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Curved movement paths and the Hering illusion: Positions or directions?

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When trying to move in a straight line to a target, participants produce movement paths that are slightly (but systematically) curved. Is this because perceived space is curved, or because the direction to the target is systematically misjudged? We used a simple model to investigate whether continuous use of an incorrect judgement of the direction to the target could explain the curvature. The model predicted the asymmetries that were found experimentally when moving across a background of radiating lines (the Hering illusion). The magnitude of the curvature in participants' movements was correlated with their sensitivity to the illusion when judging a moving dot's path, but not with their sensitivity when judging the straightness of a line. We conclude that a misjudgement of direction causes participants to perceive a straight path of a moving dot as curved and to produce curved movement paths.

The path of a hand when moving from one point on a plane to another tends to be more or less straight, with an approximately bell shaped velocity profile (Morasso, 1981). However, the paths show some systematic curvature. This modest curvature of the path has been discussed in terms of both kinematic planning (Wolpert, Ghahramani, & Jordan, 1995) and motor execution (Harris & Wolpert, 1998).

De Graaf, Denier van der Gon, and Sittig (1996) proposed a way to reconcile these two opposing views. They argued that the curvature of the hand might not be a result of deliberate planning, but a consequence of the online control of movements. If the initial movement direction is not exactly in the direction of the target, but one ends nevertheless on the target, the trajectory is necessarily curved. The mismatch between initial movement direction and target direction could either arise from the way the movement is planned or from the way it is executed. In the paragraphs below we will explain how curved trajectories can arise as a consequence of starting the movement in a wrong direction.

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The activation of arm muscles that lead to a force at the hand in a certain direction, will in general lead to a movement of that hand in a slightly different direction. This is due to the inertial properties of the human arm (Hogan, 1985). Thus if movements are controlled in the manner proposed by the equilibrium point hypothesis (Feldman, 1986), they do not have to start in the direction of the equilibrium point. By comparing human movements with movements generated by shifting the equilibrium point along a straight line, Flash (1987) showed that many kinematic characteristics of various point-to-point movements can be predicted from the mechanical characteristics of the arm. If biomechanical properties are the main cause of curvatures, the movements of the left hand should be the mirror image of those of the right hand. It has been shown that this is indeed the case for a set of centre-out movements (Boessenkool, Nijhoff, & Erkelens, 1998). This execution-based explanation for the curvature has been taken to the extreme by Harris and Wolpert (1998), who suggested that starting in the wrong direction is the optimal strategy given signal dependent noise.

On the other hand, the visual contribution to the curvature is also evident. Although most authors have discussed their results in terms of a deformation of (visual) space, some authors discussed this contribution in terms of perception of direction (de Graaf, Sittig, & Denier van der Gon, 1991). Following the assumption that only the required direction is misjudged, one would expect the hand's path to start more or less straight. This straight movement will lead at some point to detectable positional errors, which will be corrected later in the movement. The prediction is thus that movements in opposite directions have different paths, which are each other's mirror image if the directional misjudgements are the same. This is indeed what experimental paths look like (Wolpert et al., 1995, Fig. 4). Recently, we studied the effect of an oriented bar near the target on drawing movements. We found that the effect of the oriented bar on the movement path was asymmetric in a similar way: The bar had its largest effect close to the target (Brenner, Smeets, & Remijnse-Tamerius, 2002, Fig. 3). Moreover, the curvature of the pen's trajectory corresponded with the perceptual misjudgement of direction, and not with the perceptual judgement of straightness.

In general, errors in the initial direction will occur due to errors in both kinematic planning and execution. Which one is the largest will depend on the exact experimental design (direction of movement, speed, visual structures, etc.). This explains why the same author can conclude that the natural curvatures in point-to-point movements are due to kinematic planning (Wolpert, Ghahramani, & Jordan, 1994) and to motor execution (Harris & Wolpert, 1998). It would, however, be nice to know why the curvatures in the more recent paper had a different cause than those in the earlier papers.

There is a subtle difference between the examples of mechanical and visual contributions to curvature that were given above. For the mechanical contributions, the reasoning is that the errors are a direct consequence of the control system, and require no explicit corrections in order to reach the target. On the other hand, for the visual contributions the reasoning has been that initial errors need to be corrected later in the movement. Could it be that the simple control law that yields movements that start in a wrong direction but still end at the right position is also responsible for these corrections? In the next section, we will show that the answer to this question is ''yes''.

In the above, we discussed how we could understand the curvature of a trajectory as the consequence of a misjudgement of direction. Directions, positions, and curvature are attributes of space that are physically linked. However, our perceptual system has various options for judging physically linked attributes (Smeets & Brenner, 2001a). For instance, curvature could be detected by finding different orientations at two points on the curve, or by finding a misalignment of three points on the curve. When these options give different results we have a visual illusion (Smeets, Brenner, de Grave, & Cuijpers, 2002). In order to investigate how the illusion works we will use the control law that we derive in the next section to analyse how the path that the hand takes is influenced by the illusion. We will let participants move their hand over a background of radiating lines (the Hering illusion), and compare the results with their judgements in two perceptual experiments using the same background. We will discuss the results in relation with the proposed distinct processing of visual information for perception and action (Goodale & Milner, 1992) and the proposed distinct processing for planning and execution (Glover, 2002). We will conclude that such strong claims are not justified without a verified model of the underlying control.

