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Misjudgment of Direction Contributes to Curvature in Movements Toward Haptically Defined Targets

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The trajectories of arm movements toward visually defined targets are curved, even if participants try to move in a straight line. A factor contributing to this curvature may be that participants systematically misjudge the direction to the target, and try to achieve a straight path by always moving in the perceived direction of the target. If so, the relation between perception of direction and initial movement direction should not only be present for movements toward visually defined targets, but also when making movements toward haptically defined targets. To test whether this is so, we compared errors in the initial movement direction when moving as straight as possible toward haptically defined targets with errors in a pointer setting task toward the same targets. We found a modest correlation between perception of direction and initial movement direction for movements toward haptically defined targets. The amount of correlation depended on the geometry of the task.

Keywords: goal-directed movements, haptics, movement planning, misjudgment of direction, visual space

If participants are instructed to make a straight hand movement to a visually specified target, the movement path is slightly, but systematically, curved. This systematic curvature is shown in various tasks and circumstances. Several causes related to the biomechanics of the arm have been proposed (Boessenkool, Nijhof, & Erkelens, 1998; Bongers & Zaal, 2010; Osu, Uno, Koike, & Kawato, 1997). It is likely that biomechanical factors are particularly important in situations in which the dynamics play an important role: when moving fast. An important role for biomechanical factors is supported by the fact that some parts of the workspace show trajectories with more curvature than other parts of the workspace (Atkeson & Hollerbach, 1985; Wolpert, Ghahramani, & Jordan, 1994). However, it is clear that biomechanical arguments cannot explain all curvature. For instance, there are differences in curvature for movements with the same start and end point (Desmurget, Jordan, Prablanc, & Jeannerod, 1997; Desmurget, Prablanc, Jordan, & Jeannerod, 1999; Papaxanthis, Pozzo, & Schieppati, 2003). It has also been shown that participants can move more straight if they are asked to do so (Desmurget et al., 1997; Desmurget et al., 1999; Osu et al., 1997).

One biomechanical explanation of why movements are curved is based on the nonlinear relation between positions in space and joint angles (Hogan, Bizzi, Mussa-Ivaldi, & Flash, 1987; Morasso, 1981). If movements are planned to be straight in joint space, they will be curved in the workspace (Flanagan & Ostry, 1990; Hollerbach & Flash, 1982; Kaminski & Gentile, 1986; Rosenbaum, Loukopoulos, Meulenbroek, Vaughan, & Engelbrecht, 1995; van Beers, Haggard, & Wolpert, 2004). However, movements may be planned in the workspace rather than in joint space (Abend, Bizzi, & Morasso, 1982; Flash & Hogan, 1985; Ghilardi, Gordon, & Ghez, 1995; Gordon, Ghilardi, & Ghez, 1994; Haggard, Hutchinson, & Stein, 1995; Hollerbach & Flash, 1982; Morasso, 1981), or in a combination of the two (Cruse, Wischmeyer, Bruwer, Brockfeld, & Dress, 1990; Van Thiel, Meulenbroek, & Hulstijn, 1998).

A second possible biomechanical reason for following a curved trajectory is that a straight trajectory in the workspace need not be optimal. Models that produce curved trajectories include ones that minimize torque change (Barreca & Guenther, 2001; Uno, Kawato, & Suzuki, 1989), energy consumption (Alexander, 1997; Cruse, 1986), or joint rotation (Nakano et al., 1999). However, Kistemaker, Wong, and Gribble (2010) showed that energy consumption and torque change were not being optimized in fast planar arm movements. None of the above models can explain the entire range of curvature in movement trajectories (Gielen, 2009).

Beside the various biomechanical origins of curvature in goal-directed movements, there may also be perceptual causes. Two possibilities have been raised: a distortion of visual space (Flanagan & Rao, 1995; Wolpert, Ghahramani, & Jordan, 1994; Wolpert, Ghahramani, & Jordan, 1995) or a misjudgment of direction (Brenner, Smeets, & Remijnse-Tamerius, 2002; de Graaf, Sittig, & Denier van der Gon, 1991, 1994; Smeets & Brenner, 2004).

A distortion of visual space would make a curved movement trajectory give the visual impression of being straight. Wolpert, Ghahramani, and Jordan (1994) asked participants to make transverse and sagittal movements in the horizontal plane with a digitizing mouse. The transverse movements that the participants made

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were generally curved, whereas the sagittal movements were almost straight. These movements were compared with a curvature-perception experiment, in which the participants had to judge whether the trajectory of a moving dot was curved to the left or to the right, to asses what participants perceived as straight. What participants perceived as straight was correlated with the curvature in their transverse movements. The authors concluded that a perceptual distortion of visual space caused the curvature in goal-directed movements. In a later experiment, Wolpert, Ghahramani, and Jordan (1995) altered the visual feedback about the movements of the unseen hand in small increments so that straight movements would gradually look more and more curved. Participants spontaneously curved their movements in the direction opposite to the perturbation to reduce the visually perceived curvature. Wolpert et al. concluded that hand trajectories were planned in visually based coordinates and that the desired trajectory is straight in visual space.

The second perceptual explanation is a misjudgment of direction at the start of the movement. In this explanation, the misjudgment of direction causes the initial direction of the movement to deviate systematically from straight toward the target. Direction continues to be misjudged during the movement, but by constantly reevaluating the direction errors are corrected as the movement progresses and the target is still reached, but by following a curved path. The explanation of a misjudgment of direction is consistent with the existence of populations of direction-selective cortical cells that are activated just before movement onset (Georgopoulos, Schwartz, & Kettner, 1986). This inspired de Graaf and colleagues (1991) to test whether direction is a control variable for goal-directed movements. They showed that similar errors are made in judging the direction toward a target as are found in the initial movement direction of a movement toward the same target.

