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RESEARCH ARTICLE

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The effect of visuomotor displacements on arm movement paths

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Abstract The gently curved paths evident in point-to-point arm movements have been attributed to both an imperfect execution of a planned straight-hand path or as an emergent property of a control strategy in which an intrinsic cost, dependent on arm dynamics, is minimised. We used a virtual visual feedback system to test whether path curvature was mainly determined by the visually perceived or actual location of the moving limb. Hand paths were measured for movements between three pairs of targets under both veridical and uniformly translated visual feedback. This allowed us to decouple the actual and perceived hand location during movement. Under different conditions of visual feedback the curvature of the hand paths did not correlate with either the visually perceived location of the limb or the actual location but rather with the relative displacement between the actual and visually perceived limb locations. The results are consistent with the hypothesis that in planning a movement the internal estimate of intrinsic coordinates, such as joint angles, is at least partially derived from visual information.

Key words Arm movements · Displaced visual feedback · Planning · Motor control · Curvature

Introduction

The paths taken by the hand in point-to-point arm movements are generally gently curved (Morasso 1981; Atkeson and Hollerbach 1985; Hollerbach and Atkeson 1987). The ubiquity of this path curvature is generally accepted to contain information about how arm movements are planned and/or controlled. Different theories of movement control try to explain or reproduce this experimentally observed curvature based on different premises. Current theories of arm movement planning can be divided into those which propose that movements are planned in extrinsic space, such as hand space (Flash and Hogan 1985; Flash 1987), and those which propose planning in intrinsic space, such as joint space (Uno et al. 1989; Osu et al. 1997). Most theories which propose that a point-to-point movement is first planned in extrinsic coordinates, prior to being transformed into intrinsic variables for execution, assume that the planned path is straight. For example, the minimum jerk model proposes that only the kinematics of the movement are planned. However, the model was modified to suggest that it is the equilibrium point of the hand which has a minimum jerk trajectory (Flash 1987). In this model, hand path curvature results from an interaction of the equilibrium point control with the dynamics of the arm. Another possible source of movement curvature, for movements planned as straight in extrinsic space, has been demonstrated as perceptual in origin. That is, we perceive our curved hand paths as straighter than they really are since our perception of space is itself curved (Wolpert et al. 1994). For planning models based on intrinsic coordinates, path curvature is hypothesised to result from planned straight paths in intrinsic coordinates (movements in extrinsic space are therefore curved simply as a result of the non-linear relations between Cartesian coordinates and, for example, joint angle coordinates) (Osu et al. 1997) or emerge as a result of a control strategy which seeks to minimise a cost dependent on intrinsic properties such as joint torque change (Uno et al. 1989).

The present study sought to investigate whether hand path curvature depends mainly on the visually perceived or actual location of the moving limb. Using a virtual visual feedback system, a visuomotor rearrangement was introduced by uniformly translating visual feedback of the hand position transversely, relative to its actual position. Using this perturbation it was possible to dissociate the contributions to path curvature of the visual location of the hand and the actual location of the hand. This was achieved by comparing conditions in which the visual location was the same but the actual hand position was

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varied and, conversely, the condition in which the actual hand location was the same but the visual position varied.

Five hypotheses for the origin of movement curvature were considered, each of which predicted different changes in path curvature under the visuomotor rearrangement. If curvature depended solely on the perceived visual location of the moving limb, independent of the actual location of the limb, then this would be evidence in favour of a planned trajectory in visual space – extrinsic. If the paths depended only on the actual location of the moving limb, independent of the visually perceived location, then this would be evidence in favour of an intrinsic planning and control strategy – intrinsic. If, in contrast, the path curvature depended on the relative offset between the actual and perceived location of the limb, this would point to the relationship between the intrinsic and extrinsic coordinates as a source of movement curvature – relative. Two other hypotheses were considered in which curvature would result from the feedback correction of an initial deviation of the actual finger either towards the displayed visual target – end point attraction – or away from the displayed visual target (Howard and Tipper 1997) – end point avoidance.

Results from the first experiment showed that curvature of the hand paths did not correlate solely with either the perceived location of the limb or the actual location of the limb but rather with the relative displacement between the actual and perceived limb locations. As subjects were aware of the displacement of visual feedback in the first experiment, a second experiment was performed to examine the effects of a slowly and surreptitiously introduced visual perturbation (Kagerer et al. 1997). As in the first experiment, the curvature changed depending on the relative displacement between actual and visually perceived limb locations. This change was independent of whether or not the subject was aware of the imposed displacement.

Materials and methods

Subjects

Twelve naive, normal, right-handed students (age range 18–32 years), who gave their informed consent prior to their inclusion, participated in this study. Six subjects took part in experiment 1, and eight subjects in experiment 2. Two of the subjects took part in both experiments.

Experimental setup

In both experiments subjects sat with their head in a chin rest and looked down on a virtual plane in which two-dimensional targets were presented. The virtual plane was set at the surface of a table on which subjects rested their hand. Targets and feedback of finger position were provided by projecting the screen from the Silicon Graphics workstation with a cathode ray tube (CRT) projector (Electrohome Marquee 8000 with P43 low-persistence phosphor green tube, Rancha Cucamonga, CA) onto a horizontal rear projection screen suspended above the subject's head (Fig. 1). A horizontal front-reflecting semi-silvered mirror was placed face up below the subject's chin (30 cm below the projection screen). The subject viewed the reflected image of the rear projection screen. An IRED (infrared-emitting diode) was mounted on the tip of the subject's index finger. An Optotrak 3020 (Northern Digital, Waterloo, Ontario) was used to record the position of the marker at 400 Hz. The Optotrak was driven from the SGi, where the position data was stored for later analysis.