FORMATION OF CURVED TRAJECTORIES

The model

It has been suggested that the curvature of some movements is caused by misperceiving the direction towards the target, despite localizing the target correctly (de Graaf et al., 1996). To investigate whether such a misjudgement of direction can explain complete trajectories, we formalize this misjudgement in a model. We assume that participants have a constant misperception of the direction towards the target (α, anticlockwise is positive). This situation is equivalent to a subject walking to a target when wearing prisms (Rushton, Harris, Lloyd, & Wann, 1998)? The hand will thus always move towards the target with an error α relative to the required direction of motion (see Figure 1). If the target is at the origin of the reference frame, and the hand is at (x, y), the required direction of motion of the hand is $\phi = \arctan(y/x)$. The complete path is therefore given by the differential equation:

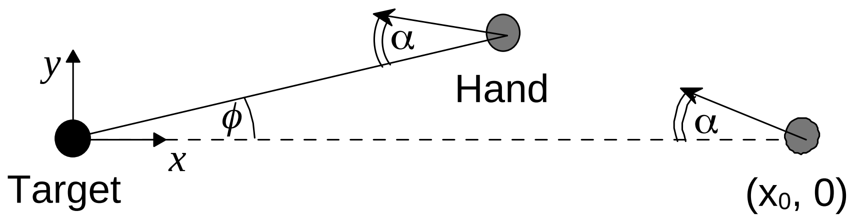

Figure 1. Schematic definition of the variables for the model. The hand is shown at its initial position (x_0, 0) and some time later during the movement.

$$\frac{dy}{dx} = \tan(\arctan(y/x) + \alpha) \tag{1}$$

We expect the angle a to be small, and we can choose the reference frame so that the hand starts at (x_0, 0), so that the required direction ϕ is initially zero. For these small angles we can approximate the tangent of an angle by the angle itself (if expressed in radians). For this situation, the equation can be solved analytically; the solution is:

$$y = x\ln(x/x_0)\alpha \tag{2}$$

This path has its extreme deviation (magnitude –0.37 x_0 α) at 0.37 x_0, thus, when 63% of the distance to the target is covered. The curve starts at an angle a relative to the line connecting the start and target, and ends perpendicular to this line. These angles are independent of the distance x_0 to the target, as was found experimentally for the starting direction (de Graaf et al., 1996). The large angle at the end of the movement is not compatible with the assumption of small angles that was needed to derive Equation (2). Thus the shape of the last part of the path is not described very well by Equation (2). We therefore used a numerical solution of Equation (1) to fit to the experimental data.

Comparison with experimental data

To see whether our model can explain visually induced curvatures, we fit Equation (1) to published data on the effect of target orientation on the movement path (Brenner et al., 2002, Fig. 5A). In that experiment, participants had to move as straight as possible in about 1 s to a target dot on an oriented bar. In separate blocks of trials, participants either had to pursue the pen with their eyes or to fixate the target. For each of these conditions we took the difference between the movement paths in which the bar was oriented upward and those in which the bar was oriented downward (thin curves in Figure 2). We fit Equation (1) to the data by varying the angular error α. The best fit was obtained for a $\alpha = -0.76^\circ$ when fixating the target and for a $\alpha = -1.09^\circ$ when pursuing the pen. The resulting model curves (thick curves in Figure 2) resemble the data very well.

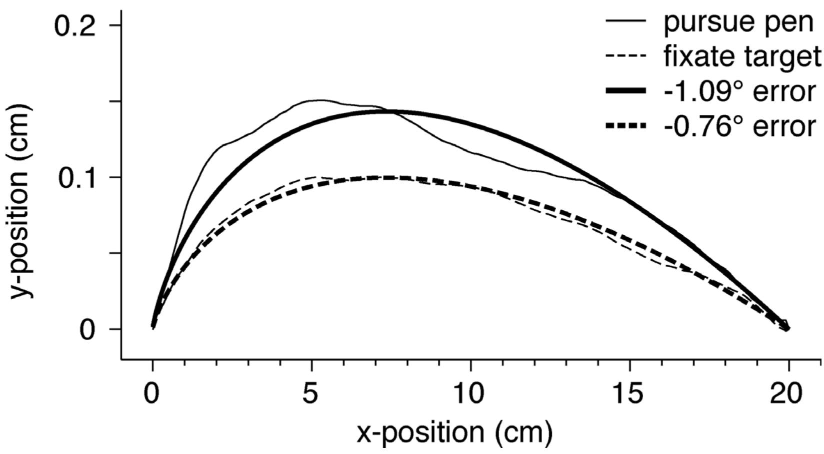

Figure 2. The effect of an oriented bar on the path of a movement from the right to the left. Thin curves: Experimental data from an earlier study (Brenner et al., 2002) for fixating the target (dashed line) and pursuing the pen (continuous line). Thick curves: Best fitting model paths, assuming a constant error in the judgement of direction (α in equation 1). Despite having only one fit-parameter, the model can reproduce the experimental movement paths very well.