A relation between movement curvature and direction perception was also found in studies from our lab (Brenner et al., 2002; Smeets & Brenner, 2004). Brenner et al. (2002) explored the influence of an oriented bar on the curvature of movements toward that bar in a movement task and a perception task. The orientation of the bar affected both the curvature in the movement trajectory and the curvature of a moving dot's path. The critical finding was that the orientation of the bar did not affect curvature judgments for a static curved line, which implies that the curvature in hand movements is not caused by a general distortion of visual space. From this combination of results, Brenner et al. concluded that a misjudgment of direction caused a part of the curvature in the movement path. Further support for this conclusion was provided by Smeets and Brenner (2004). They argued that if curvature is attributable to starting in the wrong direction, the deviation from a straight line should be asymmetrically distributed, with errors building up in the initial part of the trajectory. They reported that curvature is asymmetrically distributed over the paths, with larger deviations in the second half of the path.

If a misjudgment of direction when planning goal-directed movements contributes to a curved trajectory, the relation between initial movement direction and misjudgment of direction should not only hold for visual targets, but also be present in other modalities. In haptics, large systematic errors in perception of direction are made in a pointer setting task (Kappers & Koenderink, 1999). If the movement curvature is partly caused by a misjudgment of direction, the large systematic errors in haptic perception of direction should lead to errors in initial movement direction for movements toward haptically defined targets.

Experiment 1

In Experiment 1a, we will compare the initial movement direction in movements toward haptically defined targets with orienting a pointer toward the same targets. For comparison, we will also examine the initial movement direction in movements toward visually defined targets with orienting a pointer toward the same targets in Experiment 1b. If errors in initial movement direction and in orienting a pointer are correlated, it is likely that a misjudgment of initial direction contributes to the curvature in goal-directed movements. As we expect larger directional errors in the haptic modality than in vision, we expect a higher correlation in Experiment 1a than in Experiment 1b.

Method

Participants and experimental setup. This study is part of a program that has been approved by the ethics committee of the faculty of Human Movement Sciences. A group of 10 participants signed an informed consent form before participating in the study. There were 9 right-handed participants and 1 left-handed participant. The participants were seated in front of a table (see Figure 1). In Experiment 1a they were blindfolded. On the table were three start locations on the right and two target locations on the left for right-handed participants, and the opposite for the left-handed participant. This resulted in six combinations of start and target location. The start locations were holes with a diameter of three mm. A pinhead with a diameter of about three mm was situated at the target location of the current trial. A pointer could be placed in one of the three holes that served as start locations. The pointer was seven cm long, three mm wide, and could rotate around a pin at its center. The start and target locations were placed in such a way that they were comfortably reachable for all participants, without extreme joint angles. The positions were the same for all participants. The combinations of start and target location were either 51 or 40 cm apart. Data were recorded with an Optotrak system at a sampling rate of 200 Hz.

Procedure. Each experiment consisted of two tasks, a pointer-setting task and a slow movement task. The order of the tasks and experiments was randomly assigned across participants. Each task had 60 trials, 10 for every combination of start and target location. The order of the trials was semirandom, ensuring that both the start and target location differed between consecutive trials.

In the slow movement task in Experiment 1a, the participants felt the target with the nonpreferred hand during the whole trial and were instructed to move with the tip of the index finger of the preferred hand over the table from start to target location. Right-handed participants moved to the left, and the left-handed participant to the right. Participants were instructed to move as straight as possible toward the target, and to make sure to arrive at the target. They were not explicitly instructed to move at a certain speed, but the instruction regarding accuracy made them move quite slowly. An infrared emitting diode (IRED) was attached to the nail of the index finger of the participant's preferred hand to record the slow movements. In the pointer-setting task participants oriented a pointer that was at one of the start locations toward a

