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The curvature of human arm movements in the absence of visual experience

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Abstract It has been suggested that the spatial path of the hand is an important controlled feature of normal human arm movements and that the desired path is a straight line through external space. Recent experiments have suggested that distortions in visual perception of external space may lead to errors in its representation and thus influence the curvature of movements. The movements of blind and normal blind-folded subjects were therefore compared in a task requiring point-to-point hand movements in six directions across a horizontal worktop. Movement curvature varied with direction in both groups but was significantly higher for the blindfolded control subjects. Thus, the normals' distorted visual experience of straight lines in some orientations may lead them to make curved movement paths. The perception of curvature was also tested in the two groups in a task in which they traced the curved edge of a ruler. The blind group were slightly better at this task, although the difference was not significant. We conclude that visual experience influences point-to-point hand movements, leading to higher curvature for movements made in the fronto-parallel plane by sighted subjects due to visual distortions. These data therefore support the hypothesis that the spatial path followed by the hand is influenced by sensory inputs and is a controlled feature of human reaching movements. The data argue against the hypothesis that movement curvature is a result of optimising only the dynamics of the limb control.

Key words Trajectory control · Movement curvature Congenital blindness · Curvature perception · Human

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Introduction

In point-to-point arm movements, the hand typically follows a slightly curved path, which in the horizontal plane is most curved for movements in the vertical axis, pronounced in the fronto-parallel axis, and least obvious in the antero-posterior axis. Although the extent of curvature varies slightly from subject to subject, it is one of the consistent features of human arm movements (Morasso 1981), and there is an active debate about the cause of the curvature. Two fundamentally different hypotheses have been proposed. One hypothesis suggests that the trajectory is planned so as to optimise control variables related to the dynamics of the arm movement, minimising the total squared change of torques producing the movement (Uno et al. 1989a). The optimal minimum-torque-change trajectory is slightly curved, particularly in the fronto-parallel plane. Thus the arm is proposed to follow accurately a trajectory planned in intrinsic (joint or muscle) co-ordinates without reference to the path followed in extrinsic co-ordinates. A simpler scheme using joint interpolation (Hollerbach and Atkeson 1986; Hollerbach et al. 1986) also proposes control of intrinsic variables rather than of the spatial path of the hand movement. However, the alternative hypothesis proposes that the path is actually planned in extrinsic co-ordinates and the desired path is straight (Flash and Hogan 1985). Three possible reasons for the observed deviations from this desired straight path have been suggested: (1) the controller is inaccurate or incomplete and the curves are an unavoidable error in performance; (2) a straight-line trajectory is defined in an intermediate representation, such as a series of equilibrium positions (Flash 1987) or muscle lengths (Bullock and Grossberg 1988), and the limb dynamics and joint interactions lead to the actual trajectory being curved; and (3) there is a visual misperception of a straight line, and the hand follows what is perceived by the subject as a straight path in exteroceptive space (Wolpert et al. 1994). One or all of these could contribute to movement curvature.

Wolpert et al. (1994) reported that subjects do in fact misperceive the curvature of a line traced by a small light moving across the workspace, and they showed a strong correlation between the size and direction of the misperception and the curvature of arm movements recorded in the same subjects. They suggested that misperception of visual feedback of hand position could contribute about half of the observed curvature of the trajectories. There are quite marked visual distortions of Euclidean space (Foley 1980), and there have been other recent reports that visually guided movements are inaccurate in some directions consistent with such distortions (de Graff et al. 1991). In general there is only a good match between perceived and veridical space in the antero-posterior axis or at a distance of 1–4 m in the fronto-parallel plane and hence outside the reach of the hand.

This normal misperception of the fronto-parallel plane could thus lead to curved movement trajectories if the goal is to follow a straight line in visual space (Wolpert et al. 1994, 1995). Alternatively the curvature of the movement trajectories might be not be caused by visual misperception, but might be due to minimum-torque-change optimisation or the difference between virtual and actual trajectories, and yet might itself contribute to miscalibration of the visual system. For example, if an arm movement were thought to be straight, the visual system might treat the sight of the hand moving across the workspace as a known reference and therefore modify visual perception on the basis of the perceived hand movement (Festinger et al. 1967). To examine these questions we have recorded the arm movements of blind subjects and blindfolded controls to test whether their visual experience influenced their motor behaviour. We have also tested both groups' perception of curvature when running a finger along the edge of a gently curved ruler. According to the hypothesis that visual distortions lead to movement curvature, and that there are no obvious proprioceptive distortions, we predict that blind subjects should show lower movement curvatures. An alternative prediction, based on the hypothesis that the sensory system is calibrated by the motor system, is that the blind subjects should show a misperception of curvature in a proprioceptive test that is correlated to their movement curvature.