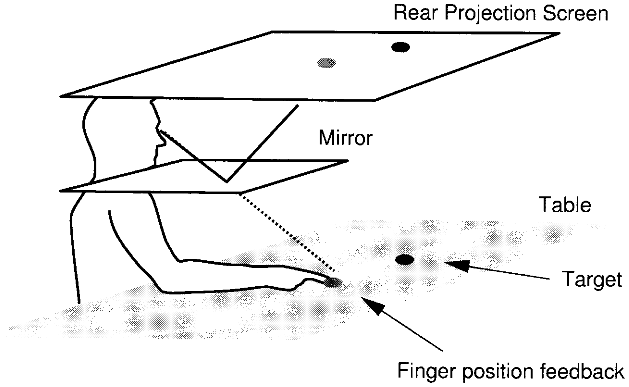

Fig. 1 Experimental apparatus for measuring arm movements on a table using virtual visual feedback. Looking down at the mirror the subject sees the virtual image of the finger and targets

Prior to the experiments the position of the IREDs relative to the projected image position was calibrated. By illuminating the semi-silvered mirror from below, the virtual image and the IRED could be lined up by eye. A linear regression fit of image position to IRED position was performed and this was then used on-line to position the targets and finger feedback images. Cross-validation sets gave a mean calibration error of less than 0.2 cm.

During the experiment an opaque sheet was fixed beneath the semi-silvered mirror thereby preventing any direct view of the arm. Finger feedback was then provided as a 1-cm-diameter yellow disc (cursor) in the virtual scene. The targets were presented as 1.5-cm-diameter blue discs.

Experimental design: experiment 1

Six subjects participated in experiment 1. The subjects were asked to reach "naturally" between targets with their hand resting on the table, and their finger in contact with the table – no instructions were given as to the movement path. The subjects' task was to move their arm so as to place the finger cursor within an illuminated target. Subjects were considered to be on target when the finger cursor was within 1 cm of the target and their speed was less than 3.0 cm s^{-1}. As soon as the subject arrived at the target, another target appeared and the subject was required to move the finger cursor to this target with a movement duration of approximately 700 ms. Subjects were given feedback of their timing performance in the form of a change in the target's appearance at the end of their movements signifying either too fast (target turned red), too slow (target turned green) or just right (within 150 ms of desired duration-target turned white). Before each session subjects practiced making movements of the correct duration. Subjects settled down extremely quickly and were consistently satisfying the timing criteria within 25 movements. For all movements the finger cursor was continuously present – full visual feedback.

The subjects made point-to-point movements between three different pairs of targets corresponding to movements labelled Left, Centre and Right, illustrated in Fig. 2. For each of these three movements the targets were 20 cm apart and lay in a horizontal plane at 37.6 cm below the level of the subjects' eyes.

The experiment consisted of seven conditions made up of three with veridical visual feedback and movements made either

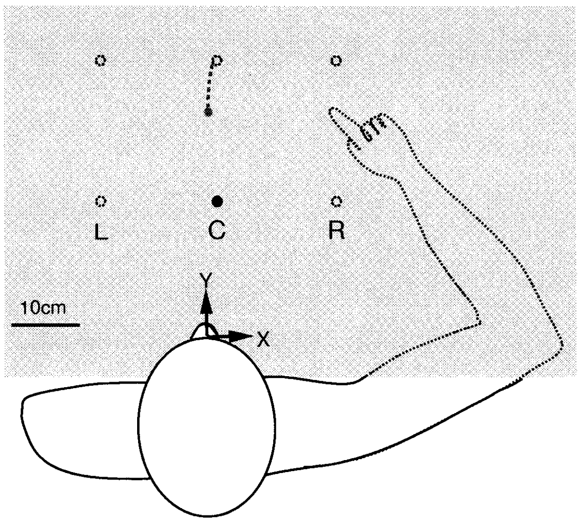

Fig. 2 The coordinate system of data capture is shown: the z-axis points out the plane and the origin is centred midway between the subject's eyes. Targets lie in the horizontal plane, $z=-37.6$ cm. Movements were made between pairs of targets in the sagittal direction (the x-coordinate for each pair of targets was the same). The pairs of targets were Centre ($x=3$ cm), Right ($x=20$ cm) and Left ($x=-14$ cm). The three pairs of targets were parallel to each other with Left and Right 17 cm on their respective sides of the Centre pair. For all pairs of targets, their y-coordinates were 20 cm apart. The *dashed lines* indicate that for all movements the subject had vision of only the virtual target for the current move (*black-filled circle*) and the finger cursor (*grey-filled circle*). Virtual targets and visual feedback of finger position, the finger cursor, were displayed either displaced leftwards, rightward or undisplaced with respect to the actual finger position. Here the subject is illustrated making movement Right, towards the body with visual feedback displaced 17 cm left

Centre, Right or Left, two with visual feedback displaced 17 cm right and movements made either Center or Left and two with visual feedback displaced 17 cm left and movements made either Centre or Right. Each condition was presented a block of 80 movements, 40 movements away from, and 40 movements towards the body. There were 560 movements in total and rests were given between each block. The seven conditions are summarised in Table 1. In the displaced visual feedback conditions the virtual scene (targets and finger cursor) were displaced 17 cm left or right. For example, Fig. 2 illustrates a subject making movement Right, towards the body, with visual feedback displaced 17 cm left of his position. The subject's visual perception is that the movement is Centre. A similar situation of displaced visual feedback exists in situations in which subjects receive visual feedback on a monitor remote from the workspace in which the movements are actually made.

For the first outward and return movements in the displaced visual feedback blocks, targets were displayed for the actual finger as well as the displaced finger cursor to orient the subject. For the remainder of the movements in the block (78), only the displaced virtual targets were displayed. For example, Fig. 2 illustrates a subject making movement Right with visual feedback displaced 17 cm left of his position. For both the first movement away from, and the first movement towards, the body in this block, the subject would have been presented with both the displaced targets, shown in the figure as black-filled circles, and targets for the actual hand, hollow circles of movement Right.

Before starting the experiment each subject was familiarised with the setup and timing constraint. All subjects were performing without difficulty well within these 25 practice movements.