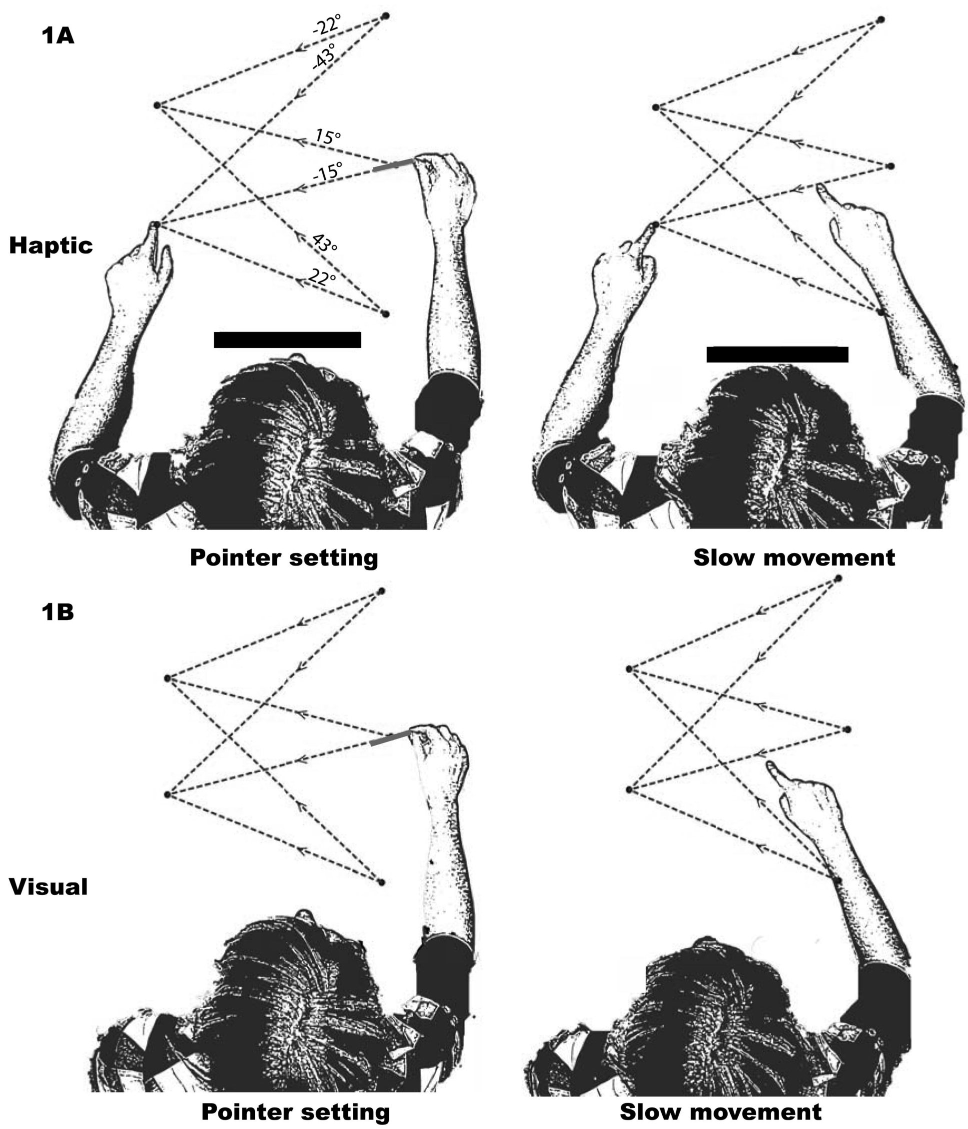

Figure 1. Experimental setup for Experiment 1 (top, Experiment 1a; bottom, Experiment 1b), as seen from above for a right-handed participant. The three start locations (or locations where pointer is placed) are on the right, and the two target locations on the left. The pointer-setting task is shown on the left with an example how the pointer (red line) was placed, and the slow movement task is on the right. The dashed lines indicating the six possible combinations of start and target locations were not visible in the experiment.

target location. For recording the orientation of the pointer, IREDs were placed on both its ends. The participant rotated the pointer with the preferred hand, and felt the target with the other hand. Once they reported that the pointer had the correct orientation, the orientation was recorded for 1 second.

In Experiment 1b, the participants were seated in front of the same table as in Experiment 1a, but in this experiment they moved their hand or oriented the pointer toward a visually presented target (Figure 1b), rather than toward a target that they felt. The participants could see everything from start location to target location and were not limited in where they were allowed to look, but were instructed to keep their head at the same position. They were allowed to see their hand, because it has previously been shown that visual feedback about the hand does not affect the curvature (Palluel-Germain, Boy, Orliaguet, & Coello, 2004) or the initial movement direction (de Graaf, Sittig, & Denier van der Gon, 1994) of hand movements over a surface.

Data analysis. We defined the start and end point of the movement as the points at which the signal could no longer be distinguished from noise. The trajectory was defined as noise if the movement direction of two subsequent pairs of samples differed by more than 90 degrees from the main movement direction. The transitions between movement and noise were determined by moving backward and forward in time from the moment of peak velocity. These transitions were defined as the beginning and the end of the movement. The initial movement direction was defined by a line between the start location and where the trajectory reaches a radial distance of 3.5 cm from the start location. We chose a radial distance of 3.5 cm because this matched the distance between the tip of the pointer and its pivot point. This distance corresponded to 6 – 9% of the movement path. The angle between this line and the line from start to target location was the initial error in the movement task. A deviation away from the participant (clockwise for the right-handed participants) was defined as positive. The error in the pointer-setting task was defined as the angle between the pointer and a line connecting start location and target location.

For each participant in each task, median errors were determined for each combination of start and target location. Medians were used because there were occasional outliers and by using the median we did not have to detect or define outliers. A regression analysis was performed to examine to what extent errors in perception are responsible for errors in initial movement direction. To consider the trends within subjects despite large (random) differences between participants (i.e., to consider the correlations between the six points per participant), we used a Generalized Estimating Equation (GEE) to define the relation between errors in initial movement direction and errors in perception of direction.

To separately examine the correlations between the tasks that arise from participant-specific biases and ones that arise from errors specific to combinations of start and target location, we also conducted two additional regression analyses. To take into account that the errors in both the pointer setting task and the initial movement direction have uncertainty, orthogonal least square (OLS) regression analyses were performed. To examine the participant-specific biases, the means of the median errors for the six combinations of start and target location were calculated per participant, and an OLS regression was performed. To examine the errors specific to combinations of start and target location, a second OLS regression was performed on the mean of the median errors for the 10 participants per combination of start and target location.

The regression analyses described above are best understood by considering the two extremes of the possible relationship between the error in initial movement direction and the error in the pointer-setting task. If the direction is misjudged systematically and the hand moves in the perceived direction, we would expect a slope that approaches 1 and an intercept of about 0 (points scattered around the unity line). On the other hand, if directions are not misjudged systematically, or if the judgments of direction that determine how the hand moves are unrelated to judgments of direction when setting the pointer, no correlation is expected in the data.

