

RESEARCH ARTICLE

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Hand and joint paths during reaching movements with and without vision

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Abstract This study examines whether the kinematics of pointing movements are altered by the sensory systems used to select spatial targets and to guide movement. Hand and joint paths of visually guided reaching movements of human subjects were compared with two non-visual conditions where only proprioception was available: (1) movements of the same subjects with blindfolds, and (2) movements by congenitally blind subjects. While hand-path curvatures were overall quite small, sighted subjects wearing a blindfold showed a statistical increase in hand-path curvature compared with their visually guided movements. Blindfolded subjects also showed greater hand-path curvature than blind subjects. These increases in hand-path curvature for blindfolded subjects did not always lead to a decrease in joint-path curvature. While there were differences between blind subjects and sighted subjects using vision for some movement directions, there was no systematic difference between these two groups. The magnitude of joint-path curvature showed much greater variation than hand-path curvature across the movement directions. We found variation in joint-path curvature to be correlated to two factors, one spatial and one geometrical. For all subject groups, joint-path curvature tended to be smaller for sagittal-plane movements than for transverse or diagonal movements. As well, we found that the magnitude of joint-path curvature was also related to the relative motion at each joint. Joint-path curvature tended to increase when movements predominantly involved changes in shoulder angle and was minimal when movements predominantly involved elbow motion. The consistently

small curvatures of hand trajectory across blind and sighted subjects emphasize the powerful tendency of the motor system to generate goal-directed reaching movements with relatively straight hand trajectories, even when deprived of visual feedback from very early in life.

Key words Reaching movements · Blind · Visual perception · Motor learning

Introduction

A key feature of goal-directed reaching movements is that the hand follows a fairly straight path (Morasso 1981; Abend et al. 1982). Even when the mechanics of the movement alter the trajectory of the hand, subjects will tend to adjust their motor patterns to re-establish a relatively straight hand path (Lackner and Dizio 1994; Shadmehr and Mussa-Ivaldi 1994). However, debate continues on the significance of these findings. It has been argued that straight hand trajectories support the notion that the CNS plans a reference hand trajectory, and any deviations from a straight line result from limb biomechanics (Flash and Hogan 1985, 1987; Bullock and Grossberg 1988). In contrast, others support a more dynamic control scheme and suggest that small hand curvatures are a result of an imprecise planner (Uno et al. 1989; Dornay et al. 1992). In either case, relatively straight hand trajectories are considered to reflect an important constraint on how the CNS plans and executes reaching movements.

An interesting dimension added to this debate comes from recent studies illustrating that visual perception alters the kinematics of hand motion during reaching (Wolpert et al. 1994, 1995; Flanagan and Rao 1995; but see Imamizu et al. 1994). Flanagan and Rao (1995) compared point-to-point movements when a computer monitor provided visual feedback of the movement trajectory in either hand or joint space. With visual feedback of hand trajectory, subjects maintained relatively straight hand trajectories at the expense of curved joint trajectory

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ries. In contrast, visual feedback of joint-angle trajectories resulted in straighter joint-angle trajectories at the expense of more curved hand trajectories. Therefore, subjects tended to linearize movements based on visual perception (feedback) of the movement, regardless of the underlying mechanical conditions of the task. Further evidence of the contribution of visual perception to hand-path curvature is provided by Wolpert et al. (1994). Their study took advantage of a natural visual distortion, which makes straight transverse lines appear concave (Foley 1980). Wolpert et al. (1994) found a significant correlation between the size and direction of the misperception of the transverse plane and the curvature of arm movements along this plane. This finding suggested that subjects perceived, because of the visual distortion, that they were moving relatively straight, while in fact the actual movements were more curved. Taken together, these studies demonstrated that visual perception of movement, and not just motoric constraints, can influence hand trajectory during movement.

While vision has been shown to have a strong influence on hand trajectory formation, vision is not always available to identify targets in space or to provide online feedback of limb trajectory, such as when we reach for a light switch in the dark. For blind individuals, target selection and movement feedback must always occur without the benefit of vision. The question we pose in this study is whether or not there are changes in limb trajectory when different sensory systems are used to identify spatial targets and contribute to ongoing movement feedback. Visually guided reaching normally involves visual and proprioceptive systems. We compared visually guided movements with two different non-visual conditions, in which only proprioception was used. First, we compared the movement performance of individual subjects with and without a blindfold to assess how temporary loss of vision affects movement trajectory. Second, we compared movement trajectory between sighted subjects and subjects who were either born blind or lost vision soon thereafter, thus having had minimal visual experience to guide movement. It has been shown that blind subjects produced straighter hand paths compared with blindfolded sighted subjects for transverse planar movements (Miall and Haggard 1995), as predicted by visual misperception of the transverse plane (Wolpert et al. 1994). In this report we extend this comparison to normal conditions for these two populations. That is, we compare pointing movements by blind subjects with movements by sighted subjects using vision.