Materials and methods

Subjects

Eleven blind subjects and ten blind-folded control subjects were tested, with permission from the local ethical committee. All were naive to the purpose of this experiments and had not previously been tested in similar experiments.

Of the 11 blind subjects (aged 15–56 years, mean 21.4 years; three women, eight men), 7 were blind from birth while the others had some residual vision in one eye during early childhood (mean age at complete loss of vision, 7.8 years, range 2–11 years). The blind group were mainly recruited from the sixth form of a residential school for the blind, whose students are selected partly on the basis of their self-sufficiency and may therefore have somewhat better motor skills than other blind subjects of that age range. One congenitally blind subject was excluded from the detailed analysis because of his inability to make targeted arm movements (Fig. 3A). No significant differences in movement patterns could be detected between the remaining blind subjects on the basis of their visual experience (see Results).

Ten control subjects (aged 18–36 years, mean 27.8 years) were recruited from students and staff of this department; three were women.

Two blind subjects and one control subject were left-handed and used their left hand throughout. For display and analysis of the results, their data have been reflected from left to right and then treated as equivalent to the data from right-handers. Thus in Figs. 2 and 3, the x-axis may be treated as running from contralateral to ipsilateral to the hand being tested.

Task

Point-to-point movements

Movements of 30–42 cm were made between six pairs of targets on a large digitising table, sampling at 133 Hz the position of a hand-held computer mouse with 0.1-mm resolution (GTCO RUD table; 80×100 cm). The subjects were trained to make each movement using an auditory tone triggered in a zone 2.5 cm around each target. They were instructed to make comfortable movements of moderate speed and to reach to and stop at the target as accurately as possible; no instructions were given about the path to follow between the targets. The subjects were trained and tested in each movement direction in turn and were told of the direction of movement that would be recorded (e.g. the outward movement between antero-posterior target pairs). The sequence was (1) contralateral to ipsilateral movements in the fronto-parallel plane; (2) the reverse movement; (3) proximal to distal antero-posterior; (4) the reverse; (5) contralateral to ipsilateral diagonal; and (6) ipsilateral to contralateral diagonal. During training, the subjects were initially guided to the start and end targets for one movement. They were then allowed 40 training movements with an auditory tone at the start and end positions and were verbally or manually directed back to a target if uncertain of its location. Most subjects were able to move accurately between the targets before the end of the 40 training movements. Immediately after training, 20 test movements were recorded with auditory feedback, to ensure a correct starting position, but with no tone at the target location. During recording the subjects were given no feedback of their final position but were directed back onto the start position as occasionally required. On completion of the block of 20 recorded movements, they would be offered a brief rest and then trained and tested on the next movement direction.

Perceived curvature

Following the movement task, subjects were tested on their ability to identify the direction of curvature of a gently curved ruler using a binary forced-choice paradigm. The subject traced along the lower edge of a 50-cm ruler, which rested on a smooth formica tabletop and which could be bent in either direction so that its centre was up to 4 cm from a line joining its two ends (maximum curvature 1.28 m^{-1}; radius of curvature 78 cm). Three orientations of the ruler were tested, corresponding to the three movement orientations (fronto-parallel, antero-posterior and diagonal), with six trials at each of nine curvatures for each orientation. The subjects were instructed to move along the length of the ruler, tracing its edge with the index finger of the same hand as used for the movement task. They were allowed to make multiple movements in both directions at their own speed along the ruler before verbally reporting its perceived direction of curvature.