Results

On average, participants took 3.3 ± 1.6 s to make the movements toward haptically defined targets and 2.0 ± 1.1 s to make the movements toward visually defined targets (means ± standard deviations). As expected, there were systematic errors in both tasks (results are shown in Figures 2 and 3). Regression analyses were performed to examine to what extent errors in perception could be responsible for errors in initial movement direction. Figure 2A shows the median errors of initial movement direction and of the pointer-setting task for Experiment 1a. The data points scattered around the unity line, but with a slope that was considerably

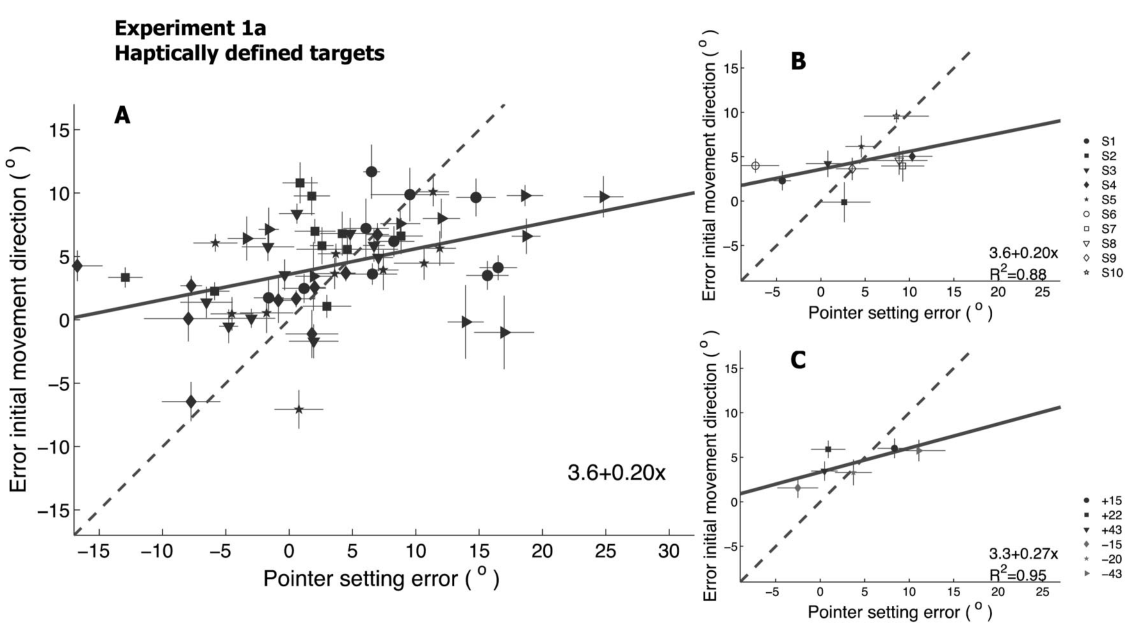

Figure 2. Results of Experiment 1a. Relation between the error in the pointer-setting task and the error in the initial movement direction. A, Each data point represents the median value for one participant and one of the combinations of start and target location. The error bars represent the SEM across the 10 trials. B, Each data point represents the mean of the six medians of one participant. The error bars represent the SEM across combinations of start and target location. C, Each data point represents the mean of the 10 medians for one combination of start and target location. The error bars represent the SEM across participants.

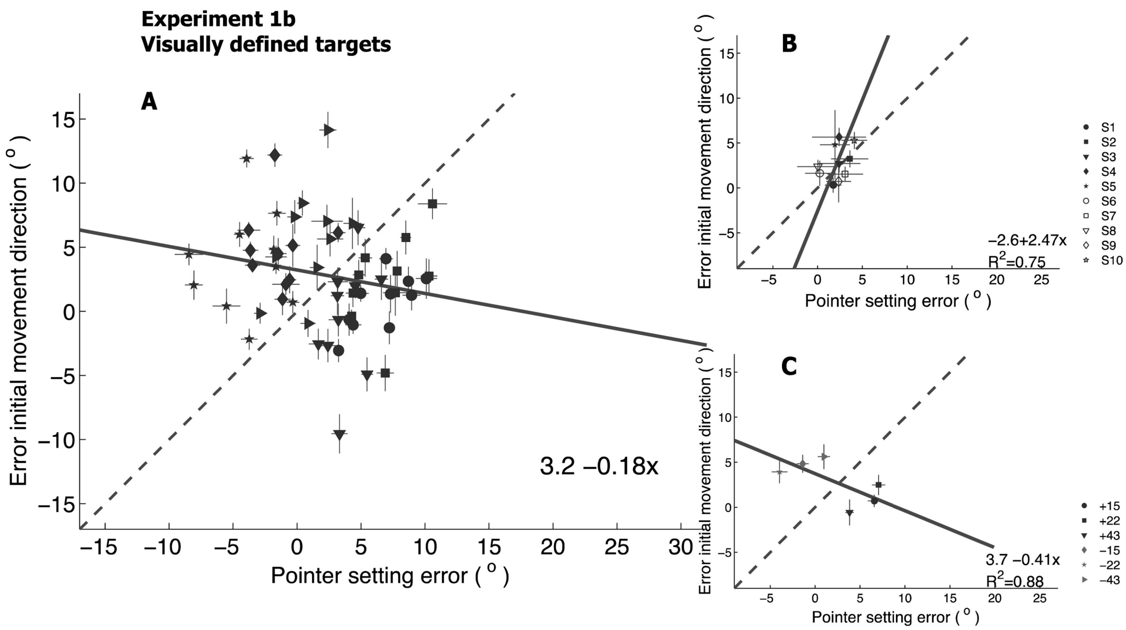

Figure 3. Results of Experiment 1b. Relation between the error in the pointer-setting task and the error in initial movement direction. Details as in Figure 2.

smaller than 1, for all three analyses. The GEE regression analysis showed that the errors were related by a slope of 0.2 ($p < .01$, C.I. = 0.10 – 0.30). The OLS regression analyses revealed similar slopes to those of the overall analysis across participants after averaging the median errors across the six combinations of start and target location (0.20; $R^2 = 0.88$; Figure 2B) and across combinations of start and target location after averaging the median errors across participants (0.27; $R^2 = 0.95$; Figure 2C).