Materials and methods

Subjects

The movements of seven sighted subjects (three male, four female, all right handed), ranging in age from 23 to 30 (mean=25), were analyzed in this study. In addition, seven congenitally blind subjects (three male, four female, all right handed), ranging in age from 18 to 41 (mean=26.1), were also used in this study. They were

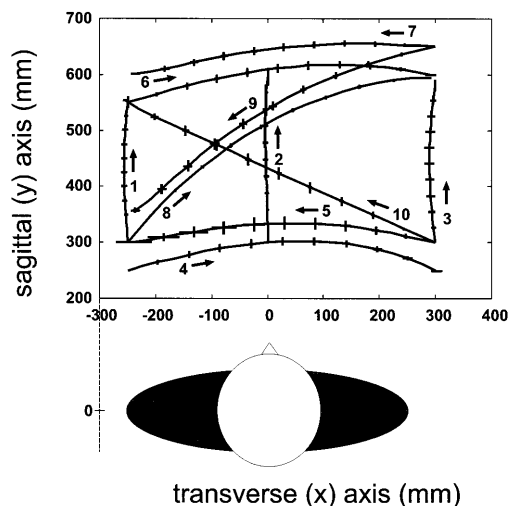


Fig. 1 Average hand paths (with standard error bars) for sighted subjects with their eyes open. The numbered arrows indicate the assigned movement number. The paths for movements 4, 7, and 9 have been displaced 50 mm for clarity

all blind either at or within eighteen months of birth and had no other handicaps. Each subject was naive to the nature of the experiment and signed a consent form outlining the procedures, approved by the University Human Research Ethics Committee, prior to participating in the study.

Procedure

Subjects sat in front of a board placed at chest height. Fixed to the board were six small squares of Velcro, positioned so that the distances between them would cover a large area, but remain well within the subjects' work-space boundaries (Fig. 1). Targets consisted of two round plastic cylinders (60 mm in height, 15 mm radius), which could be attached to the Velcro squares in order to specify start and end locations. Subjects were positioned so that the proximal targets were 30 cm anterior to their shoulders and their midline was aligned with the two mid-sagittal target locations.

Reaching movements were performed with the right arm, the dominant arm for all subjects. A total of ten movement directions were performed (Fig. 1): three sagittal movements starting from the left, midline, or right (movements 1–3); four transverse movements either 30 cm (movements 4, 5) or 60 cm (movements 6, 7) from the mid-frontal plane, starting from the left and the right; three diagonal movements starting from the left and the right (movements 8–10).

The experimenter guided the hand of the blindfolded and blind subjects to the start and end targets. They were then allowed to make 3–10 self-guided practice movements between target locations, given the instructions that movements should be smooth, at a "natural" speed, and with no terminal correction or torso movement. The end target was then removed and subjects were instructed to move, upon a "go" signal, between the start target and the remembered end target. They were asked to maintain their hand above the table at the end location until a tone sounded (2 s after the "go" signal). They then returned to the start target or rested if necessary. Five trials were collected for each of ten target pairs, for a total of 50 trials. The order of the ten movements was randomized for each subject.

Sighted subjects were first tested while wearing a cloth blindfold and then with their eyes open. The reverse order of movement tasks was never tested to avoid the potential use of visual memory of target locations in the blindfolded conditions. Although this fixed order of the tasks is not optimal, there are two reasons why we do not believe the blindfolded condition altered the subsequent

Table 1 Average hand- and joint-path linearity ratios (\pm standard deviations) for each visual group

Movement	Hand-path linearity ratio (\pm SD)			Joint-path linearity ratio (\pm SD)		
	Blind	Blindfold	Vision	Blind	Blindfold	Vision
1	0.054 \pm 0.026	0.075 \pm 0.041	0.032 \pm 0.016	0.029 \pm 0.015	0.017 \pm 0.007	0.020 \pm 0.012
2	0.039 \pm 0.013	0.057 \pm 0.047	0.027 \pm 0.010	0.022 \pm 0.005	0.036 \pm 0.027	0.025 \pm 0.012
3	0.074 \pm 0.055	0.059 \pm 0.033	0.056 \pm 0.035	0.070 \pm 0.043	0.048 \pm 0.036	0.049 \pm 0.042
4	0.068 \pm 0.032	0.095 \pm 0.033	0.095 \pm 0.023	0.364 \pm 0.221	0.189 \pm 0.120	0.199 \pm 0.132
5	0.052 \pm 0.031	0.102 \pm 0.040	0.067 \pm 0.026	0.262 \pm 0.143	0.110 \pm 0.067	0.147 \pm 0.053
6	0.064 \pm 0.020	0.064 \pm 0.029	0.070 \pm 0.025	0.331 \pm 0.214	0.511 \pm 0.259	0.330 \pm 0.199
7	0.054 \pm 0.035	0.062 \pm 0.032	0.046 \pm 0.026	0.296 \pm 0.185	0.428 \pm 0.146	0.489 \pm 0.198
8	0.074 \pm 0.044	0.110 \pm 0.043	0.109 \pm 0.038	0.171 \pm 0.075	0.114 \pm 0.065	0.112 \pm 0.065
9	0.070 \pm 0.018	0.093 \pm 0.017	0.074 \pm 0.032	0.236 \pm 0.133	0.133 \pm 0.033	0.214 \pm 0.038
10	0.046 \pm 0.028	0.048 \pm 0.023	0.035 \pm 0.026	0.213 \pm 0.129	0.077 \pm 0.032	0.058 \pm 0.025