Analysis

Movement averaging

The recorded time sequences of x-y positions of each movement were digitally filtered to 10 Hz, digitally differentiated, and a ve-

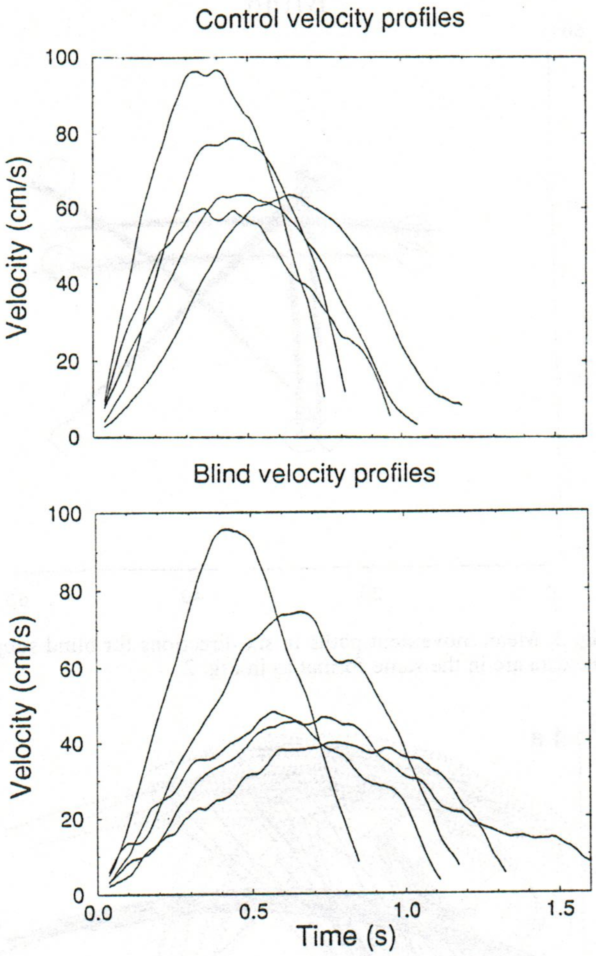

Fig. 1 Typical velocity profiles of movements in the fronto-parallel plane from blind-folded control subjects (*top*) and blind subjects (*bottom*). Each trace is a single movement from a different subject, digitally differentiated and smoothed (9-point running average). Both groups produced typical bell-shaped velocity profiles; there were no significant differences in movement durations between the groups or in any movement direction

locity threshold of 2.5 cm·s^{-1} applied to detect the start and end of each movement. For movements along the fronto-parallel or antero-posterior axes, the threshold was applied to the velocity record in that dimension only; for the diagonal movements, the same velocity threshold was applied to the tangential velocity profile. In a minority of cases (under 1%) the movement consisted of two or more discrete velocity peaks, and the data were then visually inspected to determine the start and end time of the complete movement. Movement durations were calculated on the basis of this velocity threshold.

The time sequences were then spatially resampled to give 100 points evenly distributed along the spatial path of each movement, and the spatially sampled x and y data points averaged to give the mean and standard error of position at 100 equidistant points in the path.

Measures of curvature

Two separate but complementary measures of movement curvature have been calculated. First, the perpendicular distance of the midpoint of each spatially resampled movement from a straight line between its start and end positions was measured. This is the measure of curvature used by Wolpert et al. (1994) and is based on the assumption that the movement makes a single half-sinusoidal sweep to one side or the other. It also corresponds to the measure of perceived curvature when tracing the ruler edge. A sweep away from the body or towards the contralateral hand is scored as of negative curvature. It is not a measure of the curvature along the whole path, however, so an S-shaped, sigmoidal movement between the start and end positions would score rather low on this measure.

Second, the spatially resampled paths were averaged by a generalised Procrustes analysis technique (GPA; Gower 1975; Haggard and Richardson, in press) to calculate a mean path, and a linear regression line was fitted to this mean path. The mean of the absolute values of the 100 residuals of the regression line was then obtained. This technique therefore gives a measure of the lateral deviation from a straight line of the consistent features of each subject's movement. It is a measure of the mean deviation from a straight line along the whole path and would record a single sweep or an S-shaped path as of high curvature. It does not record curvature direction. The instantaneous curvature of the paths was not calculated because of the noise in calculating second differentials from digitised data.

Measurement of perceived curvature

Data on perceived direction of curvature recorded in the binary forced-choice paradigm were fitted by probit analysis to detect a null curvature and standard deviation of the null for each subject in three orientations. These null points represent the perpendicular distance measured from the mid-point of the ruler to a straight line through the ruler ends, at which the subject perceived the ruler to be straight. As in the first method of measuring movement curvature, curvature of the ruler away from the subject or towards the contralateral hand was scored as negative.