The systematic biases in initial movement direction in Experiment 1b were about as large as in Experiment 1a. The biases in the pointer-setting task were larger for Experiment 1a than for 1b. The clear correlation between errors in these two parameters that was present in the haptic experiment was not present in the visual experiment (see Figure 3). The GEE regression analysis revealed a slope of −0.18, which was not significantly different from 0 ($p = .18$; C.I. = −0.45 – 0.09; Figure 3A). When averaged per participant or per combination of start and target location, the slopes became 2.47 ($R^2 = 0.75$; Figure 3B) and −0.41 ($R^2 = 0.88$; Figure 3C), respectively. When averaged per combination of start and target location, a clear separation between two sets of combinations of start and target locations was found (Figure 3C). The separation was between the movements away from the body (under the unity line) and movements toward the body (above the unity line).

Discussion

This experiment compared errors in the initial movement direction for slow movements toward haptically and visually defined targets with setting a pointer toward the same targets. If the curvature in hand movements is partly caused by a misjudgment of direction, the errors in initial movement direction should correlate with the errors in perception of direction. In Experiment 1a we found that the slopes of the analyses (see Figure 2) were significantly different from 0, but also from 1. That the slope is different from 0 suggests that the initial movement direction is partly based on the perceived direction. That the slope is considerably lower than 1 suggests that a misperception of direction only accounts for part of the variability.

For Experiment 1b we found that overall the errors in initial movement direction were not related to errors in perception of direction for visually defined target. This confirms our expectation that there would be a better correlation between errors in initial movement direction and errors in pointer settings for haptically than for visually defined targets. That there was no correlation in Experiment 1b was not expected from the literature, as visual perception of direction and initial movement direction were previously found to have similar errors (de Graaf, Sittig, & Denier van der Gon, 1991). Possibly, the systematic errors from perceptually misjudged direction in Experiment 1b are much smaller than errors from other origins. Errors in the pointer-setting task were larger for haptics than for vision, which is in agreement with the larger errors for haptics than for vision when setting two bars to be parallel (Kappers & Schakel, 2011).

When we look at Figure 3C we see a separation between the combinations of start and target location that result in movements and pointer settings that are directed away from the body and ones that are directed toward the body. We therefore performed two separate regression analyses post hoc on the combinations of start and target location away and toward the body for the averaged data shown in Figure 3A. The GEE regression analyses revealed clearly positive slopes of 0.57 for movements away from the body and 0.31 for movements toward the body (not shown). Thus, if movements toward the body and ones away from the body are treated separately, the error in initial movement direction and the error in the pointer-setting task to visually defined targets do have a positive correlation. The slope for movements away from the body is larger than the slope for movements toward the body.

A difference between our study and the study of de Graaf, Sittig, and Denier van der Gon (1991) is that they looked at movements that were mainly away from the body, whereas we looked at movements that were mainly sideways. In another study, de Graaf, Denier Van Der Gon, and Sittig (1996) showed that the pattern of errors in initial movement direction for movements to various targets shifts when the starting point and targets are all shifted to the right. Although these were still movements away from the body, and the errors in initial movement direction were not compared with errors in perception of direction, the dependence on egocentric position suggest that the relation between initial movement direction and perception of direction may be related to the body, and therefore be different for lateral and sagittal movements. As already mentioned, lateral movements are also more curved than sagittal movements in the horizontal plane (Wolpert, Ghahramani, & Jordan, 1994).

Experiment 2

In Experiment 1a, a modest relation was found between the error in initial movement direction and the perceived direction toward haptically defined targets. This modest relation was specific for haptically defined targets. No such relation was found for an almost identical experiment with visually defined targets (Experiment 1b). However, when we later analyzed combinations of start and target locations away and toward the body separately for Experiment 1b, we found clearly positive slopes, that were steeper than the slopes in Experiment 1a. Moreover, the slope for combinations of start and target locations that gave rise to movements away from the body were higher than those for movements toward the body.

de Graaf, Sittig, and Denier van der Gon (1991) found similar errors for orienting a pointer toward visual targets and for the initial movement direction toward the same targets. However, they used a different task geometry than in our study; only movements away from the body were tested. The direction to the target may determine the contribution of errors in direction judgments to both tasks. Kappers and Koenderink (1999) found larger systematic errors in pointer-setting for haptically defined targets in the lateral direction than in the sagittal direction. Even larger systematic deviations were found when participants had to set two bars to be parallel in the mid sagittal plane (Kappers, 2002). Goal-directed movements in the sagittal direction are nearly straight in the horizontal plane (Flash & Hogan, 1985; Morasso, 1981; Wolpert, Ghahramani, & Jordan, 1994), but large curvature in movement trajectories was found in the midsagittal plane (Atkeson & Hollerbach, 1985). Considering the larger systematic errors in the mid sagittal plane we repeated Experiment 1 in that plane (for movements and pointer setting away from the body). In addition, we examined the possible difference between movements away and movements toward the body. Preliminary results of this experiment were published in conference proceedings (van der Graaff, Brenner, & Smeets, 2012).

Method

A group of 10 right-handed participants gave their informed consent to participate in this study. These 10 participants performed Experiment 2a and 2c, and 8 of them performed Experiment 2b. The participants were seated in front of a board. For Experiments 2a and 2c they were blindfolded. The board was in the participants' mid sagittal plane (see Figure 4). On one side of the board there were three holes that served as start locations. On the other side of the board there were two pinheads that served as target locations. The combinations of start and target location were 51 to