sighted movements. First, blindfolded and sighted movements in a given spatial direction were interspersed, on average, by 100 movements in other spatial locations and directions (assuming five practice and five recorded movements for each movement direction). Second, while changes in hand trajectory were observed between conditions (see Results), we found no difference in other kinematic features of movement, such as movement speed. A comparison of the average movement speed grouped by distance, since the preferred speed of a reaching movement generally increases with distance, revealed no difference across visual groups ($P>0.01$). The average speeds (\pm SD) for blind, blindfolded, and with-vision were, respectively, 44.3 (\pm 8.5) cm/s, 42.1 (\pm 13.8) cm/s, and 45.0 (\pm 9.5) cm/s for sagittal movements; 67.6 (\pm 16.9) cm/s, 65.4 (\pm 16.9) cm/s, and 71.5 (\pm 15.0) cm/s for transverse movements; and 70.6 (\pm 17.4) cm/s, 66.6 (\pm 18.2) cm/s, and 72.7 (\pm 14.5) cm/s for diagonal movements.

Arm position was recorded in three dimensions using an Optotrak system (Northern Digital). Infrared-emitting diodes (IREDS) were placed on the subjects' shoulder, upper arm, lower arm, and finger tip. Subjects' wrists were immobilized with a brace. Two IREDS spanned each side of the shoulder and elbow joints in order to calculate the absolute segment angles. Limb movements were performed at chest level so that arm motion was generated predominantly by flexion and extension movements at the shoulder and elbow joints. Correct marker placement was assured by directly comparing measured joint angles at fixed arm postures with joint angles computed from the segment markers. Marker positions were sampled at a rate of 100 Hz.

Data analysis

For measures in both joint (shoulder-elbow angles) and hand (X-Y position) space, individual paths were first filtered at 10 Hz. Movement onset and offset was then identified on the paths using 10% of the peak tangential velocity. The paths were then cropped at these points and divided into 20 equidistant parts in order to calculate the mean and standard deviation at each point.

Curvature was measured in four different ways, so that the present results could be compared with those of previous studies, using various curvature measures. The measures were: (1) area between the path and a straight line drawn between the start and end points; (2) the perpendicular distance of the path's mid-point from a straight line between start and end points (Miall and Haggard 1995); (3) curvature based upon the equation $C=(VMT \times MT/DMT) - 1$, where VMT is the average tangential velocity during the movement time MT, and DMT is the straight line distance between start and end points (Turner et al. 1995); and (4) the linearity ratio, defined as the maximum deviation of the path from a straight line drawn between endpoints divided by the length of that straight line (Atkeson and Hollerbach 1985). All measures gave similar results, with the occasional exception that the deviation from the midpoint of a straight-line path (no. 2) would give a smaller curvature. In individ-

ual trials, this measure differed because the curvature was greatest towards the end of the trajectory. However, because these instances were infrequent and the remaining three measures gave similar results, only the linearity ratio (method no. 4) will be reported in this paper.

Results

Hand- and joint-path curvatures with and without vision

In general, hand-path curvatures for all movements and all subjects were quite small. Figure 2 shows the average hand path of one sagittal, one diagonal, and one transverse movement for each visual group. For sighted subjects, there was a small, yet consistent reduction in hand-trajectory curvature from blindfolded to open-eyed conditions across most movement directions (ANOVA, $P<0.05$; Tables 1 and 2). Significant reductions in hand-path curvature were observed for three of the ten movements (paired t -test, $P<0.01$ for movements 1 and 5, $P<0.05$ for movement 2). Across all movements, sighted subjects with their eyes open showed no systematic difference in hand-path curvature compared with blind subjects (ANOVA, $P>0.05$, Tables 1 and 2). Specific movements did show some differences. Blind subjects were straighter than sighted subjects with their eyes open for the transverse and diagonal movements starting from the lower left target (movements 4 and 8, $P<0.05$). However, their hand paths were more curved than sighted subjects for the sagittal movements starting from the lower left and the lower central target (movements 1 and 2, $P<0.05$). Across the entire workspace, there was a tendency for sighted subjects wearing blindfolds to produce hand paths with greater curvature than blind subjects. That is, statistical differences between blind and blindfolded subjects reflected straighter hand trajectories for blind subjects (movements 5 and 9; student's t -test, $P<0.01$ and $P<0.05$).