The model predicts the asymmetry between the initial movement direction and the direction of approach that is found in the experiment.

One might think that many other models yield similar results. For instance, one could model the movements as ending perpendicular to the oriented targets while minimizing the jerk (Smeets & Brenner, 1999) or the torque-change (Klein Breteler, Gielen, & Meulenbroek, 2001). However, such models would predict that the directional error would decrease if the movement distance increases, which has not been found experimentally (de Graaf et al., 1996).

We can conclude that this simple model (a continuous misjudgement of direction) can explain the experimentally observed curvatures as being caused by a misjudgement of direction. Note that the asymmetry in the trajectory is not due to delays in the control law, but to using the direction of movement as the controlled variable. If one were to move in a straight line in a direction that is not exactly that of the target, the error in the direction would increase as one approaches the target. Since our model proposes that the change in direction is proportional to this error, we will obtain an asymmetric path. In the next section we will use this model as a tool to investigate how the Hering illusion works.

MOVING OVER THE HERING ILLUSION

In discussing the results of Wolpert et al. (1995), we argued that the asymmetry that they found in the movement paths argues for a misjudgement of directions rather than of positions or curvature itself. To find out which attribute is distorted by the Hering illusion we studied movements made over a background of radiating lines. Why do these lines make a straight line appear to be curved? A possible explanation is that the orientation of the background line at each intersection interferes with the judgement of the orientation of the target line in a similar way as has been proposed to occur in the Ponzo and Zollner illusions (Prinzmetal, Shimamura, & Mikolinski, 2001). However, the fact that the illusion also works without the presence of a real line (Figure 3) suggests that the radiating lines either influence the judged orientation in some other way (e.g., Changizi & Widders, 2002), or induce curvature by influencing something other than orientation. Radiating lines influence the perceived path of a moving dot (Cesaro & Agostini, 1998). This has been taken to imply that the illusion influences relative positions.

The experimental results of Cesaro and Agostini (1998) suggest that the background of the Hering illusion might also influence the curvature of a movement made over it. However, since the illusion now arises on the path itself, rather than at the target, we expect the illusion not to change the judgement of the required direction of motion, but to change the perceived direction of motion of the hand when it moves over the illusion. This obviously results in the same directional error. If the background leads to a curved hand path due to its effect on the movement direction, we can therefore use the model described in the previous section to evaluate the directional error. For the reasons given in

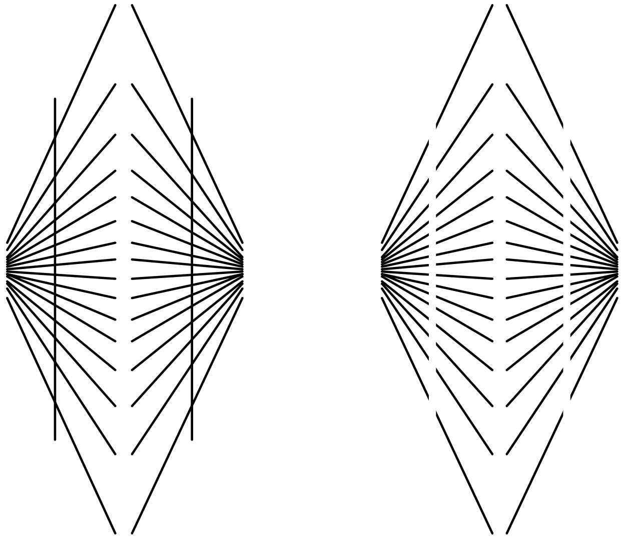

Figure 3. The static Hering illusion is present with (left) and without (right) crossings of lines. A theory based on orientation contrast at intersections is therefore not a very likely explanation for this illusion.

the preceding section, a misjudgement of direction will result in a maximal effect in the second half of the trajectory. If it is not the direction that is misjudged (but for instance relative positions or space in general; Flanagan & Rao, 1995), we expect a maximal effect of the illusion halfway through the movement.

Apparatus and stimuli

The methods used in this experiment were largely the same as those used for Experiment 2 of a previous study (Brenner et al., 2002). Participants' movements were measured at 204 Hz with a resolution of 0.02 mm using a digitizing tablet (WACOM A2). The participants sat comfortably (no physical restriction) in front of the slightly inclined surface of the tablet. They moved the special pen that is provided with the tablet across the drawing surface of the tablet, in about 1 s from an indicated starting position about 10 cm to the right of the subject's midline to a target that was 20 cm to the left of this position. As this pen leaves no mark, they had no visual feedback about their spatial performance. The experimenter gave feedback on the timing of their movements. We only used movements to the left to prevent occlusion of the background by the hand (Mon-Williams & Bull, 2000). From our earlier experiments we know that movement direction is irrelevant for the effect of visual elements on the curvature of movement paths (Brenner et al., 2002).

The starting position and the target were each indicated by a black dot (2.5 mm diameter) drawn on a sheet of paper positioned below the drawing surface of the tablet. In the space between the dots there were 16 black lines. Two orientations were tested: that shown in Figure 4, and an upside-down version. An irregular black mask surrounded the targets and the space between them. The black mask was the same on all trials, and its position was fixed. The paper with the starting position, target, and black lines was repositioned before each trial. In this way, neither the surrounding mask nor scratches on the drawing surface could help to perform the task.