Results

The blind-folded control subjects made movements typical of those reported for sighted movement (Prablanc and Martin 1992; Wolpert et al. 1995), with a smooth bell-shaped velocity profile (Fig. 1) and with a gently curved path. Figure 2 shows the mean path of their movements, spatially averaged over all 10 subjects and 20 movements per subject. The error bars are 3.92 times the standard errors and thus represent 99.99% confidence limits on the mean. The movements of the blind subjects were of very similar form to the blind-folded controls (Fig. 3), but with noticeably straighter paths in most movement directions, particularly for fronto-parallel movements (i.e. the horizontal paths indicated in Fig. 3). The extremely variable and distorted paths followed by the blind subject B8, who was excluded from Fig. 3 and excluded from the detailed analysis, are shown in Fig. 4A. Figure 4B shows the individual paths followed by one of the more typical blind subjects.

All movements were characterised by a gradual increase in variance throughout the path, indicating some scatter of the movement paths away from the mean direction. Movement amplitudes were approximately correct in all directions tested. The final positions of the movements did not significantly differ between groups; nor was there a significant group-by-direction interaction. The mean movement durations ranged from 1026 to 1170 ms; there were no significant group, direction or interaction effects in the movement durations.

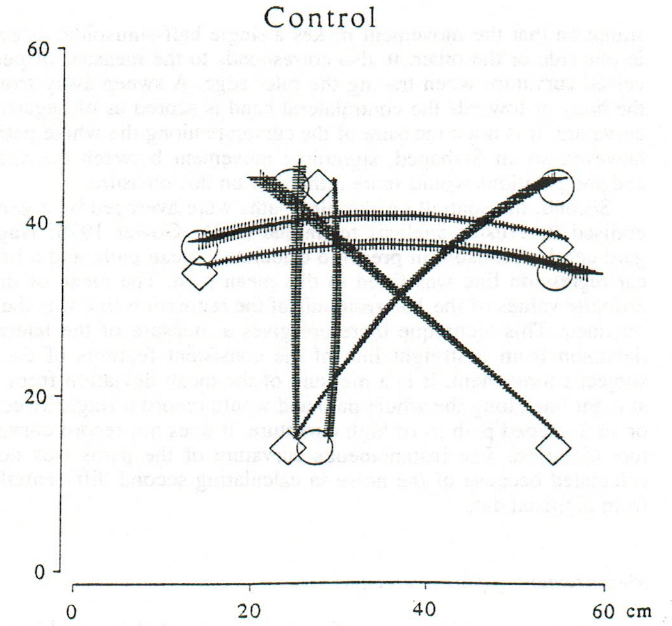

Fig. 2 Mean movement paths in six directions for blind-folded control subjects. Each trace is the mean of 190–200 movements (18–20 per subject, ten subjects) averaged after spatial resampling to give 100 data points equidistant along an individual path. The error bars are 3.92 SE or 99.99% confidence limits about the mean. *Diamonds* indicate the starting region (actually a 2.5-cm-radius circle) and *circles* indicate target positions (also 2.5-cm circles). The downward and leftward movements have been offset by 3 cm for clarity; the targets were actually in the same position as for the reverse movements. The *horizontal axis* represents the subject's fronto-lateral plane, the *vertical axis* their antero-posterior axis; the subject's shoulder was at about: x=30, y=–10). For the left-handed subject, the movements have been left-right reversed to coregister target locations

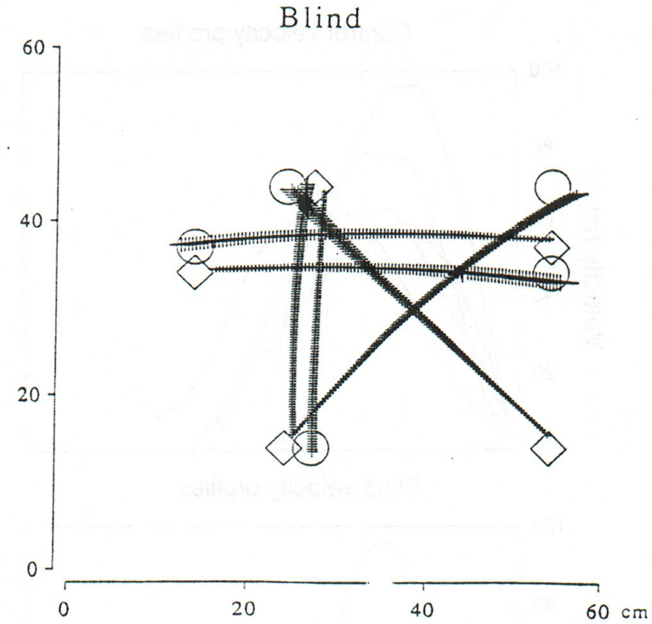

Fig. 3 Mean movement paths in six directions for blind subjects. The data are in the same format as in Fig. 2