There was no systematic difference in joint-path trajectory between blind and sighted subjects either blindfolded or with their eyes open (ANOVA, $P>0.05$; Fig. 3). One transverse movement (6; paired t -test, $P<0.01$) was significantly straighter for open-eyed conditions than blindfolded, but the opposite was found for one diagonal

Table 2 Relative linearity ratios. Double “greater than” symbols (\gg and \ll) $P < 0.01$, single “greater than” symbols ($>$ and $<$) $P < 0.05$, symbols point to the smaller value (V Vision, B blind, F blindfold)

Orientation	Movement	Hand paths			Joint paths		
		Vision-blind ^a	Blindfold-blind ^a	Blindfold-vision ^b	Vision-blind ^a	Blindfold-blind ^a	Blindfold-vision ^b
Sagittal	1	V<B		F>>V		F<B	
	2	V<B		F>V			
	3						
Transverse	4	V>B					
	5		F>>B	F>>V	V<<B	F<<B	
	6						F>>V
	7				V>B		
Diagonal	8	V>B					
	9		F>B			F<B	F<<V
	10				V<<B	F<<B	
	ALL ^c		F>>B	F>V			

^a Student’s *t*-test; ^b paired *t*-test; ^c one-way ANOVA

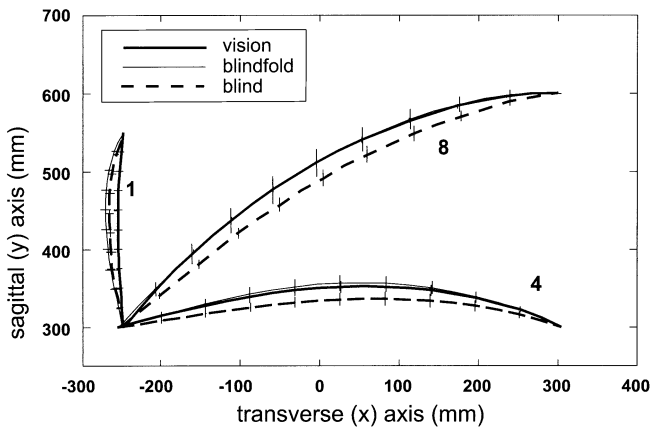


Fig. 2 Average hand paths (with standard error bars) for sighted subjects with their eyes open (*vision*), blindfolded sighted subjects (*blindfold*), and congenitally blind subjects (*blind*) for three movements

movement (9; paired *t*-test, $P < 0.01$). Blind subjects also produced greater joint-path curvatures versus eyes-open sighted subjects for one transverse and one diagonal movement (movements 5 and 10, $P < 0.01$). In contrast, ipsi-to-contralateral distal transverse movements were straighter in blind versus eyes-open control subjects (movement 7; Student’s *t*-test, $P < 0.05$). Joint-path curvatures were greater in blind versus blindfolded subjects for one diagonal, one transverse, and two diagonal movements ($P < 0.01$ for movements 5 and 10; $P < 0.05$ for movements 1 and 9).

Variation of hand- and joint-path curvature relative to spatial and geometric factors

Hand path curvature remained small and relatively consistent for movements in all spatial directions for blind and sighted subjects (Fig. 4, top panel; $F_{2,18} = 0.28$ and 1.04 , $P > 0.05$). One exception was that the sighted subjects with their eyes open produced straighter hand paths in the sagittal than in the diagonal direction ($F_{2,18} = 4.56$, $P < 0.05$).

