 'height' is no longer effective. Instead, the 'height' profile might be skewed more to the right (maximum 'height' near the end of the movement) in condition 'tilted up' compared to condition 'natural up', in order for gravity to move the digit to the tealight or the beginning of the movement might be faster so that gravity can replace muscle force at the end of the movement by decelerating the index finger as it approaches the tealight. Because such considerations may influence the movement velocity we calculated average resampled tangential velocity profiles per condition (in a similar manner as we had done for the path). We also performed a two-way repeated measures ANOVA on the mean maximum velocity per subject and condition, with orientation and constraints as factors.

Results

The extent to which the rotation of the setup affected the 'height' of the path differs between subjects (Figure 3). Overall, it seems that the maximum 'height' is higher in the tilted conditions compared to the corresponding conditions in the natural orientation. We tested this statistically using a two-way repeated measures ANOVA on the mean extreme values, with the factors orientation and constraints. We found a significant effect of orientation, $F(1, 7) = 12.9$, $p = .009$, which confirms our impression from Figure 3. The maximum 'height' was *higher* (i.e., the digit moved further above a straight line connecting the digit's starting and end position) in the 'tilted up' condition ($M = 3.6$ cm, $SD = 1.3$ cm) than in the 'natural up' condition ($M = 2.8$ cm, $SD = 0.8$ cm). Note that according to our hypothesis we would expect a *lower* maximum 'height' in the 'tilted up' condition, because in the 'tilted up' condition increasing 'height' is not an effective way to facilitate gravity to replace muscle force at the end of the movement. The profile is also not skewed to the right in the 'tilted up' condition. The minimum 'height' was higher (i.e., the digit moved closer to a straight line connecting the digit's starting and end position) in the 'tilted down' ($M = –3.0$ cm, $SD = 0.8$ cm) than in the 'natural down' condition ($M = –3.6$ cm, $SD = 1.1$ cm).

In line with our previous study (Verheij et al., 2013), we found a highly significant effect of constraints, $F(1, 7) = 221.3$, $p < .001$. There was no interaction effect between constraints and orientation, $F(1, 7) = 0.3$, $p = .6$, which is in line with our assumption that changing the orientation will only influence the part of the 'height' of the path that is not related to the local constraints.

There are no apparent systematic differences between the 'heights' of the first five trials and the 'heights' of the last five trials (Figure 4). A three-way repeated measures ANOVA on the mean extreme values of the first five trials and the last five trials, with the factors orientation, constraints, and phase revealed significant effects of orientation, $F(1, 7) = 9.3$, $p = .02$; and constraints, $F(1, 7) = 188.8$, $p < .001$; but not phase, $F(1, 7) = 0.0$, $p = 1.0$. There were no significant interaction effects (all ps $> .1$).

We calculated GT for each subject and orientation to evaluate how gravity affects the 'height' of the index finger's path. Although the shape of GT varies widely across subjects (Figure 5), for most subjects GT is more positive in the tilted orientation than in the natural orientation. Relative to a straight line from the starting position to the final position of the tip of the index finger, decreasing the downward pull by gravity by rotating the setup leads to an increase in the 'height' of the index finger's path. For most subjects the difference in GT between the two orientations is about as large as the magnitude of GT in the natural orientation (Figure 5), suggesting that GT depends to a large extent on gravity.