Movement curvature

The measures of curvature are indicated in Table 1. The two measurement methods showed that curvature was highest for a contralateral-to-ipsilateral diagonal movement, was high also for the fronto-parallel movements and was low for the antero-posterior movements. This general pattern was found for both the blind subjects and the blind-folded controls. However, the movement curvature of the blind subjects was significantly lower than that of the controls ($F_{1,18}$=5.95, P=0.025, measured by method 2). The group difference calculated by method 1 was not statistically significant ($F_{1,18}$=2.89, P=0.11) apparently because this method recorded a low curvature score for the ipsilateral-to-contralateral movements of the control group (bottom line, Table 1). Both curvature scoring methods indicated a highly significant group-by-direction interaction ($F_{1,18}$=4.87, P=0.001 for method 1; $F_{1,18}$=3.99, P=0.003 for method 2).

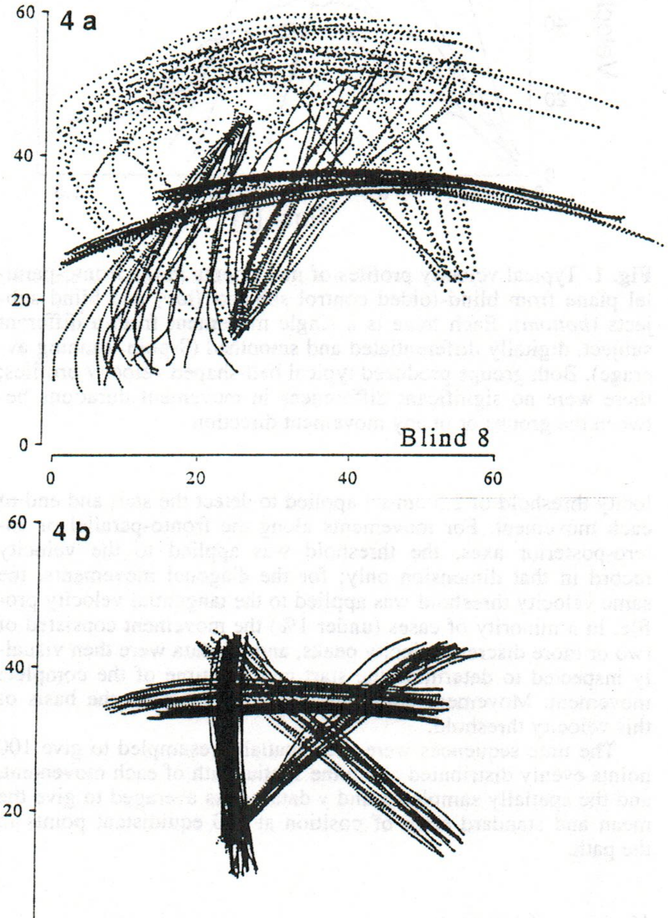

Fig. 4 Individual movements plotted for the one blind subject unable to perform the task (A) and for a typical blind subject (B). In the *upper panel* some data were clipped, as the subject reached the edge of the digitising table

Table 1 Curvature of movements. Each measure is the mean curvature (in millimetres ±SD) calculated from ten subjects making 18–20 movements each; two different methods of calculating curvature were used (see Materials and methods). The *arrows* indicate movement directions as shown in Figs. 2 and 3

Movement direction	Method 1: mid-point deviation		Method 2: mean absolute deviation	
	Blind	Control	Blind	Control
→	−9.71±7.69	−29.01±19.70	2.36±1.98	7.58±4.17
←	−10.04±6.35	−31.28±13.88	3.30±1.23	7.51±3.37
↑	−6.52±4.16	−2.63±3.96	2.00±0.88	1.24±0.50
↓	−3.23±3.16	6.57±16.11	1.47±0.48	2.55±3.33
↗	−21.40±19.12	−30.04±27.13	5.71±3.56	7.47±6.38
↖	−4.88±8.63	1.61±14.00	2.70±1.25	3.22±1.99