Participants and procedure

Participants were the authors and seven of our colleagues. Only the authors were aware of the specific hypotheses under study. Participants performed the tasks using their preferred hand, which was the right hand for all but one participant. The left-handed participant was instructed to move in the opposite direction than the other participants, and the data were mirrored for analysis. Examination of individual data showed no conspicuous differences between the authors and the other participants, or between the left- and right-handed participants, so no distinction is made in the further analysis.

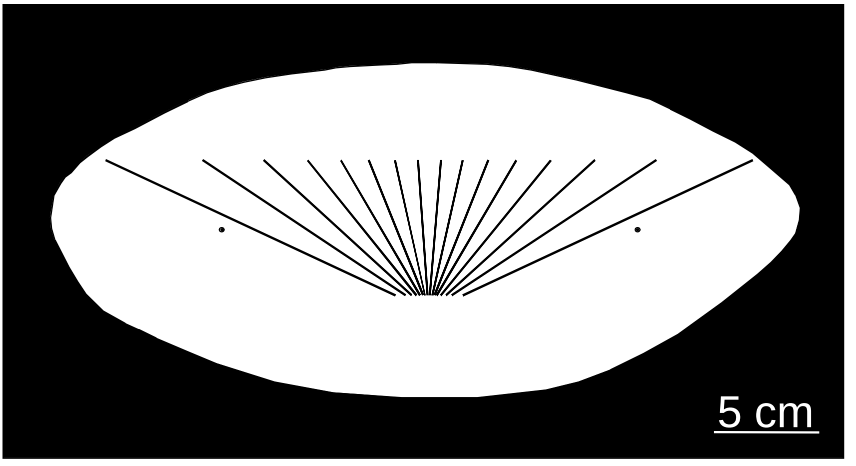

Figure 4. Example of a background used in the experiments. In the drawing experiments, the participant moved the pen from the dot on the right to the one on the left. In the perception experiments, the participants set the path of a target moving from the right to the left dot, or a line connecting the two, to appear straight.

The different orientations of the lines were presented in random order. The instruction in the movement task was to move as straight as possible. Participants were encouraged to take about one second for each movement. It is long known that fixation reduces the effect of orientation illusions (von Helmholtz, 1925, p. 196). As we previously found that a fixation instruction reduced the magnitude of the misjudgements of direction (Figure 2), we performed the experiment with two instructions. Each participant first made 20 movements (10 for each orientation) while looking at the pen and then another 20 while fixating the target.

Data analysis

The conventional way to define the onset and end of a movement trajectory is to use a velocity criterion. This method has a clear disadvantage: It disregards the parts of the trajectory traversed at a lower speed. The advantage is that this criterion only yields data in which the participants are moving. This makes a velocity criterion suitable when temporal measures (e.g., movement time) are important. As we are mainly interested in spatial performance, we chose a criterion than includes the whole trajectory, at the expense of an overestimation of the movement time. We defined the onset and end of the trajectory as those samples for which the difference with the previous/next sample was more than 90° from the main movement direction. This criterion is only met in data of a human movement when measurement noise is larger than the signal. A consequence of our criterion is that we include portions of nonmovement in our data, and thus include submovements that continue in the movement direction from the main movement. This is in line with our purpose: To find the total path along which participants reach the target.

Due to our deliberate variations in the exact positions of the starting point and target relative to the tablet, we had to align the trajectories in order to determine average paths. We therefore moved the end of the trajectory to the origin of our reference frame, and rotated the path so that the start was on the x-axis. Because participants were slightly variable in positioning the pen (about 1 or 2 mm, the size of the dots), the paths were not exactly 20 cm long. They were therefore scaled slightly (less than 2% in 98% of the trials). Subsequently, each trajectory was resampled (201 points) using linear interpolation. The deviation of the path from the straight line to the target was determined at each point, and averaged for each participant, instruction, and orientation. We calculated the difference between the paths for the two background orientations. This is the net effect of the illusion, free of any systematic curvature that is not related to the background.

To test our hypothesis, we fit the model of Equation (1) to the data. As we predicted that the illusion would only affect the direction of motion when the hand was moving over the radiating lines, we added a second fit-parameter: the portion of the path in which the movement direction is misjudged. As the background was positioned symmetrically between start position and target, we assumed that the portion in which the illusion works is also symmetric.

Results

When pursuing the pen, participants moved in 1.7 ± 0.3 s (mean ± inter-participant *SD*) to the target; when fixating the target, the movements were faster: 1.3 ± 0.3 s. The illusion influenced the participant's movements: The paths were curved in a way that more or less counteracted the known perceptual effect of the illusion (Figure 5). The influence of the illusion was clearly asymmetrical and was smaller when participants fixated the target while moving the pen. When pursuing the pen, the maximum deviation was 4.5 ± 1.7 mm at 71 ± 7% of the movement path. When fixating the target, the deviations were smaller: 1.9 ± 1.3 mm at 68 ± 23% of the movement. The deviation was not significantly different from zero at the moment the pen entered the illusion after 1.5 cm of movement ($p > .05$). The first position at which the deviation is significantly different from zero is at 2.1 cm when pursuing the pen.