Table 1 Movements made for the seven conditions of experiment 1. Movement Right was 17 cm right of movement Centre while movement Left was 17 cm left of Centre. In the displaced visual feedback conditions, visual feedback of finger position, the finger cursor, as well as the virtual targets were either displaced right or left by 17 cm

Visual feedback	Move	Display	Number in batch
Veridical	Centre	Centre	80
Veridical	Right	Right	80
Veridical	Left	Left	80
Displace right	Centre	Right	80
Displace right	Left	Centre	80
Displace left	Centre	Left	80
Displace left	Right	Centre	80

Table 2 Movements made for the seven conditions of experiment 2. Movement Near Right was 8 cm right of movement Centre while movement Near Left was 8 cm left of Centre. In the displaced visual feedback conditions, visual feedback of finger position, the finger cursor, as well as the virtual targets were either displaced right or left by 8 cm. In the surreptitiously displaced visual feedback conditions, the finger cursor was slowly displaced right or left by 8 cm over 40 movements

Visual feedback	Move	Display	Number in batch
Veridical	Centre	Centre	80
Veridical	Near right	Near right	80
Veridical	Near left	Near left	8o
Displace right	Centre	Near right	80
Displace right surreptitiously	Centre	Near right	80
Displace left	Centre	Near left	80
Displace left surreptitiously	Centre	Near left	80

Experimental design: experiment 2

Eight subjects participated in experiment 2. The experimental setup was the same as in experiment 1. As in experiment 1 the subjects made point-to-point movements of 700-ms duration, between three different pairs of targets 20 cm apart. As before subjects were asked to rest their hand on the table with their finger in contact with the table. Movements were all in the sagittal direction, 3 cm left of centre – Centre; 8 cm right of, and parallel to, this central move – Near Right; and 8 cm left of, and parallel to, this central move – Near Left. The targets for movement Centre were identical to those of experiment 1.

The experiment consisted of seven conditions made up of three with veridical visual feedback and movements made either Centre, Near Right or Near Left, two with movements made Centre but visual feedback displaced 8 cm right in one condition and 8 cm left in the other (these five conditions are a subset of those of experiment 1 but with a smaller visual displacement) and two new conditions in which moves were made Centre but visual feedback was surreptitiously displaced 8 cm right in one condition or surreptitiously displaced 8 cm left in the other. In these surreptitiously displaced conditions subjects initially made movements either Near Left or Near Right and then gradually the visual feedback location was shifted so that in order to perceive the finger cursor as moving between the virtual targets the actual finger had to move between the Centre targets. Each condition was presented in a block of 80 movements, 40 movements away from, and 40 movements towards, the body – 560 movements in total. Rests were given between each block. All seven conditions of experiment 2 are listed in Table 2.

The perturbation was introduced slowly at 2 mm per movement so that the subjects did not notice the shift. It took 40 movements to achieve the full 8-cm displacement. The smaller displacement of 8 cm was chosen instead of the 17 cm of experiment 1 so that subjects would be unaware of the visual perturbation in the surreptitiously displaced visual feedback conditions. For a full 17-cm displacement subjects become aware of the discrepancy between proprioceptive and visual feedback at least in the parts of the workspace under examination here. An 8-cm displacement was therefore chosen as a compromise between a large enough displacement to produce curvature effects and a small enough one not to alert the subject to the perturbation.

Data analysis

To calculate mean hand paths with standard error ellipses, the finger position data for each movement was resampled at 50 evenly spaced points over the duration of the movement. The start of the movement was defined as the time when the hand speed first exceeded 3 cm s^{-1}. Hand speeds were calculated from the finger position data by first differencing and then filtering with a Butterworth second-order, zero-phase lag, low-pass filter with a 15-Hz cutoff. To remove variability due to small changes in the starting location of the movement, the trajectories were translated to align the first point on the starting target.

In order to assess movement curvature, the perpendicular distance in the *XY* plane between the movement path and the straight line between the start and end of the movement was calculated and resampled at 50 evenly spaced points along this line. The midpoint deviation was used as a measurement of movement curvature in the analyses. The mean midpoint deviation for each subject and condition was calculated in each direction in each condition over the last 30 trials for experiment 1 and the last 20 trials for experiment 2. Only in the last 20 trials of experiment 2 was the visual perturbation complete in the surreptitiously displaced visual feedback condition. In order to test for significant changes in curvature between conditions, two-tailed *t*-tests, paired for subjects, of these mean midpoint deviations were made. Based on the results of experiment 1, both two-tailed and one-tailed *t*-tests were used to test for significant changes in curvature between conditions in experiment 2. To assess for any change in curvature over the course of each condition, linear regressions of midpoint deviation against trial were performed for the last 30 trials in each direction of experiment 1 and the last 20 in each direction of experiment 2. The regressions were calculated separately for each subject. The slopes of the regressions, one per subject, were tested for significance using a two-tailed *t*-test.

Simulation

To examine the effect of an incorrect internal estimate of arm configuration on movement paths, we simulated a simple two-degree-of-freedom arm, assuming that the internally calculated position of the limb is biased toward the visually perceived location. We used the model of Hoff and Arbib (1993) for a planned minimum jerk feedback trajectory in extrinsic space. This model was designed to produce minimum jerk trajectories to targets using a feedback mechanism even in the presence of intra-movement changes in target location. The model defines a desired rate of change of acceleration, that is jerk, of the hand at each time step based on the current estimate of arm's state [$x=(x, \dot{x}\,\ddot{x})$ of finger position, velocity and acceleration in extrinsic coordinates], the target location, and movement time remaining. In the current simulation the model was modified to include the effect of an incorrect internal estimate of hand position, with correct estimates of both the target location and the remaining movement time. In these simulations it was assumed that the internally estimated hand position was biased towards the visually perceived location. It has recently been shown that, using proprioception alone, hand positions closer to the shoulder are localised more precisely than those further away (van Beers et al. 1998). Therefore the magnitude of the bias was modelled as increasing linearly with the distance of the hand from the shoulder. At each point in time the model specifies the desired change in hand acceleration, as defined in Hoff and Arbib (1993); however, the corresponding desired change in shoulder and elbow joint accelerations for the two-joint arm is calculated based on the biased, and hence incorrect, internal estimate of hand position. This change in joint accelerations is then applied to the arm to update its state. Therefore, the effect of the biasing of the estimated hand location causes an incorrect desired change in acceleration to be applied to the arm, which causes the hand to deviate from a straight-line path. The magnitude of bias was chosen to provide a qualitative fit to the data. When the hand was 55 cm from the shoulder, the bias was 2 cm. The bias was 1.1 cm for the most proximal hand position and 2.0 cm for the most distal. Link lengths were taken as 35 cm for the upper arm and 43 cm for the lower arm. The targets for the simulated movements were taken to be at the same positions in the horizontal plane as those of experiment 1. The simulations were run using a MATLAB integration routine for movements of 700-ms duration.