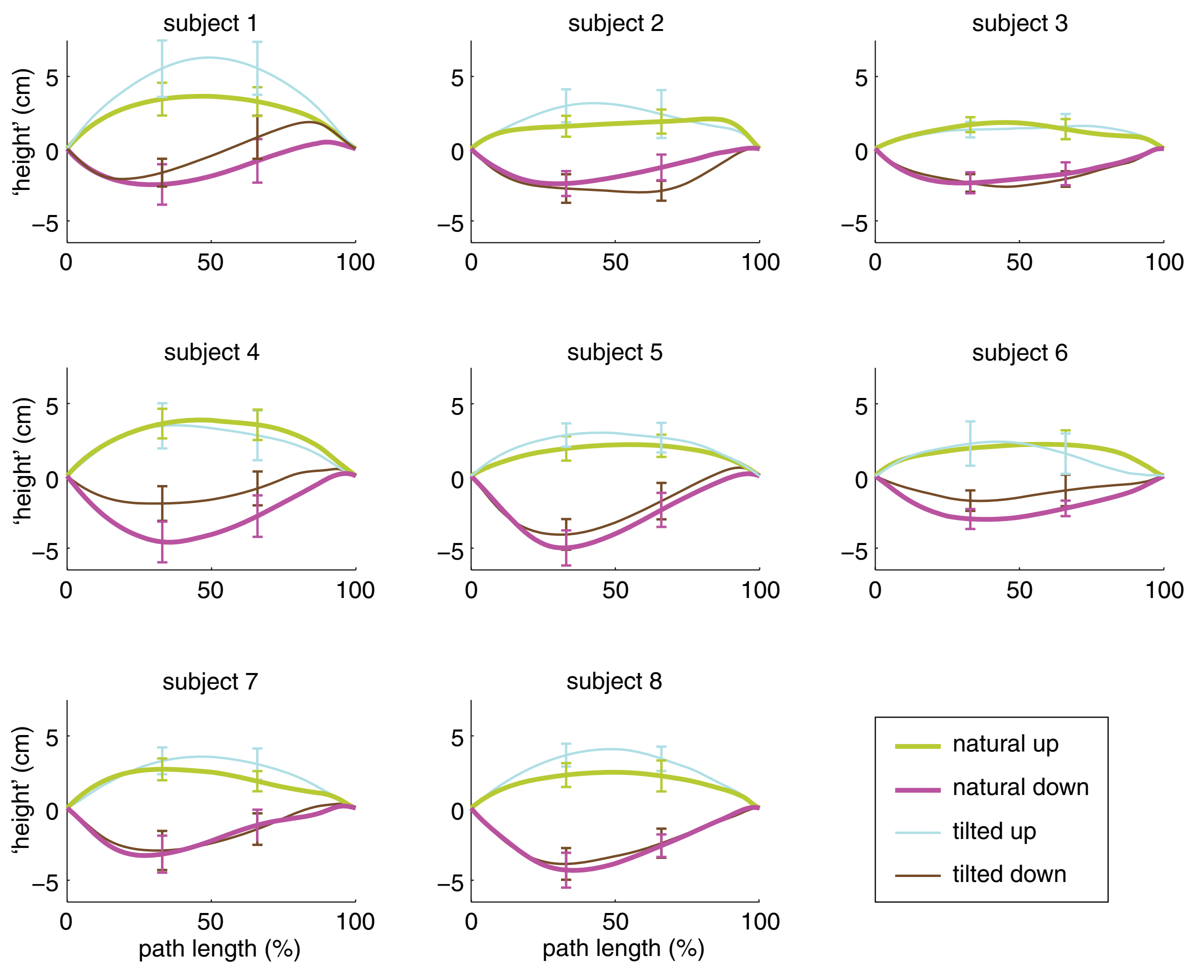

FIGURE 3. The average 'height' per subject and condition. The error bars indicate the associated standard deviations at one third and two thirds of the path length. (Color figure available online).

The shape of the average tangential velocity profile was similar for all conditions (Figure 6). Maximum velocity was larger when subjects started above the rod than when they started below the rod, $F(1, 7) = 9.4$, $p = .02$. There was no significant effect of orientation, $F(1, 7) = 4.4$, $p = .08$, or interaction between orientation and constraints, $F(1, 7) = 1.9$, $p = .2$, on the maximum velocity.

Discussion

We examined whether gravity affects the 'height' of the index finger's path by rotating the whole setup, including the subject, relative to gravity. This rotation resulted in a decrease of the component of gravity that is orthogonal to the main direction of movement to 34% of the normal value. We hypothesized that humans integrate gravity into the movement plan by launching their hand upward, knowing that gravity will bring it down again to end at the goal position, in order to lower the muscle force near the end of the movement to end more precisely. According to this hypothesis, decreasing the downward pull by gravity by rotating the setup would lead to a decrease in the 'height' of the index finger's path (unless subjects failed to consider the rotation). Contrary to our hypothesis, we found that rotating the setup led to an increase in the 'height' of the index finger's path (where 'height' is defined in the direction orthogonal to the main direction of the movement). We can therefore reject our hypothesis.