The net effect of the background and the model that we fit to these paths are shown in Figure 6. For the data obtained when participants fixated the target, the

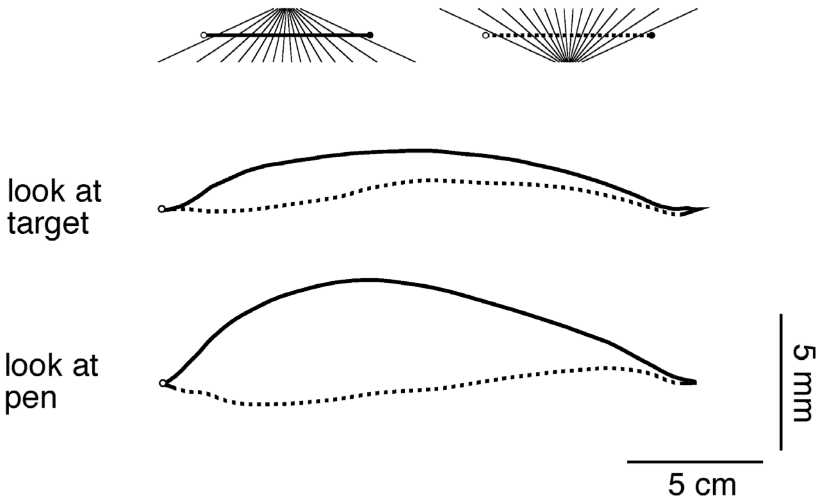

Figure 5. Overall average trajectory for each kind of background and instruction. Each trajectory is the average of 10 replications for each of the 9 participants (total of 90 paths). The two line types (dashed and continuous) represent the two orientations of the background, indicated by the schematic figures at the top. Instructions: To look either at the *target* or at the *pen*. For clarity, different scales are used for the movement components in the required direction, and those in the orthogonal direction.

best fit was for a misjudgement of direction of –1.29°, and no misjudgement within 2.3 cm from the start and target. When the participants fixated the target, the best fit was obtained for a –3.67° misjudgement of direction, and no misjudgement within 2.2 cm from the start and target.

Discussion

In many respects the effect of the Hering illusion on the movement paths (Figure 6) resembles the effect of the oriented targets (Figure 2). The movement paths were clearly curved, with the peak deviation in the second part of the movement. The asymmetry in the paths is inconsistent with explanations based on relative positions (Cesaro & Agostini, 1998) or deformation of space (Flanagan & Rao, 1995). The instruction to fixate the target resulted in a smaller deviation from a straight line than the instruction to look at the pen. Except for the magnitude of the effect, the main difference between this and the previous experiment is what happens near the target and starting position. For the oriented targets (Figure 2), the angle between the direction of motion and the direction between target and start is large

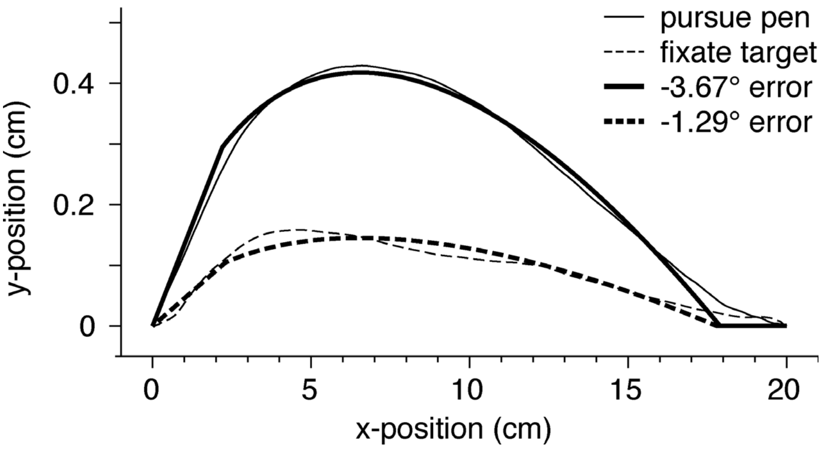

Figure 6. The effect of the radiating lines (Hering illusion; Figure 4) on the path of a drawing movement from the right to the left. Thin curves are the experimental data for two fixation instructions. Thick curves are the model paths, assuming a constant misjudgement of direction (Equation 1). Two parameters were fitted: the directional misjudgement of the illusion, and the part of the path in which the illusion is active.

at motion onset and reduces during the movement. For the Hering illusion (Figure 6), this angle was very small (not significantly different from zero) for the first 2 cm. The results of the two experiments also differ near the target. Whereas the paths toward the oriented targets remain curved, the path over the Hering illusion is a straight line to the target over the last 2–3 cm, independent of the fixation instruction. Our model based on a constant misjudgement of the direction captures these differences to a large extent; note that the data near the end differ even more between the two experiments than the models do.