Results

Experiment 1

All subjects found the task natural and easy to perform. The subjects' mean hand paths in the plane of the targets (*XY*) for the last 30 movements in each direction for each of the conditions of Table 1 are shown in Fig. 3. The *X*-axis scale has been magnified to clarify the movement curvature. The movements under veridical visual feedback (*shown in black*) show typical straight or gently curved paths for all movement locations. However, the movement curvature, for movements at the same location, changes when the visual feedback is displaced right or left.

When visual feedback of finger location is displaced right or left with respect to actual finger location, the movement path curvature changes from that of the veridical visual feedback condition in a systematic manner. There are two systematic features to the change in curvature. First, the change in curvature from the veridical feedback condition is in opposite directions when the visual feedback is displaced right and left (Fig. 3b,e). Second, the movement curvature is in the opposite direction under the same visual displacement when movements are made towards or away from the body (compare the top and bottom rows of Fig. 3). Therefore, movements Centre away from the body (Fig. 3b) are curved in opposite directions depending on whether feedback is displaced right or left (dark grey and pale grey), while for movements towards the body (Fig. 3e) the pattern is reversed. The same effects are observed for movements Left (Fig. 3a,d) and Right (Fig. 3c,f).

The pattern of observed curvature is consistent with a dependence on the relative displacement of actual and perceived finger locations. For example, when moving Left but with feedback displaced 17 cm to the right (Fig. 3a,d, dark-grey traces) the curvature is similar to moving Centre with visual feedback displaced 17 cm to the right (Fig. 3b,e, dark-grey traces). Similarly, when moving

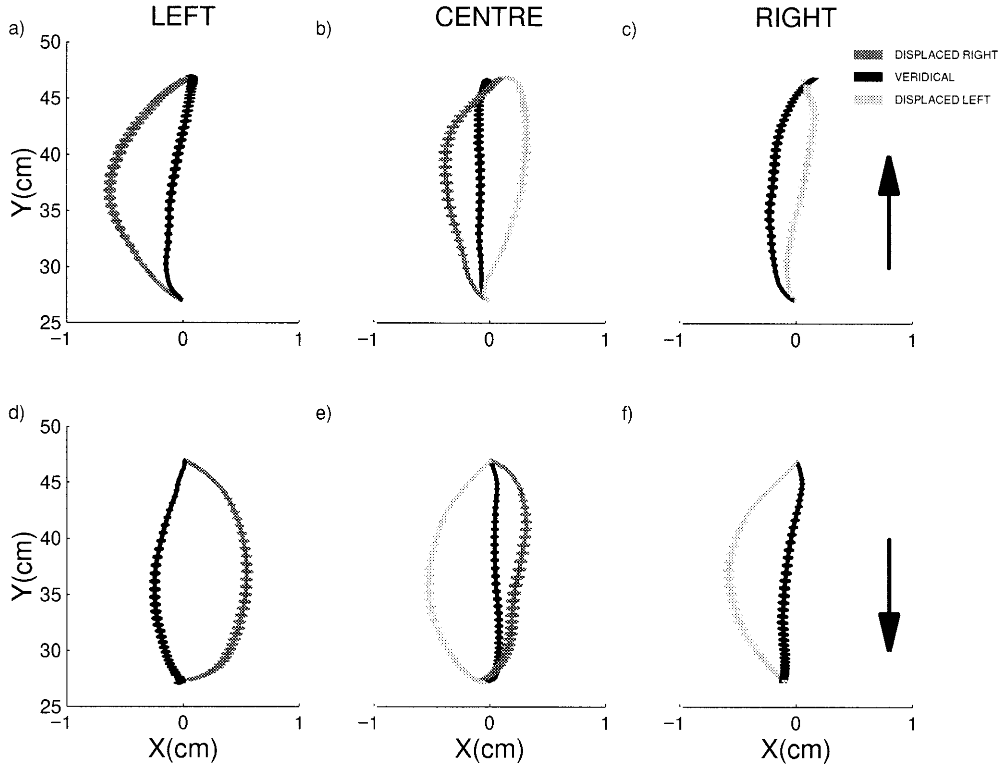

Fig. 3a–f Mean hand paths, for all subjects, for the last 30 movements in each direction of each condition. Paths are shown in the plane of the targets (*XY*) with standard error ellipses for the three different movement types under the three different visual feedback conditions. *Top panels* show movements away from the body and *bottom panels* towards the body; *arrows* indicate the direction of movement. **a, d** Movements Left; **b, e** movements Centre; **c, f** movements Right. Movements with veridical visual feedback are shown in *black*, with feedback displaced 17 cm right in *dark grey* and feedback displaced 17 cm left in *light grey* (n=180)

Right with feedback displaced 17 cm to the left (Fig. 3c,f, pale-grey traces) the pattern of curvature is similar to moving Centre with feedback displaced 17 cm to the left (Fig. 3b,e, pale-grey traces). Returning to the hypotheses of the "Introduction", this pattern of curvature does not correlate with movement location alone. If this were the case, then in each of the panels, which display movements made at the same actual location, the hand paths would be similar. The pattern does not correlate with displayed finger location alone. If this were the case then, for example, movements which are all displayed centre but actually made either Left (Fig. 3a,d, dark-grey traces), Centre (Fig. 3b,e, black traces) or Right (Fig. 3c,f, pale-grey traces) would show similar curvature. End point attraction or avoidance effects can also be ruled out as the origin of the change in curvature as these would predict changes of the same sign for movements away from and towards the body. For example, when the subject was moving Left away from the body with visual feedback displaced 17 cm right, attraction to the visual target (which is to the right of the actual hand position) would cause a deviation rightwards, as opposed to the measured leftwards deviation (Fig. 3a, dark-grey trace). Similarly when moving towards the body, attraction to the visual target (which is again to the right of the actual hand location) would again cause deviation to the right. A similar argument applies for target avoidance effects. Both these effects would imply deviations of the same nature for movements away from, and towards, the body. In contrast, for all movements Left, Centre and Right the measured changes in curvature with visual feedback location are in opposite directions for movements away from and towards the body (compare top and bottom rows of Fig. 3).