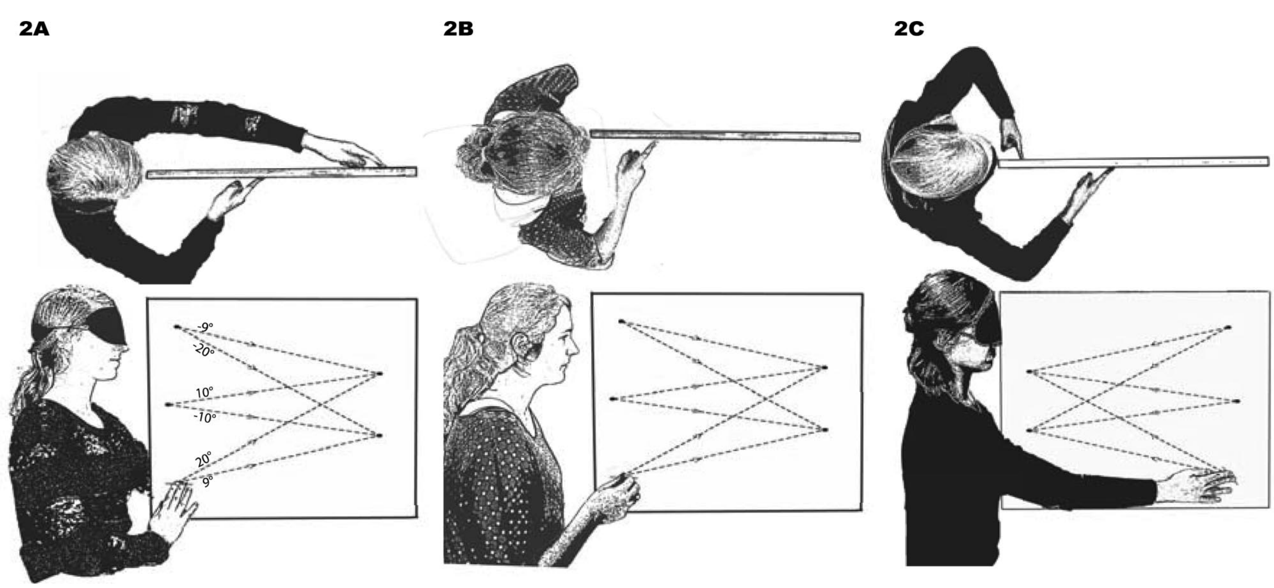

Figure 4. Experimental setup for Experiment 2. Top, Top view of the slow movement task. Bottom, Side view of the pointer-setting task.

58 cm apart. For Experiments 2a and 2c the participants felt the target with their left hand on the left side of the board. They oriented the pointer or moved with the right hand on the right side of the board toward where they felt their left finger on the left side of the board. For Experiment 2b participants oriented the pointer or moved their hand toward visually defined targets. By rotating the board 180 degrees, we could change the task geometry. For Experiments 2a and 2b the start locations were situated at the near end of the board, and the target locations at the far end of the board, so that the participants made movements or oriented the pointer away from the body. For Experiment 2c the start locations were at the far end of the board. In all cases, an upward deviation was defined as positive.

Results

On average, participants took 3.1 ± 1.4 s to make the movements in Experiment 2a, 2.3 ± 2.3 s in Experiment 2b and 3.2 ± 1.8 s to make the movements in Experiment 2c. Participants ended on average 1.2 ± 2.2 cm below and 3.2 ± 2.4 cm in front of the target when making movements in Experiment 2a, and 0.6 ± 2.1 cm below and 2.4 ± 2.4 cm in front of the target when making movements in Experiment 2c.

The relationship between pointer settings and initial movement direction was similar to what we found for the horizontal plane in Experiment 1, both for haptically defined targets and visually defined targets. There were positive slopes for the relation between initial movement direction and pointing for haptically defined targets, but not for visually defined targets (Figures 5, 6, and 7). The slope for movements and pointing toward haptically defined targets away from the body (0.39; CI = 0.23 – 0.53; Figure 5A) was slightly steeper than the slope for movements and pointing toward the body (0.22; CI = 0.09 – 0.35; Figure 7A) and than the slope in Experiment 1. There was no relation between errors in initial movement direction and pointing toward visually defined targets (0.06; CI = −0.10 – 0.22; Figure 6A).

To further explore the difference between Experiment 2a and 2c we also calculated the slope of the combinations of start and target location per participant. The mean slope was 0.95 for movements away from the body (Experiment 2a) and 0.29 for movement toward the body (paired t test $t(9) = 1.94$, $p = .085$). All dots are near the unity line for Experiment 2a, whereas the dots are to the right of the unity line for Experiment 2c. The dots being to the right of the unity line indicates a systematic bias to orient the pointer upward.

Discussion

In this experiment we compared the relation of misjudgment of direction to the initial movement direction in the midsagittal plane. We confirmed our findings from Experiment 1 that the initial movement direction was related to the perception of direction for haptically defined targets, but not for visually defined targets. A possible explanation is that systematic errors in judging the direction toward visually defined targets are too small in comparison to other systematic sources of movement variability to introduce a clear relation between initial movement direction and perception of direction.

There was an overall bias to orient the pointer upward in the pointer-setting task when orienting the pointer toward the body that was not seen when orienting the pointer away from the body. This systematic bias was not present in the initial movement direction, suggesting that we know the direction toward the target, but make an error in judging the orientation of the pointer. The felt orientation of a bar is known to be systematically biased (Kappers & Koenderink, 1999).