The size of the illusion-free part of the path is more than the 1.5 cm that separates the start and target from the background lines. We suggest that several factors play a role in this. As our participants took more than one second to traverse the complete path, the straight parts correspond with about 110 ms, the delay needed for visual information to influence hand movements (Brenner & Smeets, 1997). The illusion may start to work as the perceived direction of motion (affected by the illusion) is compared with the required direction of motion (not affected by the illusion). To explain the lack of effect of the illusion near the end one could argue that as the time to reach the target is less than the visuomotor delay, participants switch their strategy from ‘‘move straight’’ to ‘‘stop at the target’’.

COMPARING PERCEPTION AND ACTION

The effect of visual illusions on motor behaviour has frequently been used to test the two-visual-systems hypothesis (reviewed by Carey, 2001). We therefore wondered whether there was any relationship between the curvature in movements over the Hering illusion and the judgements of straightness of a line in this illusion. In order to find out we measured the participant's perceptual susceptibility to the illusion.

Apparatus and stimuli

For our perception task, the same background as presented in the action task was presented on a computer screen (120 Hz; 39.2 × 29.3 cm; spatial resolution of 815 × 611 pixels, refined with antialiasing techniques). In addition, a curved line connected the starting point and target. The line had a constant radius of curvature: It was a portion of a circle with variable diameter. Participants sat facing the monitor at a distance of about 50 cm. Again, they were not restricted physically, but they were not allowed to move appreciably nearer to or further from the screen. The black mask that was used in the action experiment was attached to the screen. Similar variations in the position and orientation of the stimulus to those in the action experiment were programmed in order to avoid the possibility of using local slopes or imperfections of the monitor to perform the task.

Participants and procedure

The same nine participants that participated in the drawing task also participated in this experiment. The different orientations of the lines were presented in random order within each condition. As one cannot pursue a straight line, and looking at your hand is what many participants reported to find the most natural condition, we decided to use a ''look where you want'' condition as the equivalent of the pursuit condition. We always asked the participants to first adjust a line until it was straight with no restrictions on gaze, and subsequently to repeat the task while fixating the left end. The radius of curvature of the circle-segment could be adjusted in such a way that the maximal deviation from a straight line changed linearly with the movement of the mouse (range ±2.5 cm). The line remained visible until the participant indicated that it was straight by pressing a button. Each orientation of the background was presented 10 times in both conditions.

Data analysis

We characterized our participants' settings by the deviation of the middle of the line. The settings were averaged for each participant, viewing instructions, and background. To obtain a single comparable value for the drawing task we determined the deviation in the middle of the path. This value halfway is of course smaller than the peak deviation (in the drawing task, but not in the line-setting task). Moreover, the absolute magnitude of the deviation that would be judged straight in the line-setting task will depend on the shape of the stimulus (we may have obtained different values if we had used a Gaussian instead of a circle-segment). Comparing the average magnitude of the illusion across tasks is therefore not a very fruitful exercise. Instead we decided to concentrate on the correlation in the effect of the illusion between participant-viewing instruction combinations (Franz, Fahle, Bülthoff, & Gegenfurtner, 2001).

Results

Figure 7 shows that our participants very consistently set curved lines in response to the background. The effect was 1.4 ± 0.5 mm (mean ± standard deviation). This was smaller than the effect on the movement path (2.4 ± 2.0 mm). More importantly, the variations that the background caused in the judgements were not correlated with the variations it caused in the movement paths ($r^2 = .13$, $p = .15$).

Discussion

This comparison shows a nice dissociation between the information used in the two tasks. But does this dissociation support the two-visual-systems hypothesis? As opposed to what is often predicted by proponents of the two-visual-systems hypothesis (Aglioti, DeSouza, & Goodale, 1995), the illusion had a *larger* effect on the action (drawing) than on perception (setting a line straight). It has been demonstrated before that apparently subtle details in a perceptual task can have large influences on the magnitude of the apparent effect of the illusion (de Grave, Brenner, & Smeets, 2002). This is because perceptual judgements of a property (e.g., straightness) can be based on various physically related attributes (e.g., directions and relative positions) that are judged using a different metric (Smeets et al., 2002). Before concluding that the curvature of a hand movement is based on different visual processing than are perceptual judgements of straightness, we therefore decided to try another perceptual task.

A SECOND COMPARISON OF PERCEPTION AND ACTION

Probably, a static line is not the best comparison for our motor task. The line is continuously visible, and orientation detectors can measure its orientation. This is not the case for the path of the pen. In order to compare the production of a straight path with the perception of its straightness, we decided to ask our participants to set the path of a moving dot to be straight.