Our experimental results are qualitatively in line with a direct effect of gravity's downward pull: when gravity hardly counteracted curvature in the 'height' direction the index finger moved 'higher'. Although gravity is not taken into account in movement planning in the way we proposed, it may be taken into account in movement planning in some other way. Further research is needed to examine the possible integration of gravity into the movement plan, because a direct effect of gravity's downward pull does not explain

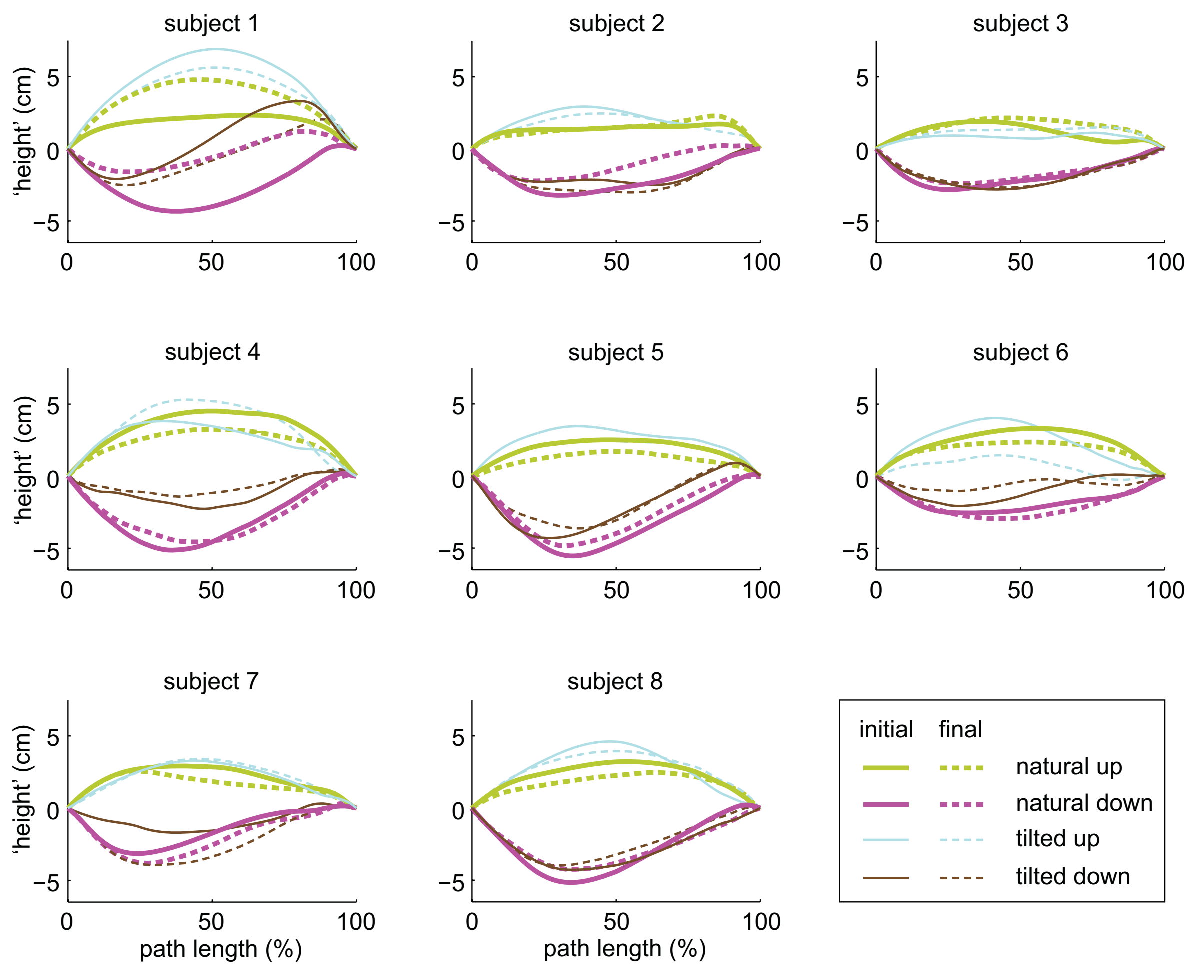

FIGURE 4. The average 'height' per subject and condition for the first five trials (solid lines) and the last five trials (dashed lines) of each condition per subject. (Color figure available online).

why the component of the 'height' of the path that is not related to the local constraints at the start and end of the movement (Figure 5) curves upward for some subjects.