Table 2 Perception of curvature. Each measure is the mean null curvature (in millimetres±SD) of ten subjects. The null curvature for each subject was calculated from a binary forced-choice test involving six movements at nine different curvatures for each of three orientations (see Materials and methods). The *arrows* indicate movement directions in the same orientation as in Figs. 2 and 3; subjects were allowed to make multiple movements before reporting their perceived curvature

Movement direction	Null curvature (perceived as straight)	
	Blind	Control
↔	−0.85±7.85	−3.63±6.76
↕	−3.02±3.26	−5.28±4.75
⤢	−5.92±5.04	−8.08±7.85

Since we expected the effects of visual experience to be most pronounced in the fronto-parallel plane, we performed planned comparisons of the data to test this. This analysis did reveal significant group differences in the curvature of movements measured by method 1 when comparing just the fronto-parallel and antero-posterior movements ($F_{1,18}$=4.976, P=0.039), or when comparing the fronto-parallel and diagonal movements ($F_{1,18}$=5.684, P=0.028). It also revealed very significant group-by-direction interactions for the fronto-parallel and antero-posterior movements ($F_{3,54}$=12.162, P<0.0001); a smaller but still significant interaction for the fronto-parallel and diagonal movements ($F_{3,54}$=4.233, P=0.009); but no significant interaction for the antero-posterior and diagonal movements.

The movement curvature of the congenitally blind subjects did not differ significantly from that of those who had had some residual vision in early childhood (below the age of 2–11 years).

Perception of curvature

The blind subjects had a smaller mean null curvature in the perceptual task in all three orientations than the controls (Table 2). The mean curvature of the perceived straight line for the blind group was 3.26 mm versus 5.66 mm for the control group, but this difference did not reach significance; nor was there a significant group-by-direction difference. The mean curvature was in the same direction as the mean curvature of the movements for each group at each orientation. However, there was no significant correlation between the measured curvature of subjects' movements and their perceived curvature measurements (Fig. 5). The perception of curvature did not differ significantly between the congenitally blind subjects and those with some residual vision in early childhood.

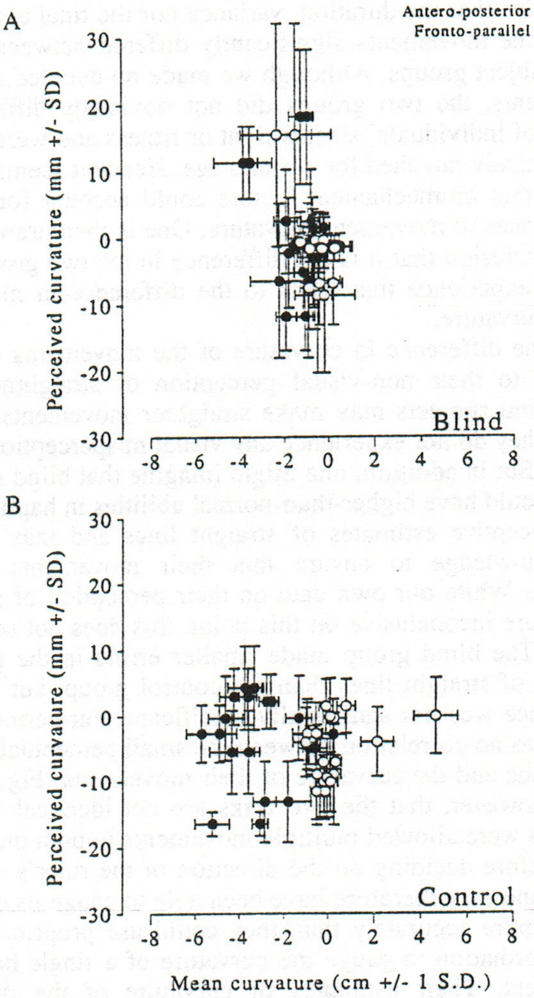

Fig. 5 The relationship between mean movement curvature and perceived curvature for the blind group (A) and the control subjects (B). In each graph, the perceived null point determined with a binary forced-choice procedure in two orientations has been plotted against the mean movement curvature for movement in those directions. The correlation coefficients did not reach significance in either group at any orientation. Diagonal movements and perceived curvature measurements have been omitted, allowing the differences in perceived curvature between the two groups to be compared more easily

Discussion

These results indicate that there are measurable differences in the curvature of movements made by blind subjects and blind-folded control subjects when moving the hand between two targets. The movements of the two subject groups were otherwise quite similar. For example, the mean durations of movements in all directions and in both subject groups were almost identical. The spatial variance of the paths was also very similar and showed a similar increase in variance during each movement. Neither the duration, variance nor the final accuracy of the movements significantly differed between the two subject groups. Although we made no detailed measurements, the two groups did not obviously differ in terms of individuals' size, weight or fitness and were approximately matched for sex and age. Hence it seems unlikely that biomechanical factors could account for the differences in movement curvature. One is then drawn to the conclusion that it is the difference in the two groups' visual experience that leads to the difference in movement curvature.