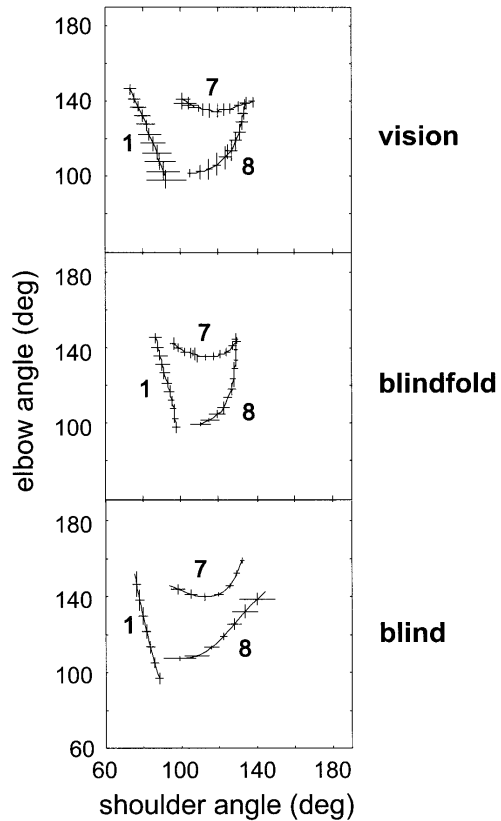


Fig. 3 Average joint paths (with standard error bars) produced by one sighted subject using vision and while wearing a blindfold (subject no. 10, upper and middle panels), and one blind subject (subject no. 7, lower panel). The number beside each path corresponds to the movement numbers in Fig. 1

In contrast, we found that joint-path curvature varied systematically with movement direction, although there was no single trend observed in joint-path curvature across the different visual conditions. Joint paths were most curved for transverse movements, less curved for diagonal movements, and straightest for sagittal movements. Figure 3 shows joint paths for three representative movements for one sighted (upper and middle pan-

els) and one blind subject (lower panel). It can be seen that transverse movements crossing the body (movement 7) had a larger joint-path curvature than sagittal movements (movement 1) for visual and non-visual conditions. The bottom panel of Fig. 4 illustrates the large and systematic variation in joint-path curvature for movements in the three different spatial directions across subjects, where transverse movements (4–7), involving mostly shoulder rotation, are curved, while sagittal movements (1–3), comprised of mainly elbow rotation, are quite straight. Overall, the magnitude of joint-path curvature

was larger than hand-path curvature for both transverse and diagonal movements. In a one-way ANOVA, joint-path curvature was significantly different between the three movement orientations, across both blind and sighted subjects (for blind, blindfolded, eyes-open: $F_{2,18} = 24.73, 18.43, \text{ and } 12.5; P < 0.0001$).

The variability of joint-path curvature was different across movement direction, and was overall greater than hand-path curvature (Fig. 4). A test of equality of variances (Snedecor and Cochran 1980) found that the overall variance of joint-path curvature was significantly greater than hand-path curvature across movements and visual groups ($P < 0.01$). For joint-path curvature, individual tests revealed that the variance of transverse movements was greater than that for diagonal and sagittal movements. The variance for diagonal movements was, in turn, greater than for sagittal movements ($P < 0.01$). There were no significant difference in the variance of hand-path curvature between different movement directions, or in the variance of either hand- or joint-path curvature between the different visual groups ($P > 0.05$).

The magnitude of joint-path curvature was also found to vary systematically with the relative motion at the shoulder and elbow joints. Joint-path curvatures were always small for movements predominantly involving only elbow motion, whereas they tended to be larger for movements predominantly involving shoulder-joint motion. Movements involving similar motion at the shoulder and elbow joint were intermediate to these two extremes. This finding can also be observed in Fig. 3, where transverse movements involving mostly shoulder rotation are curved, while sagittal movements comprised of mainly elbow ro-