We did not observe practice effects. There were no consistent differences between the trajectories of the first five trials and the last five trials, and there was no significant difference in the extreme values (maximum 'height' or minimum 'height') between these two phases of five trials. Thus although starting and ending movements below a rod, and moving the hand upward while leaning backward by 70°, are not very common movements in daily life, people do not appear to move so inappropriately on the first trials that they needed to adjust their movements. Therefore we think that the effect of gravity in our task is likely to be representative for the effect of gravity in more natural tasks.

We found that GT varies widely across subjects. Because of this variation we think that we have now identified only one factor, gravity, of multiple factors that together result in GT. The variation in the contributions of the factors between subjects presumably causes the variation in GT. Further experimental research is needed to verify this. In our previous study (Verheij et al., 2013) we found that, averaged over the subjects, the 'height' of the index finger's path for the condition 'natural up' and 'natural down' was larger than the averaged 'height' measured in this experiment, while the conditions were similar. In that study we attributed GT to a general tendency to curve upward. From Figure 5 of the present study we can see that not all subjects tend to curve upward. We do not know what caused this difference between our previous and the present study, but it cannot be directly related to tilting the subject because the difference is also present in the natural orientation of the present study.

It could be that other factors than gravity that influence the 'height' of the index finger's path differed between the two orientations. One such factor might be viewing angle (Baker, Donoghue, & Sanes, 1999; Ustinova, Perkins, Szostakowski, Tamkei, & Leonard, 2010). The viewing angle differed slightly between the conditions because most