Midpoint deviation from a straight line between the first and last point of the movement was used to quantify the effects illustrated in Fig. 3. Figure 4 shows midpoint deviations, averaged over all subjects for batches of 10 movements, over the course of each condition, 40 movements in each direction. Paired t-tests (paired for subject) of the slopes of regressions of midpoint deviation against trial number for the last 30 movements in each direction showed no significant slope for any condition (P <0.05). Therefore the change in curvature was stable over this period. There was no significant difference between mean midpoint deviations for movements with the same relative difference between actual and perceived finger location (paired two-tailed t-tests). Therefore, for movements Left with visual feedback, displaced right mean midpoint deviation is similar to that of movements Centre with visual feedback displaced right. Similarly, curvature for movements Right with visual feedback displaced left is most similar to that of movements Centre with visual feedback displaced left. In contrast, movements at the same location with different visual feedback location show significantly different midpoint deviations, and hence curvature (two-tailed paired t-test P <0.05). One exception was movement Centre towards the body in which the difference in mean midpoint deviation for veridical visual feedback and feedback displaced right was not significant (P=–0.065). Also, movements at the same visually perceived location but different actual location show significantly

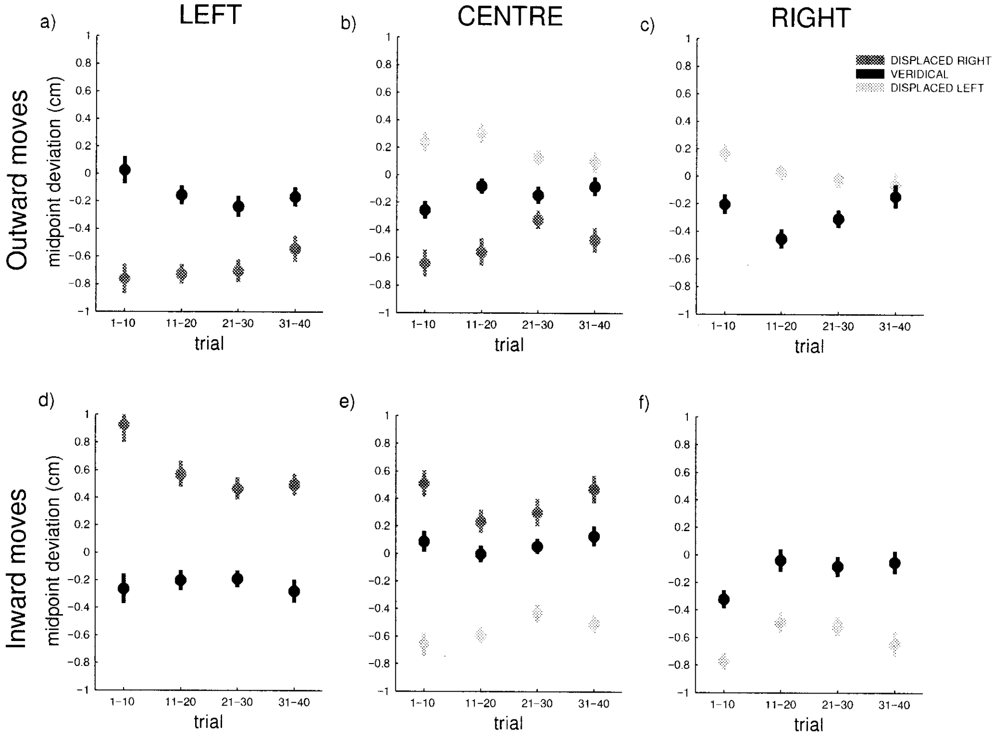

Fig. 4a–f Mean midpoint deviations for all subjects in batches of ten movements in each direction with standard error bars for the three different movement types under the three different visual feedback conditions. *Top panels* show movements away from the body and *bottom panels* towards the body. **a, d** Movements Left; **b, e** movements Centre; **c, f** movements Right. Midpoint deviations for movements with veridical visual feedback are shown in *black*, with feedback displaced 17 cm right in *dark grey* and feedback displaced 17 cm left in *pale grey* (n=60)

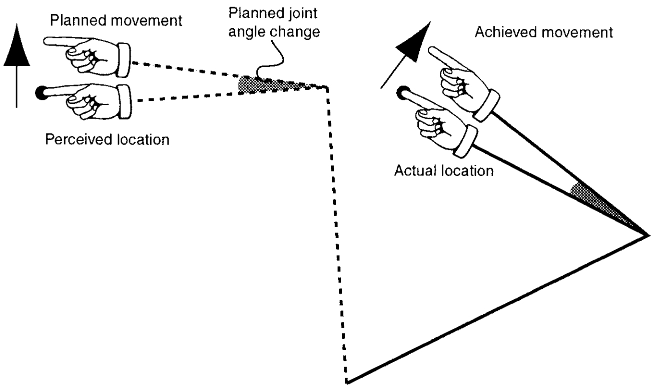

Fig. 5 Schematic of a movement away from the body with visual feedback displaced left. The movement is planned for the visually perceived location of the arm, shown in *dotted lines*. Here the desired movement is shown as resulting from just one joint angle change for simplicity of illustration. If this planned joint angle change is then applied to the actual limb shown in *solid lines*, the movement achieved deviates rightwards from the movement planned

different mean midpoint deviations (paired t-test, $P<0.05$). Two exceptions were movements Centre and Right away from the body both displayed centre (P=0.465) and these same movements both displayed right (P=0.305).

The observed change in curvature with visual displacement can be interpreted as the result of a planning strategy in which visual information biases the internal estimate of the position of the limb towards the perceived visual location. Under this hypothesis the intrinsic coordinates of the arm, such as joint angles, are biased by the perceived visual location. When making a movement, changes in intrinsic coordinates are calculated based on this incorrect estimate of intrinsic coordinates. These calculated joint angle changes are therefore inappropriate for the limb's actual position and will cause the hand to deviate from the usual path in the manner observed. For the purposes of illustration consider Fig. 5, a schematic of a movement away from the body with visual feedback displaced left. If we assume (again for illustration) that proprioceptive information is completely dominated by visual information, then the subject believes the hand is at the visual location and hence plans the movement for the corresponding limb position (dotted lines in Fig. 5). Consider the changes in joint angles that would move the limb at the visually perceived location in the direction illustrated. In this schematic the planned movement is achieved by a clockwise rotation at the elbow. When this change in joint angle is applied to the actual limb (solid lines in Fig. 5), the hand deviates rightwards from the straight path. Similarly, for movements towards the body the deviation would be leftwards as is observed.