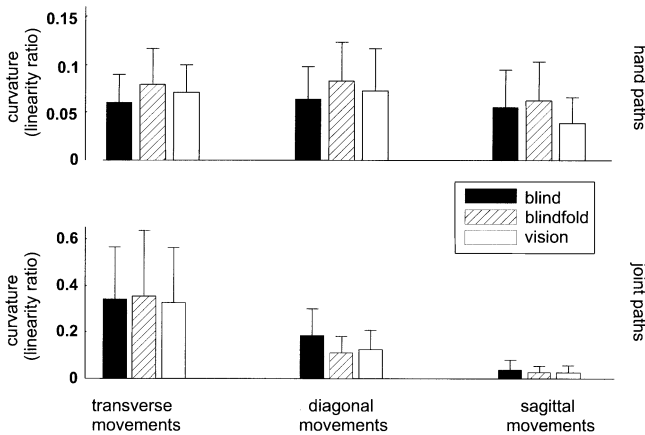
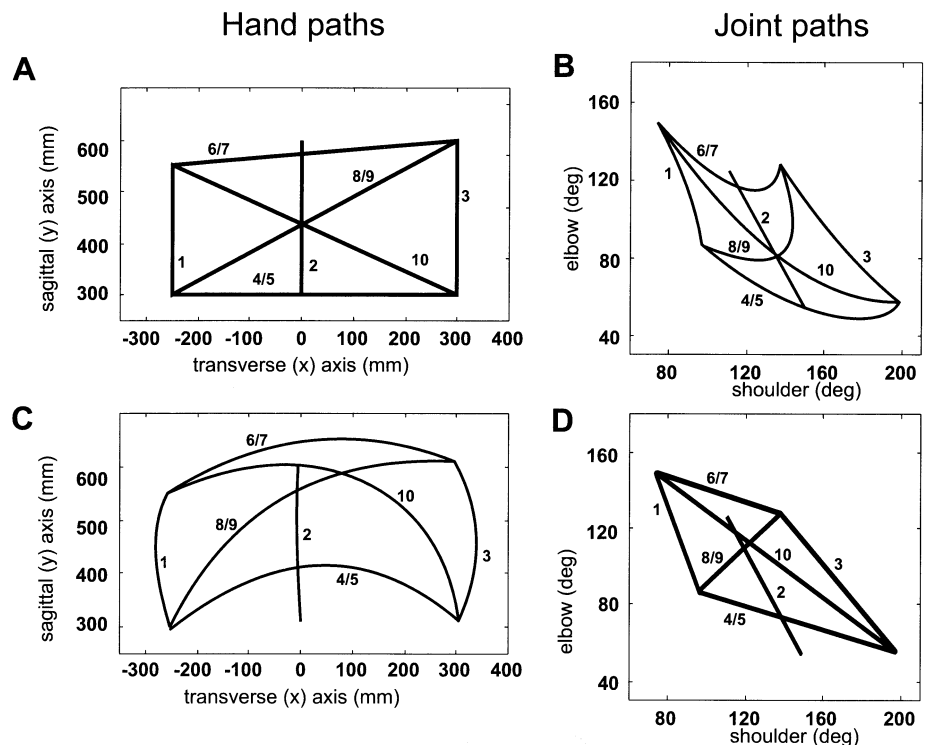


Fig. 4 Histograms depicting average hand-path (*top panel*) and joint-path (*bottom panel*) curvature for each of the three visual conditions grouped by movement direction. Note that the *vertical scale* in the upper panel is four times smaller than that of the lower panel

Fig. 5A–D Trigonometric relations between hand and joint paths. The *numbers* beside the paths correspond to the assigned movement numbers used in previous figures. Straight hand paths (**A**) between targets produce curved joint paths (**B**). Straight joint paths (**D**) produce curved hand paths (**C**)



tation are quite straight. Relative joint motion was divided into three groups: (1) “mostly shoulder”, where shoulder motion was at least 50% greater than at the elbow; (2) “mostly elbow”, where elbow motion was at least 50% greater than at the shoulder; and (3) roughly “equal” motion at both joints. For the visual and non-visual conditions analyzed in this study, joint-path curvature was significantly different between these three relative joint-motion groups (ANOVA for blind, blindfolded, eyes-open: $F_{2,18} = 11.3, 12.39, \text{ and } 5.62; P < 0.01$). It is interesting to note that all three visual conditions analyzed in this study showed similar dependencies between joint-path curvature and the relative motion at the shoulder and elbow joints. Within each category of joint motion (e.g., mostly shoulder, equal, mostly elbow) there were no significant differences in the linearity ratio between visual groups (ANOVA, $P > 0.01$). Unlike joint paths, hand-path curvature showed no systematic variation with the relative motion at the shoulder and elbow joints (for blind, blindfolded, eyes-open: $F_{2,18} = 0.38, 0.66, \text{ and } 0.05; P > .05$).

To better understand the interaction between the spatial direction and the relative joint motion of limb movement, we looked at the nature of coupling between hand and joint paths for each of the movements studied in this experiment. We employed a simple two-segment model of the arm to understand how linear hand trajectories are transformed into joint-angle space and vice versa. Link lengths were chosen to match the length of the forearm and upper arm of one of the seven sighted subjects, and the hand and both limb segments were assumed to stay in the horizontal plane. Linear hand trajectories between the start and end target positions were converted into joint-angle space for each of the ten movements. Correspondingly, linear joint-angle trajectories for each movement were converted into hand space. Figure 5 illustrates how linear hand trajectories for the ten movements (Fig. 5A) generate complex joint-angle trajectories (Fig. 5B). For straight-line sagittal movements (1–3), there are only moderate changes in joint-angle curvature. Diagonal and transverse movements, which predominantly involve shoulder-joint motion, transform into large joint-angle curvatures. In general, the curvature in shoulder- and elbow-joint angle for movements in different directions are qualitatively similar to those observed in Fig. 3. Conversion of linear joint-angle trajectories (Fig. 5D) also generate complex changes in hand trajectory (Fig. 5C). Sagittal movements are generally straight, as observed for human reaching movements, whereas transverse and diagonal hand trajectories are very curved. However, unlike some of the paths depicted in Fig. 5C, hand paths with large curvatures were never observed in either blind or sighted subjects, nor was a systematic relationship found between hand path curvature and different spatial movement directions (Fig. 4).