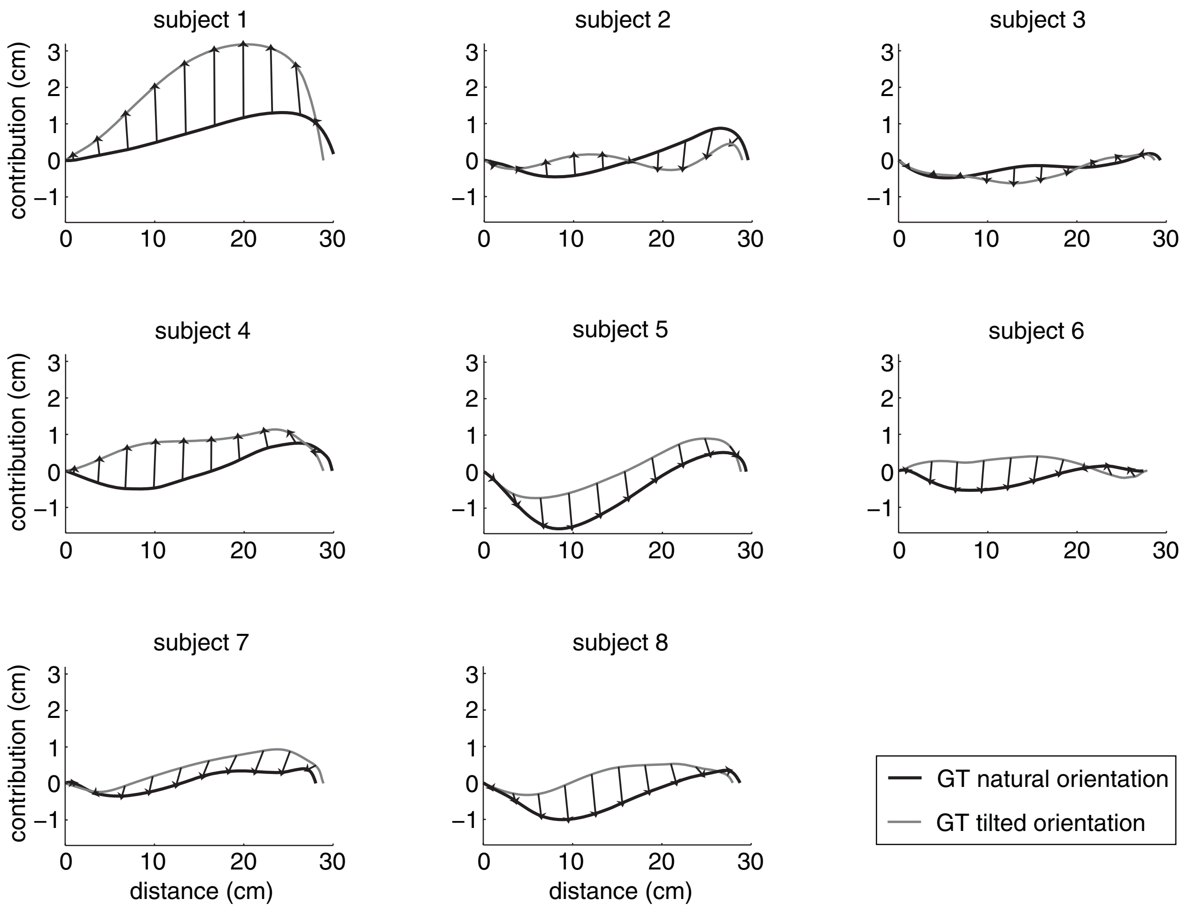

FIGURE 5. The component of the ‘height’ of the path that is not related to the local constraints at the start and end of the movement (GT) for the tilted and natural orientation. The arrows connect samples from the same percentage of path length and point from GT of the first orientation to GT of the second orientation that the subject was exposed to.

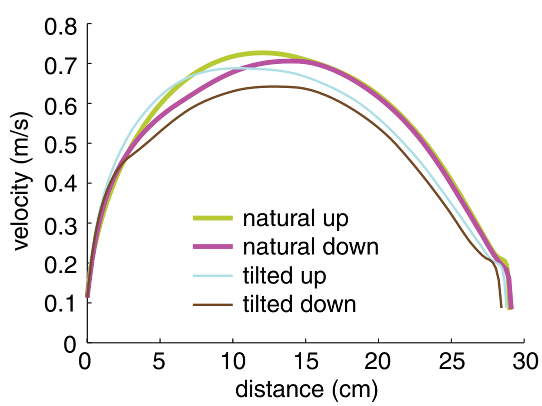

FIGURE 6. The tangential velocity as a function of the distance, per condition, averaged over subjects. All averaging was done in terms of percentage of path length. (Color figure available online).

subjects leaned forward a bit in the natural conditions, such that their head was not touching the headrest (Figure 1A), while their head rested on the headrest in the tilted conditions. However, subject 7, who did not show an observable difference in head position, shows the same effect of orientation as most other subjects (Figure 5). We found that the velocity profile did not differ between the two orientations. We are not aware of any other factors that differed between the two orientations and that may therefore have influenced the difference in ‘height’ of the index finger’s paths.

In sum, we found in a previous study that the height of the index finger’s path is determined by local constraints at the start and end of the movement together with a general tendency that is unrelated to the local constraints. In this study we found that this general tendency is partly caused by gravity. Gravity affects the vertical curvature in human horizontal grasping movements by decreasing the height of the path.

ACKNOWLEDGMENTS

This work was supported by a grant from the Netherlands Organization for Scientific Research (NWO), Vici grant 453-08-004.

REFERENCES

Baker, J. T., Donoghue, J. P., & Sanes, J. N. (1999). Gaze direction modulates finger movement activation patterns in human cerebral cortex. *The Journal of Neuroscience*, *19*, 10044–10052.

Berret, B., Darlot, C., Jean, F., Pozzo, T., Papaxanthis, C., & Gauthier, J. P. (2008). The inactivation principle: Mathematical solutions minimizing the absolute work and biological implications for the planning of arm movements. *PloS Computational Biology*, *4*(10), e1000194.

Crevecoeur, F., Thonnard, J.-L., & Lefèvre, P. (2009). Optimal integration of gravity in trajectory planning of vertical pointing movements. *Journal of Neurophysiology*, *102*, 786–796.

Furuya, S., Osu, R., & Kinoshita, H. (2009). Effective utilization of gravity during arm downswing in keystrokes by expert pianists. *Neuroscience*, *164*, 822–831.

Gaveau, J., & Papaxanthis, C. (2011). The temporal structure of vertical arm movements. *PLoS ONE*, *6*(7), e22045.