A fuller demonstration of this effect on movement curvature is seen in Fig. 6, which shows simulation results, for the different conditions of experiment 1, for a simple two-degree-of-freedom arm, assuming that the internally calculated position of the limb is biased toward the visually perceived location (see "Materials and methods"). The simulated paths show initial hand deviation and subsequent movement curvature similar to that observed experimentally; cf. Figs. 6 and 3.

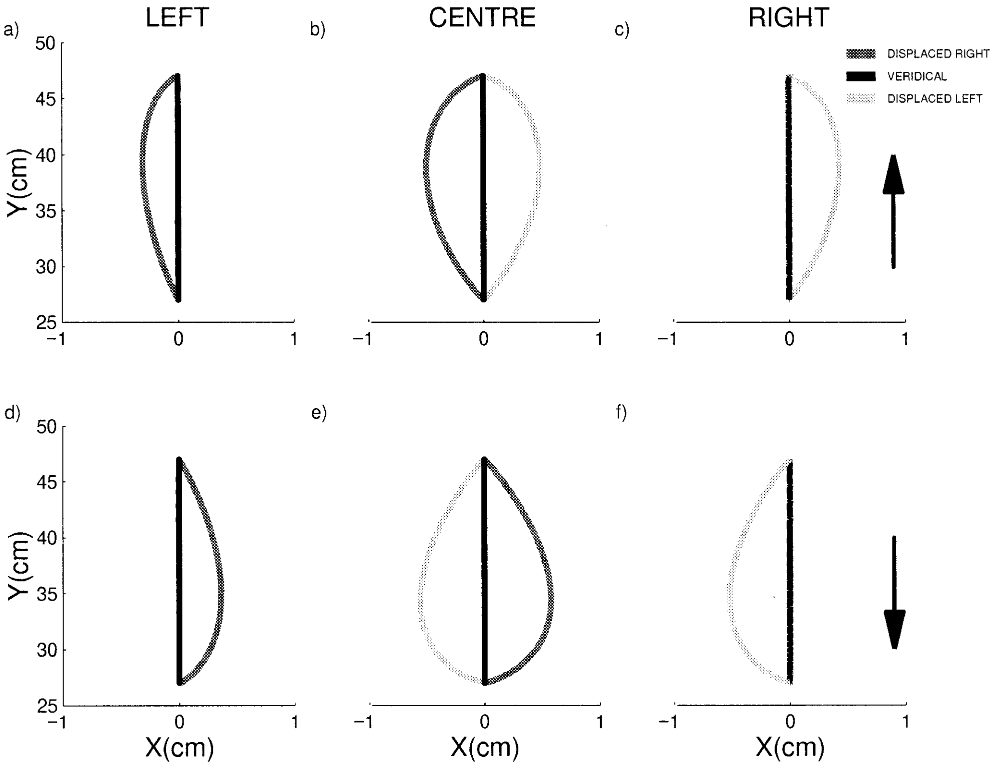

Fig. 6a–f Illustrative simulation results for a two-degree-of-freedom arm assuming a planned minimum jerk feedback trajectory in which the internal estimate of hand position is biased toward the visually perceived location of the limb. The magnitude of the bias was modelled as increasing linearly with the distance of the hand from the shoulder and was between 1.1 and 2 cm over all hand locations. *Top panels* show movements away from the body and *bottom panels* towards the body. **a, d** Movements Left; **b, e** movements Centre; **c, f** movements Right. Movements with veridical visual feedback are shown in *black*, movements in which the limb position estimate is biased towards the right in *dark grey* and biased towards the left in *pale grey*

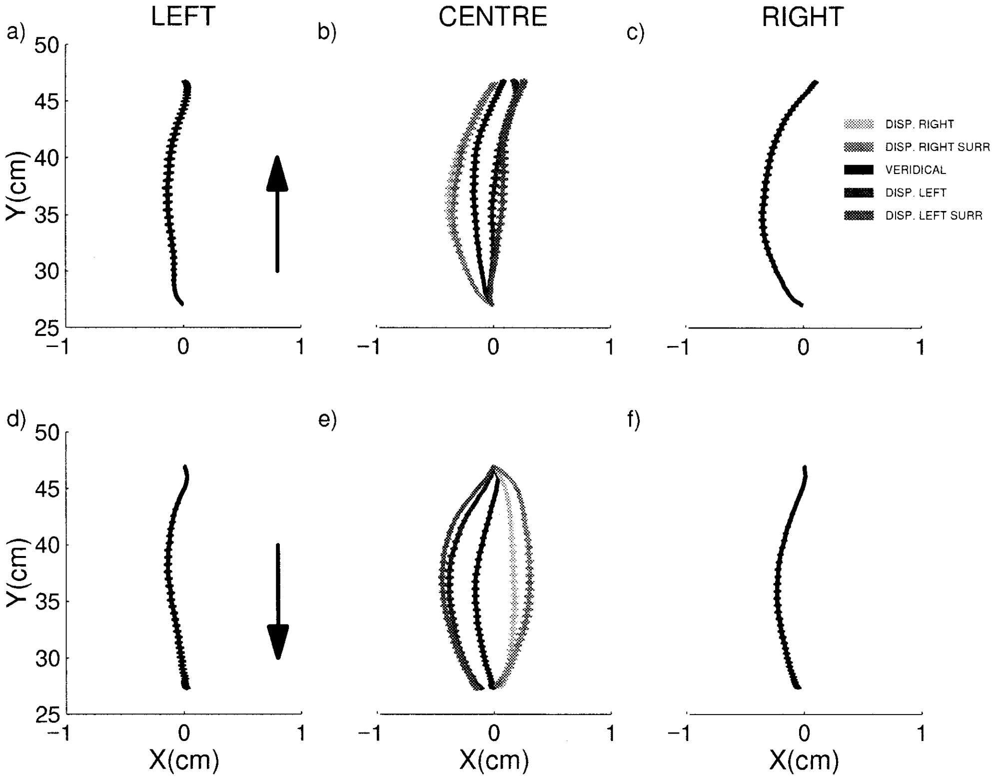

Fig. 7a–f Mean hand paths, for all subjects, for the last 20 movements in each direction in each condition of experiment 2 in the same form as Fig. 3. *Top panels* show movements away from the body and *bottom panels* towards the body; *arrows* indicate the direction of movement. **a, d** Movements Near Left; **b, e** movements Centre; **c, f** movements Near Right. Movements with veridical visual feedback are shown in *black*. Movements with visual feedback displaced 8 cm right are shown in *pale grey*, displaced 8 cm left in *dark grey* (n=160)