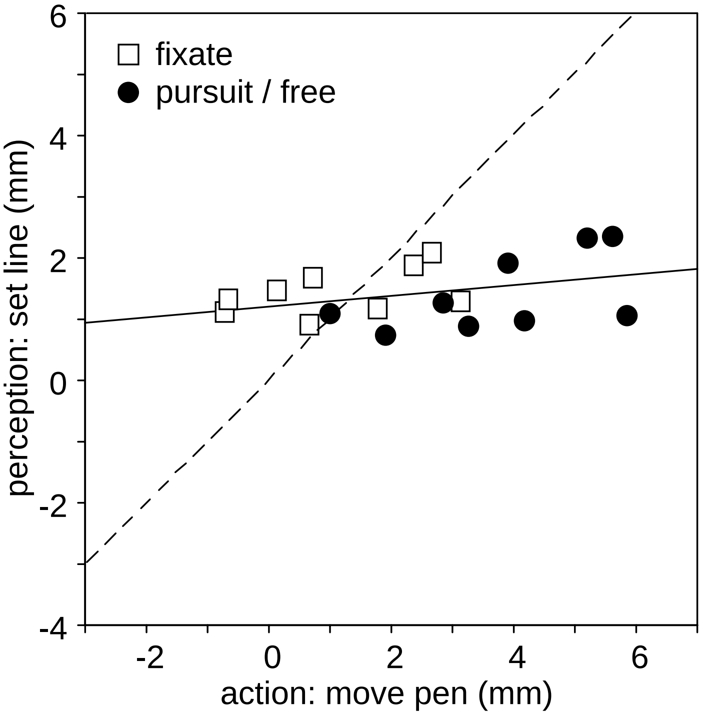

Figure 7. Magnitude of the illusion (for each participant for both viewing instructions) in two tasks. The continuous line shows the best linear fit; the dashed line indicates an equal effect. The task was either to move a pen along a straight path or to set a line to appear straight. For the first task, the viewing instructions were ''fixate target'' or ''pursue pen''. For the second task, the viewing instructions were ''fixate target'' or ''look where you please''. The large variability between participants and viewing instructions in the drawing task is not paralleled by similar variations in the line-setting task, where we see a small but very consistent effect of the illusion.

Methods

The equipment used was the same as when setting a line straight in the previous section. Instead of a curved line connecting the starting point and the target, a moving dot was presented. The dot moved repeatedly along a circle-segment (with a 0.5 s interval between movements) at a constant horizontal speed. It took the dot 1 s to move from the starting position to the target.

The participants and procedure were the same as when setting a line to appear straight. The two conditions were presented in the same fixed order: First adjusting the path along which a dot was moving while pursuing the dot with one's eyes, and subsequently adjusting the path along which a dot was moving while fixating the target.

Results

Figure 8 shows that the results of setting the dot's path straight were just as variable as the straightness of the participants' movements. The two measures were correlated across participants and viewing conditions ($r^2 = .51$, $p = .0009$). The slope of the regression was .76, which did not differ from the predicted unity slope ($p = .21$). If both viewing conditions are fitted separately, both resulting slopes differ neither from zero nor from unity ($p > .08$). We also tested (not shown) whether there was any correlation between the results for the two perceptual tasks. There was none ($r^2 = .04$, $p = .92$).

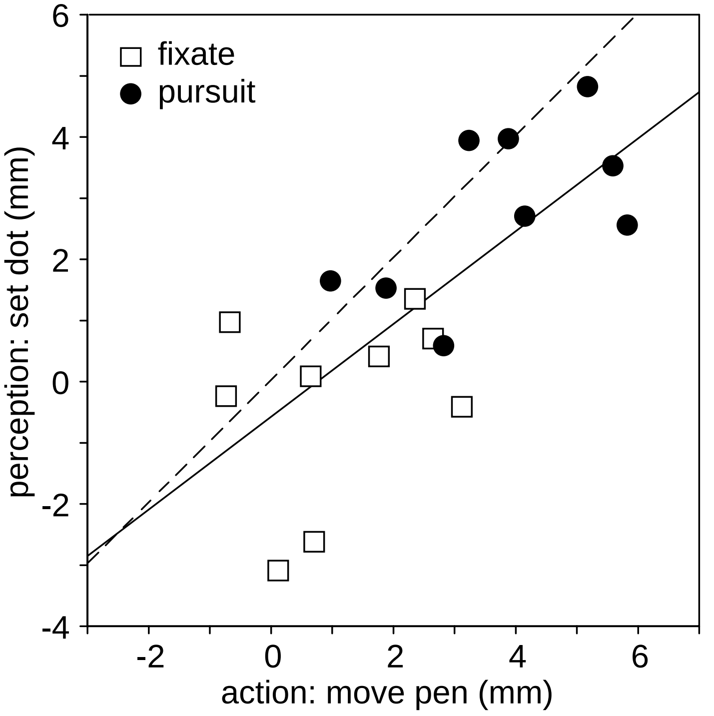

Figure 8. Magnitude of the illusion (for each participant in both viewing instructions) in two tasks. The continuous line shows the best linear fit; the dashed line indicates an equal effect. The task was either to move a pen along a straight path or to set a moving dot's path to appear straight. For the first task, the viewing instructions were ''fixate target'' or ''pursue pen''. For the second task, the viewing instructions were ''fixate target'' or ''pursue dot''. The large variability between participants and viewing instructions in the drawing task is paralleled by similar variations when setting a moving dot's path straight.

Discussion

We found that the curvature that the background induced in the hand's movement path when moving straight is correlated with the curvature that the background induced in a moving dot's path that was judged to be straight. This finding is similar to the good correlation between judging the curvature of a moving cursor and drawing that Wolpert et al. (1994) reported for the natural curvature that is independent of a background. We conclude therefore that our perceptual task (setting a moving dot's path straight) is based on the same visual information as drawing (i.e., that the direction of the dot's motion is misjudged, and not the curvature of its path).