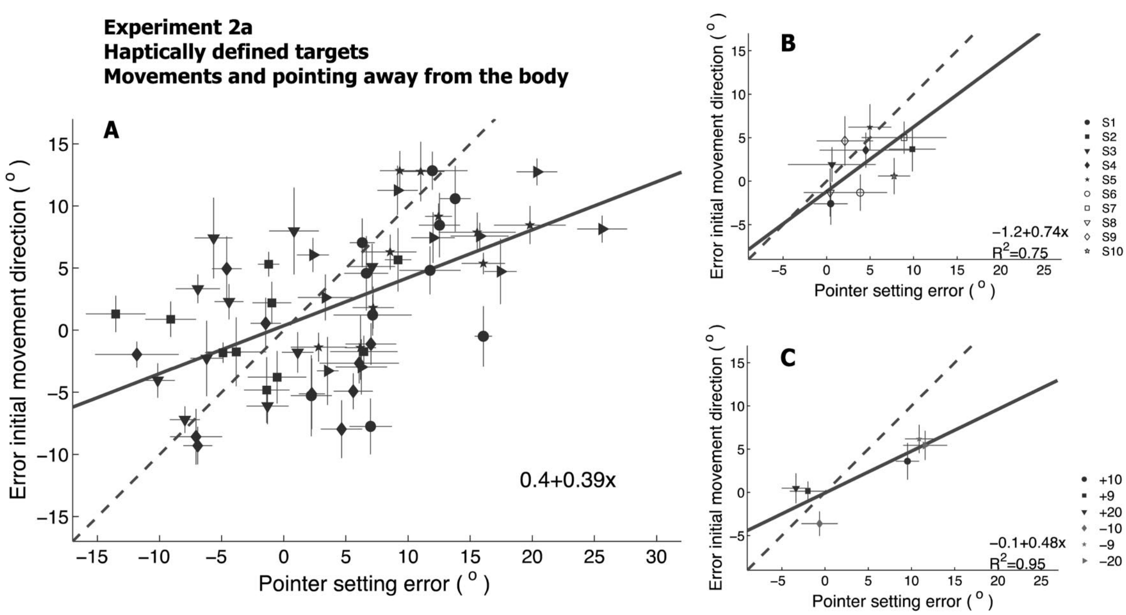

Figure 5. Results of Experiment 2a. Relation between the error in the pointer-setting task and the error in initial movement direction. Details as in Figure 2.

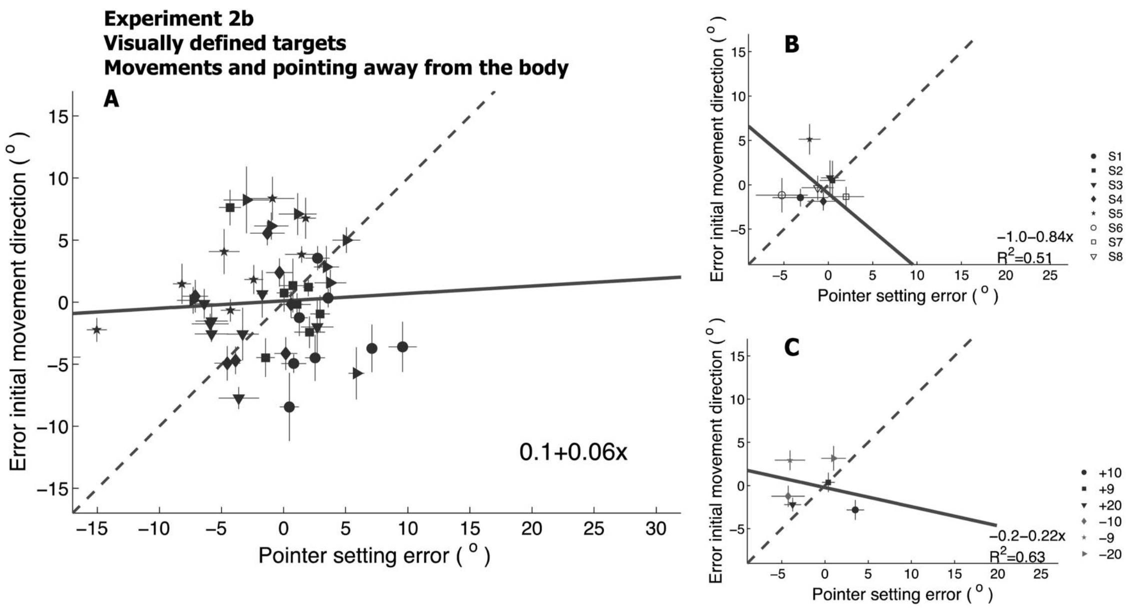

Figure 6. Results of Experiment 2b. Relation between the error in the pointer-setting task and the error in initial movement direction. Details as in Figure 2.

General Discussion

In this study we investigated the relation between the perception of direction and the initial movement direction toward haptically defined targets. If the curvature in goal-directed movements is caused by a misjudgment of direction, the initial movement direction of goal-directed movements should be related to errors in judging direction. We found that errors in initial movement direction were indeed related to errors in perception of direction for movements toward haptically defined targets. For all three experiments toward haptically defined targets, the errors in initial movement direction were correlated with the errors in the pointer-setting task.

Miall and Haggard (1995) found no relation between haptic perception and movements toward haptically defined targets, which might seem to contradict our findings. However, the important difference between their experiments and ours is that they