Experiment 2

All subjects found the task natural and easy to perform and did not notice the slowly introduced visual perturbation in the surreptitiously displaced visual feedback condition. At the end of the session subjects were asked whether or not they noticed the perturbation. Figure 7 shows, for each of the conditions of experiment 2, the mean hand paths in the plane of the targets (*XY*) for the last 20 movements in each direction. The *X*-axis scale has been magnified to clarify the movement curvature. Movements under veridical visual feedback are gently curved (black). Paired *t*-tests (paired for subject) of the slopes of regressions of midpoint deviation against trial number for the last 20 movements in each direction showed no significant slope for 13 out of 14 conditions × direction *(P*$<$0.05). One exception was for movements towards the body for visual feedback displaced surreptitiously 8 cm right. Therefore the change in curvature was stable over this period. When the visual feedback was displaced laterally right or left, the movement curvature changed in the same way as in experiment 1. The changes were generally smaller than those measured in experiment 1 consistent with the smaller displacement of 8 cm (compared with 17 cm of experiment 1).

For the displaced feedback conditions there was no significant difference in the average midpoint deviations between conditions in which the displacement was surreptitious or non-surreptitious (paired two-tailed *t*-test, paired for subject, $P<0.05$). However, as in experiment 1, movements at the same location, Centre, with different visual feedback location show significantly different midpoint deviations, and hence curvature, in both directions for both surreptitiously and non-surreptitiously displaced visual feedback conditions (one-tailed paired *t*-test, $P<0.05$). One exception was movement Centre away from the body in which the difference in mean midpoint deviation for veridical visual feedback and feedback displaced right surreptitiously was not significant ($P=0.108$). One-tailed *t*-tests were used to test for the same sign of curvature changes as those of experiment 1.

The similarity of the path curvature in these conditions of displaced and surreptitiously displaced visual feedback (Fig. 7) shows that this effect is independent of awareness of the separation of actual and visually perceived limb location.

Discussion

We found that under different conditions of veridical and displaced visual feedback the curvature of the hand paths did not correlate solely with either the perceived location of the limb or the actual location of the limb, but rather with the relative displacement between the actual and perceived limb locations. Furthermore, this change in curvature with visual feedback location was independent of the subjects' awareness of the imposed displacement. There were two systematic features to the change in curvature with the relative displacement of actual and visually perceived finger location. First, the change in curvature from the veridical feedback condition was in opposite directions when the visual feedback was displaced right and left. Second, the movement curvature was in opposite directions under the same visual displacement when movements were made towards or away from the body.

The hypotheses

Here it was hypothesised that changes in path curvature under conditions of displaced visual feedback could provide information about the origin of movement curvature. If curvature depended only on the actual location of the limb, this would be evidence in favour of intrinsic planning. If the curvature depended only on the perceived location of the limb, then this would suggest extrinsic planning. If the curvature depended on the relationship between the perceived and actual location of the limb, then the altered relationships between the extrinsic and intrinsic coordinates could be identified as the source of movement curvature. Other possible patterns of curvature change were considered, consistent with end point attraction and end point avoidance effects. The measured curvature did not correlate with either the displayed finger location alone or the actual movement location alone. Instead path curvature showed a dependency on the relative displacement of actual and perceived finger locations. The measured curvature is inconsistent with target avoidance, attentional effects, and also with target attraction and end point control effects.

Planning or execution

In this work differences in path curvature were observed for movements of the same duration, at the same location in the workspace, but under different displaced visual feedback conditions (left and right). These differences are therefore unlikely to be related to the mechanics of movement execution but instead reflect the nature of the sensorimotor transformations required to plan the movements. They are also unlikely to be due to any differences in initial starting joint configuration under different displaced visual feedback for the following reasons. The finger had to be within 1 cm of the target at the start of the movement so any difference in initial starting configuration would have been small. In addition, it was found that large changes in initial joint angle configuration (for example, for movement Left, Centre and Right under veridical visual feedback in Fig. 3) showed smaller changes in curvature than those made at the same location under different visual feedback conditions (for example, movement Centre visual feedback displaced right and left; Fig. 3). The results are therefore interpreted in the context of movement planning, rather than movement dynamics. This interpretation is supported by the results of a simulation in which in planning the movement an incorrect visuomotor transformation is applied, such that the derived internal estimate of hand position is biased towards the visually perceived location of the limb. The simulated hand paths show the same pattern of curvature changes under the different visual feedback conditions as the measured paths. In the simulations it was assumed that a minimum jerk trajectory is planned for the hand paths (extrinsic planning). The curvature arises because the internal estimate of arm configuration is incorrectly estimated. However, our results do not, in general, exclude intrinsic planning. For a minimum torque change strategy an initial estimate of the joint angles at the start of the movement is required; if this estimate were incorrect this strategy could also produce a change in curvature.

Task conditions such as the location of the target information in relation to movement location have previously been shown to produce differences in the pattern of variable errors in pointing task conditions (Messier and Kalaska 1997). These were also interpreted as reflecting differences in the early stages of movement planning in the different conditions. Directional biases in pointing movements have been shown to change in a systematic manner with the initial starting position (Ghilardi et al. 1995). These changes were interpreted as arising from the nervous system, underestimating the distance of the hand from the body. The changes in curvature observed in the current work are consistent with the directional deviations measured by Ghilardi et al. (1995). However, our results would suggest that the directional biases measured in that work could have been related to the difference between the actual and visually displayed hand position as well as the distance of the hand from the body.