The difference in results between the two perceptual tasks is not surprising. The tasks differ in many apparently small details. For instance, the start position and target are equivalent when setting a line straight, but not when setting a moving dot's path straight. It shows again that many subtle differences in the design of the task will influence the extent to which an illusion influences that task, independent of whether a task is a perceptual judgement or a motor task (Smeets et al., 2002).

GENERAL DISCUSSION

When trying to move in a straight line, participants could use various strategies. Many studies have assumed that participants plan a straight line, and subsequently follow that trajectory. Planning a straight line requires a metrical spatial representation to construct this line in. Many researchers assume the existence of such a representation in the visual, visuomotor, or motor domain (see for instance the contributions of Awater, Kaernbach, & Müsseler, 2004). However, it has been argued that the concept of a metrical representation of space is not very useful (O'Regan & Noe, 2001; Smeets & Brenner, 2001a). How do subjects try to move along a straight line if they do not plan this line?

We present evidence for a movement strategy that is independent of any spatial representation: participants constantly try to move their hand in the direction of the target, just as they do when walking to a target while wearing prisms (Rushton et al., 1998). We modelled this strategy, and applied it to the results of two data sets from experiments in which participants were asked to move as straight as possible. In both experiments, the effect of visual structures on the movement path was studied. The model predicted correctly that the visual structures should have the largest effect in the second part of the movements in both experiments.

The model was inspired by the results of de Graaf et al. (1996), who found that participants misjudge the direction of the movement that was to be made. They concluded from their finding that moderately paced and slow movements are coded as vectors. Our conclusion is somewhat different, if not the opposite.

We think that the endpoint of the movement is the main variable in such movements (Van den Dobbelsteen, Brenner, & Smeets, 2001). Our present results, and also those of de Graaf et al. (1996), show that we are not very good at ''vector coding'', because we make systematic errors in the direction in which we move. Despite systematic errors in the vector, the endpoint is reached. We plan an endpoint, but in order to move our arm there *in a straight line*, we determine a vector in that direction. This vector is continuously updated. This is the opposite of the proposal that we integrate the movement until it equals the vector from the starting position to the target (Bullock & Grossberg, 1991).

According to the two-visual-systems hypothesis (Goodale & Milner, 1992), contextual visual illusions should affect perception, but not action (Aglioti et al., 1995). The conclusion of the last section was that when the tasks were carefully matched, the Hering illusion had the same effect on perception and action. One could, however, argue that drawing a straight line is a way to report the perception of straightness, rather than a motor action. We have previously argued that it is not always possible to distinguish a perceptual report from a genuine motor action, because a perceptual report is conveyed by a motor action (Smeets & Brenner, 2001b). However, others have suggested criteria for making such a distinction. These include the notion that genuine motor actions use the visual information directly, without any delay (Rossetti, 1998), and that the relevant aspect of the motor task is isomorphic with the visual information (Bridgeman & Huemer, 1998). The conclusion of our drawing experiment was that the curvature was caused by the continuous use of information on the direction of the target. In other words: A variable that is isomorphic with the movement direction is used without a delay. Thus both criteria for a genuine action are met, supporting the view that perception and action are based on the same processing of visual information. In the next two paragraphs we discuss what the fact that we do not find a perception–action dichotomy in this task means for two alternative accounts for the apparent perception–action dichotomy in other tasks.

A similar effect of an illusion on perception and action need not be a strong argument against the two-visual-systems hypothesis. For instance, if the illusion works in early vision (in the retina or V1, before the separation between the dorsal and ventral stream), even proponents of a two-visual-systems hypothesis do not predict a differential effect (Dyde & Milner, 2002). As argued in the introductory paragraphs, the information processing underlying the line-setting task might be ''early'', because it may be based on the detection of local orientation. However, the other two tasks are based on other (presumably later) aspects of vision. If also these aspects have to be considered ''early'', then obviously the value of the two-visual-systems hypothesis becomes rather limited.

It has recently been proposed that illusions affect planning of an action, but not its online control (Glover, 2002). Support for this claim was found in experimental results that show an apparent reduction of the effect of an illusion during the course of an action (Glover & Dixon, 2001). In our experimental results we see the opposite pattern: The effect of the illusion (either expressed as the curvature or the deviation from the straight trajectory) increases during the movement, and has its maximum in the second half of the trajectory. However, from our model we know that this could arise from keeping the angle between the direction of motion and the direction to the target constant (i.e., from a constant influence of the illusion). In order to determine whether the effect of the illusion remains constant, we therefore have to know which spatial attributes contributes to the observed behaviour, and in what way. A constant influence of the illusion not only explains our present experimental results, but also the experimental results on which Glover has built his claim (Smeets et al., 2002; Smeets, Glover, & Brenner, in press). To understand the effect of illusions on action, one thus needs to know how information about the various spatial attributes shape motor behaviour, and thus have a model of visuomotor control (Smeets & Brenner, 1995; Smeets et al., 2002).

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