Is the difference in curvature of the movements then related to their non-visual perception of straightness? The blind subjects may make straighter movements because they do not experience any visual misperception of space. But in addition, one might imagine that blind subjects would have higher-than-normal abilities in haptic or proprioceptive estimates of straight lines and may use this knowledge to ensure that their movements are straight. While our own data on their perception of curvature are inconclusive on this point, this does not seem likely. The blind group made smaller errors in the perception of straight lines than the control group, but this difference was not statistically significant. Furthermore, there was no correlation between the small perceptual errors made and the curvature of their movements (Fig. 5). Note, however, that the two tasks are not identical: the subjects were allowed multiple movements in both directions before deciding on the direction of the ruler's curvature and may therefore have been able to gauge its curvature more accurately than they could use proprioceptive information to gauge the curvature of a single hand movement. Their estimates of curvature of the ruler could in principle be based on a static haptic measure, but the maximum curvature tested here (1.28 m^{-1}) is well below the threshold for static detection of curvature using the fingerpad alone (about 5 m^{-1}; Goodwin et al. 1991). The mean null curvature and the mean standard deviation of the psychometric functions measured in our task represent curvatures of less than 0.2 m^{-1} (Table 2). The subjects' estimates of curvature could also be based on afferent information from pressure sensors in the fingers during movement (Easton and Falzett 1978). However, this then requires accurate estimates of their arm movement to allow the afferent information to be calibrated. Only one blind subject had any difficulty in the movement task (Fig. 4A), and this subject was also reported to have considerable difficulties in everyday spatial tasks such as locating objects or in finding paths between buildings. Interestingly, although this subject claimed to have no concept of what a curve was and so could not say whether the ruler was bent towards or away from his body, he rapidly learned to discriminate the two directions in the perception task, by reporting the curvature as being of "pattern A" or "pattern B," and achieved scores within the range shown by the other blind subjects. This suggests a separation between the perception of curvature and the spatial ability necessary to make targeted hand movements.

A further point to consider is the possible transfer of information about straight lines in exteroceptive space. Wolpert et al. (1994) showed a very significant correlation between visual misperception and movement curvature in sighted subjects (see Introduction). Might this distortion of exteroceptive space also affect the perception of curvature in our non-visual task? In our blindfolded controls, the perceptual errors were larger than those of the blind group and mainly in the same direction as the curvature of their movements, but the correlation was not significant. Therefore we cannot yet say whether the visual misperception of curvature of sighted subjects, which leads them to make curved movements, leads to a small misperception of curvature in a proprioceptive task (Fig. 5B).

However, the important point about these results is that they lead to the conclusion that the path of the movement is affected by the subjects' sensory experience. Hence our data do not support the argument that only the limb dynamics are considered in planning and executing a point-to-point movement (Uno et al. 1989a; Kawato 1994). If the trajectory planning process was concerned only with some dynamic function such as the minimum-torque-change cost of the movement, then visual experience should not affect the final trajectory. In contrast our data suggest that the spatial path of the hand is explicitly represented in the trajectory planning process (Morasso 1981; Hogan 1984; Hogan and Flash 1987). Thus, in subjects with normal visual experience, visual induced distortions in the representation of exteroceptive space seem to lead to curved paths. Conversely, limited visual experience seems to lead to straighter hand paths.