Discussion

Recent studies have demonstrated the importance of visual feedback of movement on hand-path trajectory

(Wolpert et al. 1994, 1995; Flanagan and Rao 1995). Under normal conditions, the visual and proprioceptive systems are used together for movement selection and guidance. The question posed in the present study was whether there are any changes to the kinematic patterns of reaching when the proprioceptive system is used alone to select and guide movement compared with when vision is also involved. There are several findings. First, movements performed by sighted subjects with a blindfold were more curved than movements performed with vision. This suggests that movement trajectory is influenced by the sensory systems used to plan and guide movements, and that a short term loss of vision results in changes in the motor patterns to execute limb movements. However, subjects having a life-long loss of vision moved straighter than blindfolded sighted subjects. Blind subjects did not show an increase in hand path curvature compared with sighted subjects using vision. In some cases, they moved straighter than sighted subjects for transverse movements, likely because of visual misperception on the part of the sighted subjects (Wolpert et al. 1994, 1995; Miall and Haggard 1995). Second, for all subject groups, the magnitude and variation in joint path curvature for movements in different directions was greater than hand-path curvature. Variation in joint-path curvature appears to be related to spatial and geometrical factors. Linear joint paths tend to occur for sagittal movements, which predominantly involve elbow motion, whereas curved joint paths occur for transverse movements, which predominantly involve shoulder motion. These trigonometric relations reflect how spatial motion of the hand is related to angular motion of the multi-segmented limb in a complex manner. Lastly, the magnitude and variation of hand-path curvature for movements in different directions was overall quite small, as originally observed by Morasso (1981). This trend was observed for the movements with and without vision analyzed in this study, emphasizing the powerful tendency of the subjects to generate relatively straight hand trajectories even when deprived of visual feedback from early in life.

Changes in hand-path trajectory with short-term removal of vision

This study illustrates that short-term removal of vision results in a more curved hand trajectory during pointing movements than during movements performed with vision. One possible explanation for the increase in hand-trajectory curvature under blindfolded conditions is that subjects tend to linearize their movements in a sensory system used to select and guide movements. It is known that subjects will make more curved hand paths in order to maintain linear visual feedback of limb motion (Flanagan and Rao 1995; Wolpert et al. 1995). If vision is not available and only proprioception is involved to select and guide movement, an analogous result would be for subjects to make linear joint motions during movement. This hypothesis would predict that increased

curvature of hand trajectory from blindfolded to sighted conditions would always be coupled with decreased joint-path curvature. Note that this inverse coupling between hand- and joint-path curvature is not obligatory. Increases in hand-trajectory curvature can lead to either an increase or a decrease in joint-path curvature, depending on movement direction and whether hand-path curvature is clockwise or counter-clockwise.

Both hand and joint motion were recorded in this study in order to investigate whether subjects shifted from a linear hand- to a linear joint-path strategy when changing from sighted to blindfolded conditions. However, we found that increases in hand trajectory were not always coupled to decreases in joint-path trajectory from sighted to blindfolded conditions. Statistical differences between blindfolded and sighted joint-path curvatures were observed for two movement directions, but, in one of these cases, joint-path trajectories were actually straighter when vision was used.

It may be that short-term removal of vision results in a degradation of the subject's ability to plan and guide goal-directed pointing movements. This reduced performance may be due to the dominant use of vision to select and guide arm movements under most conditions. However, the comparable performance of congenitally blind and sighted subjects using vision suggests that humans can, with time, learn to move just as straight when only proprioception is utilized. Note that this explanation assumes that subjects are attempting to generate straight hand trajectories, whether or not vision is used to guide movement.

Consistency of hand-path curvature

One of the main findings of this study is that hand-path curvatures were consistently straighter than joint-path curvatures for movements spanning most of the workspace, regardless of whether the subjects were congenitally blind, were sighted and blindfolded, or were sighted and had their eyes open. These results augment the growing body of literature highlighting the importance of hand-path trajectory in planning and executing reaching movements (Morasso 1981; Flash and Hogan 1985; but see Suzuki et al. 1997). Recent studies have also demonstrated that, under complex changes in movement dynamics, subjects eventually adjust motor performance to once again generate relatively straight hand paths (Lackner and Dizio 1994; Shadmehr and Mussa-Ivaldi 1994; Shadmehr and Brashers-Krug 1997). In addition, the increased variability of paths in joint versus hand space across visual groups (Haggard et al. 1995; present study) suggests that straight hand paths may be produced at the expense of consistency at the joint level.