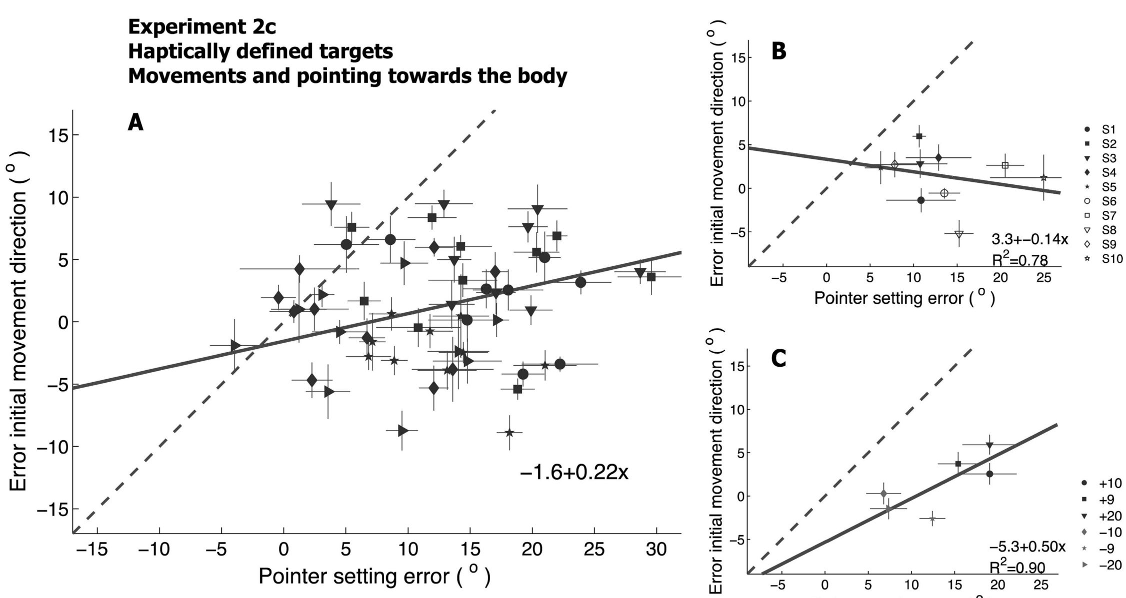

Figure 7. Results of Experiment 2c. Relation between the error in the pointer-setting task and the error in initial movement direction. Details as in Figure 2.

related movement curvature with haptically perceived curvature, rather than initial movement direction with the perceived direction to the target point. If a misjudgment of direction contributes to the curvature in goal-directed movements, a relation would not have to be present between haptic perception of curvature and curvature in goal-directed movements. Just as Brenner et al. (2002) showed that a slanted bar influences the curvature of goal-directed movements and judgments about a moving dot's path, but not judgments about a static line's curvature. The fact that Miall and Haggard did not find a relation whereas we did supports the notion that curvature is not due to a general deformation of (haptic) space.

In Experiments 2a and 2c participants received no feedback about whether they reached the location of the target, whereas in Experiments 1a, 1b and 2b they did. In Experiment 1a feedback about whether they reached the location of the target was obtained from touching the other hand. In Experiment 1b and 2b it was obtained from seeing the moving hand and the target. The feedback that the participants received in Experiments 1a and 1b could not have influenced subsequent movements much, because the errors did not clearly decrease over the course of the experiment. To examine this we calculated a separate median error for every combination of start and target location for the first half and the second half of the experiment (for every participant). There was no difference between the errors in the first half and the second half of each experiment, except for the slow movement task of Experiment 2b. For this experiment the errors were 1 degree smaller (0.72 ± 4.9 vs. -0.45 ± 4.4 degrees) in the second half of the experiment compared with the first half. Note that the lack of systematic changes in initial movement direction does not imply that there are no corrections during the movement to bring the hand to the target.

Our study shows that curvature in movement trajectories could partly be explained by a misjudgment in direction. This is analogous with the observation that participants follow curved paths when walking toward a target if their judgments of direction are artificially disrupted by making them wear prism glasses (Rushton, Harris, Lloyd, & Wann, 1998). Rushton et al. interpreted this as evidence that participants were continuously guided by their judgments of egocentric direction. If a person consistently misperceives the direction toward the goal, the person will systematically walk in a slightly different direction than straight toward the target. By constantly reevaluating the direction to the goal, and moving with a constant heading error attributable to the perceptual error, the person will reach the target by following a curved trajectory. Whether systematic misperceptions of the direction toward the target are responsible for the curvature in goal-directed movements in a similar manner as proposed for walking remains to be investigated.

In a study by de Graaf, Denier Van Der Gon, and Sittig (1996), the errors in the initial direction of slow arm movements were not influenced by the length of the trajectory or by the distance between the whole stimulus configuration and the body. de Graaf et al. interpret these results in relation to the vector-coding of movements (Bock & Eckmiller, 1986; Desmurget, Pelisson, Rossetti, & Prablanc, 1998). However, it has also been proposed that some movements are planned in terms of end points rather than movement vectors (Bizzi, Hogan, Mussa-Ivaldi, & Giszter, 1992; van den Dobbelsteen, Brenner, & Smeets, 2001). de Grave, Brenner, and Smeets (2004) proposed a combination of vector and position coding. de Grave et al. investigated hand movements on the Brentano illusion, a combination of the two versions of the Müller-Lyer illusion in which the two halves of a single line appear to be of different lengths although they are not. They argued that the illusion is an illusion of length and not of position. Therefore it will only have an effect if the judged length is relevant, and thus only if movements are coded in terms of vectors. The illusion indeed had an effect when the movement was along the illusion but not when it was from outside the illusion. However, even when moving along the illusion the effect of the illusion was smaller than expected on the basis of the perceptual effect of the illusion. How much smaller depended on the visibility of the target and the hand. This was interpreted as vector coding being combined with position coding in a manner that depends on the circumstances. Recently, more evidence for a combination of vector and position coding has been found. It has been shown that individual neurons can be tuned to target location and initial movement direction simultaneously (Pearce & Moran, 2012). Moreover, Hudson and Landy (2012) confirmed, by analyzing the scatter in endpoints of repeated movements, that both position coding and vector coding are used in the same task.

If goal-directed movements arise from a combination of vector and position coding, our results suggest that vector coding plays a larger role in movements away from the body than in movements toward the body. This may be because we have more experience with manipulating targets close to the body and therefore have a better sense of position nearby the body. Support for position coding for movements ending near the body can be found in the presence of neurons in the monkey precentral cortex which, when stimulated, give rise to movements ending near the mouth (Graziano, Taylor, & Moore, 2002). This end position was reached for different starting positions, which suggests that these neurons code the endpoint of movements toward the body rather than a movement vector.

We found a relation between the perception of direction and the initial movement direction toward haptically defined targets. This supports the idea that a misjudgment of direction could contribute to curvature in trajectories for goal-directed movements. The extent to which the errors in perception of direction and initial movement direction are related differs for different task geometries.

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