Proprioception versus vision

The results reported here provide further support for the idea that, when available, both visual and kinaesthetic information about the location of the hand is used in planning and execution of reaching movements. It is well known that in patients with large-fiber sensory neuropathy, vision of the moving limb or cursor improves movement accuracy (Ghez et al. 1995). Without vision, these patients make directional errors from movement outset, suggesting proprioception is necessary for the control of the initial feedforward part of the movement, rather than simply for feedback control (Gordon et al. 1995). In a study of variance in pointing errors in conditions in which either vision alone, proprioception alone or both were available to localise the target (van Beers et al. 1996), it was found that if both proprioceptive and visual information are available they are both used. In a study comparing pointing under conditions of veridical and displaced visual feedback of the initial position of the hand (Rossetti et al. 1995), it was found that the displaced visual feedback biased pointing movements. These results were interpreted in the context of coding of a movement vector and imply that both vision and proprioception are used in its determination. It has been shown that, using proprioception alone, hand positions closer to the shoulder are localised more precisely than those further away (van Beers et al. 1998). This would suggest that any biasing of the internal estimate of hand position by the displaced visual feedback could be less powerful when the hand is nearer to the body than far from the body. In movements Centre of the current experiments, the initial hand position is nearer to the body for moves away from the body than for moves towards the body. We might therefore expect that the effect of biasing by visual information would be smaller for movements away from the body as is found in the simulations. There is some suggestion that this is the case in the initial deviations for experiment 1 (Fig. 3b,e) and more obviously in the paths of experiment 2 (Fig. 7b,e).

Visuomotor transformation

In any reaching or pointing movement a visuomotor transformation must be performed to translate the target position in visuo spatial coordinates (and perhaps also the planned trajectory) into intrinsic coordinates, such as joint angles or muscle activations, appropriate for movement generation. Many perturbation studies have shown that we are able to adapt to changes in this visuomotor map such as occur when we wear prism glasses (Welch 1986; Redding and Wallace 1996; Kitazawa et al. 1997) or are subjected to more unusual visual perturbations (Imamizu et al. 1995; Wolpert et al. 1995; Ghahramani et al. 1996; Kagerer et al. 1997). Some of these transformations are easier to adapt to than others. For example, for movements on a horizontal surface, rotation of visual feedback in the same plane as that of the movement disturbs normal point-to-point movements dramatically. In the presence of such a visual perturbation subjects take hundreds of trials before normal movement trajectories are regained (Imamizu et al. 1995). In contrast, for movements on a horizontal surface, rotation of visual feedback out of the plane of movement is easy to accommodate, as evidenced by subjects' ability to use visual feedback on a monitor remote from the workspace to guide reaching (Ghilardi et al. 1995). In the current study, in order to achieve the task in the displaced visual feedback conditions, subjects had to use a new visuomotor transformation. The change in curvature observed here for different visual feedback and movement location relations is consistent with the idea that in translating from target location in extrinsic space to desired changes in joint angles an incorrect sensorimotor transformation was applied in which the calculated limb position was biased towards the visually perceived location of the limb.

Origins of movement curvature

It has been shown that perceptual distortion of visual space contributes to the curvature of arm movement paths (Wolpert et al. 1994; Miall and Haggard 1995) although a comparison of curvature of pointing movements made with the right and left hands suggests this contribution is small (Boessenkool et al. 1998). The perception of curvature is independent of the perception of absolute position in space. Rather, perception of curvature is dependent on estimates of relative positions in space. The present study shows that misperception of absolute position in space can also affect the curvature of movements. A study of deviations in initial movement direction in point-to-point movements suggests they arise not from a perceptual distortion of visual space but rather from a distorted internal representation of spatial relations (de Graaf et al. 1994). In either case the assumption is that the path followed by the hand in extrinsic space is a controlled feature of the movement and this planned path is straight. At least some of the observed path curvature in point-to-point hand movements is therefore hypothesised to arise from a distortion of this straight plan prior to the movement execution stage. In addition to these perceptual effects it has also been shown that the location of spatial attention can influence path curvature in point-to-point arm movements. Hand paths are seen to curve away from the location of the attentional cue (Howard and Tipper 1997).

In theories of movement control, path curvature has been attributed to imperfection at the execution stage of a planned straight equilibrium path (Flash 1987) in extrinsic space. Evidence for planning of straight-hand paths in extrinsic space has come from the observations that in the presence of either visual (Wolpert et al. 1995; Flanagan and Rao 1995) or force-field perturbations (Flash and Gurevich 1991; Gurevich 1993; Shadmehr and Mussa-Ivaldi 1994; Lackner and DiZio 1994; Gandolfo et al. 1996; Sainburg and Ghez 1995; Flash and Gurevich 1997; Goodbody and Wolpert 1998) subjects adapt without instruction so as to regain a hand path which appears almost straight in visually perceived space even if (in the case of the perturbed visual feedback experiments) the actual hand path becomes curved (Wolpert et al. 1995; Flanagan and Rao 1995). Any curvature remaining after adaptation is assumed due to one of the origins mentioned above. If, on the other hand, planning is carried out in intrinsic coordinates, curved paths are a natural result of the non-linear relations between intrinsic and extrinsic coordinates (Uno et al. 1989; Osu et al. 1997).

In the current work it was found that hand path curvature showed a dependency on the relative difference between the visually perceived and actual location of the hand. These differences were consistent with the hypothesis that the hand position in intrinsic coordinates was incorrectly calculated under displaced visual feedback conditions. Such an incorrect estimate was shown to lead to changes in movement curvature. This could imply that under normal conditions hand path curvature could be due in part to the misrepresentation of intrinsic position.

Conclusion

These results are consistent with the hypothesis that in planning a movement the internal estimate of intrinsic coordinates, such as joint angles, is at least partially derived from visual information. Under displaced visual feedback the estimate of the joint angles is biased towards the visual location and therefore an incorrect change in joint angles for the movement is estimated. When this change in joint angles is applied to the true joint angles, it causes the arm to deviate from its path in the manner observed experimentally. Furthermore this suggests that, under normal conditions, miscalculation of hand position in intrinsic coordinates could be another contributor to hand path curvature.

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