Gentili, R., Cahouet, V., & Papaxanthis, C. (2007). Motor planning of arm movements is direction-dependent in the gravity field. *Neuroscience*, *145*, 20–32.

Harris, C. M., & Wolpert, D. M. (1998). Signal-dependent noise determines motor planning. *Nature*, *394*, 780–784.

Hesse, C., Nakagawa, T. T., & Deubel, H. (2010). Bimanual movement control is moderated by fixation strategies. *Experimental Brain Research*, *202*, 837–850.

Jeannerod, M. (1981). Intersegmental coordination during reaching at natural visual objects. In I. J. Long & A. Baddeley (Eds.), *Attention and performance IX* (pp. 153–169). Hillsdale, NJ: Erlbaum.

Jones, K. E., Hamilton, A. F., & Wolpert, D. M. (2002). Sources of signal-dependent noise during isometric force production. *Journal of Neurophysiology*, *88*, 1533–1544.

Oostwoud Wijdenes, L., Brenner, E., & Smeets, J. B. J. (2011). Fast and fine-tuned corrections when the target of a hand movement is displaced. *Experimental Brain Research*, *214*, 453–462.

Papaxanthis, C., Pozzo, T., & McIntyre, J. (2005). Kinematic and dynamic processes for the control of pointing movements in humans revealed by short-term exposure to microgravity. *Neuroscience*, *135*, 371–383.

Papaxanthis, C., Pozzo, T., & Schieppati, M. (2003). Trajectories of arm pointing movements on the sagittal plane vary with both direction and speed. *Experimental Brain Research*, *148*, 498–503.

Paulignan, Y., Mackenzie, C., Marteniuk, R., & Jeannerod, M. (1991). Selective perturbation of visual input during prehension movements. 1. The effects of changing object position. *Experimental Brain Research*, *83*, 502–512.

Pinter, I. J., van Soest, A. J., Bobbert, M. F., & Smeets, J. B. J. (2012). Do we use a priori knowledge of gravity when making elbow rotations? *Experimental Brain Research*, *217*, 163–173.

Saunders, J. A., & Knill, D. C. (2003). Humans use continuous visual feedback from the hand to control fast reaching movements. *Experimental Brain Research*, *152*, 341–352.

Savelsbergh, G. J. P., & van der Kamp, J. (1994). The effect of body orientation to gravity on early infant reaching. *Journal of Experimental Child Psychology*, *58*, 510–528.

Schmidt, R. A., Zelaznik, H., Hawkins, B., Frank, J. S., & Quinn, J. T. (1979). Motor-output variability: a theory for the accuracy of rapid motor acts. *Psychological Review*, *86*, 415–449.

Schot, W. D., Brenner, E., & Smeets, J. B. J. (2010). Posture of the arm when grasping spheres to place them elsewhere. *Experimental Brain Research*, *204*, 163–171.

Smeets, J. B. J., & Brenner, E. (1999). A new view on grasping. *Motor Control*, *3*, 237–271.

Smeets, J. B. J., & Brenner, E. (2001). Independent movements of the digits in grasping. *Experimental Brain Research*, *139*, 92–100.

Trommershäuser, J., Gepshtein, S., Maloney, L. T., Landy, M. S., & Banks, M. S. (2005). Optimal compensation for changes in task-relevant movement variability. *The Journal of Neuroscience*, *25*, 7169–7178.

Uno, Y., Kawato, M., & Suzuki, R. (1989). Formation and control of optimal trajectory in human multijoint arm movement. *Biological Cybernetics*, *61*, 89–101.

Ustinova, K. I., Perkins, J., Szostakowski, L., Tamkei, L. S., & Leonard, W. A. (2010). Effect of viewing angle on arm reaching while standing in a virtual environment: Potential for virtual rehabilitation. *Acta Psychologica*, *133*, 180–190.

Van de Kamp, C., & Zaal, F. T. J. M. (2007). Prehension is really reaching and grasping. *Experimental Brain Research*, *182*, 27–34.

Verheij, R., Brenner, E., & Smeets, J. B. J. (2013). Why are the digits' paths curved vertically in human grasping movements? *Experimental Brain Research*, *224*, 59–68.

Received November 1, 2012
Revised April 15, 2013
Accepted April 17, 2013