The visual misperception of curvature demonstrated by Wolpert et al. (1994) is consistent with the curvature of the visual horopter (see, e.g. Foley 1980 or Tyler 1991 for reviews). Wolpert et al. showed that subjects perceive lines in the fronto-parallel plane which curved away from the body as being straight. Post-hoc analysis of the movement curvatures in our experiment indicated that the greatest difference between the blind and control group was in the fronto-parallel direction, with a smaller difference for the diagonal movements. This is also consistent with the visual horopter. Prablanc and Martin (1992) also reported that movements to targets displaced from the mid-line were more curved with visual feedback than without. However, Wolpert et al. (1994) report that their estimates of visual misperception can account for only about half of the movement curvature which they measured. It seems from our data that any non-visual perceptual errors are even smaller and at best could only account for a small fraction of the remaining curvature. It is therefore interesting that movement curvature was very different for the two diagonal movements tested in our experiment (Table 1); the ipsilateral-to-contralateral movement had a low mean curvature, whereas the contralateral-to-ipsilateral movement had the highest mean curvature. The misperception of curvature was also highest in this orientation (Table 2). Unfortunately we did not test the subjects' perception of curvature in the opposite diagonal orientation; neither did Wolpert et al. (1994) for their visual tasks. One would not expect the visual perception of curvature to differ greatly for these two orientations, as the visual horopter is essentially symmetrical (Foley 1980). The proprioceptive perception of curvature might well differ, however, as the two movements require very different rotations of the joints. It would therefore be a good further test of the visual or proprioceptive contribution to movement curvature to contrast the two diagonal movements.

So it is likely that one or more of the three remaining causes of curvature mentioned in the Introduction may add to the curvature of movement. The first cause, inaccuracy of the controller, cannot be excluded, and the variance of the measured paths may lend it some support. It is very clear that individual movements made by a single subject vary from trial to trial (Fig. 4B). The variance may be due to errors in the planning or in the execution of the movement. However, Oso et al. (1994) have shown that after training subjects are able to follow a specified straight-line path with lower curvature than in their unconstrained movements. This would suggest that the curvature could be avoided if the subject is instructed to move in straight lines and is able to perceive the curvature. Hocherman (1993) has shown that blind-folded subjects made errors in fast reaching movements in a task close to that used here, but the subjects were unable subsequently to make accurate corrections of these rapid movements. The subjects were also found to be as accurate at pointing with the opposite hand to target positions learned only with one hand. Hocherman therefore attributes some of the error in the movements to the representation of target localisation rather than to motor programming or motor execution. However, we found no significant difference in the terminal errors of the movements, nor in the variance about the mean paths. Castiello et al. (1993) tested the reach-to-grasp movements of blind subjects, and, while they found some significant differences in movement patterns between blind and control subjects, they concluded that visual experience was not necessary for the basic co-ordination of the two components of these movements. Thus while target representation may add to movement errors and thus contribute to movement curvature, it would not account for the differences between blind subjects and controls reported here.

The second possibility, that the path is planned in an intermediate co-ordinate set (as equilibrium positions or muscle-lengths) cannot be addressed by our results or those of Wolpert et al. (1994, 1995). Flash (1987) suggested that equilibrium trajectories might be straight, but the executed movement would be curved, depending on where in the workspace it was produced. This would largely be due to the dynamics of the limb. However, since we have no reason to suspect that the limb dynamics differ between the two groups tested here, our observed differences in hand paths would imply that the groups chose different equilibrium trajectories. It is possible that the intermediate trajectory could be influenced by visual experience, and this again suggests a clear role for sensory control of the path, but we cannot predict the effects on movement curvature.

Finally, one could consider that the trajectory planner is concerned with both the kinematics and the dynamics of a movement. In other words, the path may be partly planned in extrinsic co-ordinates without reference to limb dynamics, but modified on the basis of a dynamic cost function. This cost function might involve the mechanical effort associated with the movement (minimum torque-change or minimum muscle-tension-change; Uno et al. 1989b; see Dornay et al. 1992) or it might involve the computational complexity of the motor pattern (as related to the minimum motor command-change model; Kawato 1992). The resulting trajectory would then be a compromise between the optimally smooth and straight path in extrinsic co-ordinates and the optimal simple or smooth control signals required to achieve that path. This may then account for the very large curvature observed in some movement directions (Uno et al. 1989a) and also allow for the fact that hand curvature varies under different situations. In some tasks the only constraint is the hand direction and speed at the target position (e.g. when hitting a ball), but in others the paths' straightness is critical (e.g. when drawing on paper). Cruse et al. (1993) have shown that a cost function based on a subjective measure of ″joint comfort″ can also fit some movement paths. Thus it would seem most likely that the actual movement paths reflect a combination of cost functions operating in several different metrics.

We conclude that the fact that the blind subjects did not display a marked non-visual misperception of curvature, and that they made significantly straighter movements than controls, supports the hypothesis that visual misperception of curvature in sighted subjects contributes to the curvature of their movements.

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