While hand trajectory tends to be preserved for point-to-point movements, it is not clear how this information is utilized in the planning and execution of goal-directed movements. One possibility is that hand trajectory is explicitly defined in the series of putative sensorimotor

transformations involved in converting visual target information into motor output to muscles (Soechting and Flanders 1991; Kalaska and Crammond 1992). Neuronal activity in many cortical regions implicated in goal-directed reaching movements, such as primary motor cortex, dorsal premotor cortex, and parietal area 5, covaries with the direction of hand movement (Georgopoulos et al. 1982; Kalaska et al. 1983; Caminiti et al. 1991; Crammond and Kalaska 1996). However, recent experiments developed to uncouple or dissociate different variables of movement illustrate that the discharge of cells in these cortical regions is sensitive to many parameters other than hand trajectory (Kalaska et al. 1989; Crutcher and Alexander 1990; Boussaoud 1995; Kalaska and Crammond 1995; Scott and Kalaska 1997; Scott et al. 1997; Sergio and Kalaska 1998; Shen and Alexander 1997a,b). For example, cell discharge in dorsal premotor cortex covaries with a variety of factors, including arm geometry (Scott et al. 1997), target location (Shen and Alexander 1997b), and even gaze angle (Boussaoud 1995). While psychophysical studies continue to demonstrate that hand trajectory is an important feature in goal-directed reaching movements, the existence of an explicit neural correlate of this variable continues to be elusive.

Another possibility is that hand trajectory is determined largely at a perceptual, rather than motoric level. Flanagan and Rao (1995) showed that subjects produced straight hand paths when viewing their movements in hand space, but learned to produce straighter joint paths when viewing their movements in joint space. Further, Wolpert et al. (1994) demonstrated that a visual distortion in the transverse plane contributed to hand-path curvature. They found a significant correlation between actual and perceived curvature, suggesting that subjects perceived their curved movements to be straight due to visual distortion. This supposition was supported by a later study, in which subjects adapted to an increase in perceived curvature by altering their actual hand movement so that the perceived curvature was reduced (Wolpert et al. 1995). The implication from these studies is that subjects preferred visually straight movement feedback, regardless of the actual trajectory of the hand in space. That is, they preferred to "see" rather than execute straight movements.

However, visual feedback in itself is not sufficient to explain why subjects tend to generate straight hand paths during movement. Congenitally blind individuals, who have never received visual feedback during motor learning, still generate roughly straight reaching movements (present study; Miall and Haggard 1995). Without vision, proprioception provides the only source of feedback to perceive and correct deviations from straight-line hand paths. Spindles are known to be intimately involved in limb-position sense and kinesthesia (Gandevia et al. 1992). The initial sensory representation of movement provided by spindles does not simply define joint angle, since the mechanical advantage and fiber orientation of muscles often vary with joint angle (An et al. 1981; Otten 1987; Young et al. 1993), and spindles in bi-

articular muscles reflect motion at both spanned joints. It remains debatable how these signals are converted to perceive arm position and aid movement control (Flanders et al. 1992; Scott and Loeb 1994; Lacquaniti et al. 1995; Scott et al. 1997).

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References

- Abend W, Bizzi E, Morasso P (1982) Human arm trajectory formation. *Brain* 105:331–348
- An K, Hui FC, Morrey BF, Linscheid RL, Chao EY (1981) Muscles across the elbow joint: a biomechanical analysis. *J Biomech* 14:659–669
- Atkeson CG, Hollerbach JM (1985) Kinematic features of unrestrained vertical arm movements. *J Neurosci* 5:2318–2330
- Boussaoud D (1995) Primate premotor cortex: modulation of preparatory neuronal activity by gaze angle. *J Neurophysiol* 73:886–890
- Bullock D, Grossberg S (1988) Neural dynamics of planned arm movements: emergent invariants and speed-accuracy properties during trajectory formation. *Psychol Rev* 95:49–90
- Caminiti R, Johnson PB, Galli C, Ferraina S, Burnod Y (1991) Making arm movements within different parts of space: the premotor and motor cortical representation of a coordinate system for reaching to visual targets. *J Neurosci* 11:1182–1197
- Crammond DJ, Kalaska JF (1996) Differential relation of discharge in primary motor cortex and premotor cortex to movements versus actively maintained postures during a reaching task. *Exp Brain Res* 108:45–61
- Crutcher MD, Alexander GE (1990) Movement-related neuronal activity selectively coding either direction or muscle pattern in three motor areas of the monkey. *J Neurophysiol* 64:151–163
- Dornay M, Uno Y, Kawato M, Suzuki R (1992) Simulation of optimal movements using the minimum-muscle-tension-change model. In: Moody JE, Hanson SJ, Lippmann RP (eds) *Advances in neural information processing systems*, vol 4. Morgan Kaufmann, San Mateo, pp 627–634
- Flanagan JR, Rao AK (1995) Trajectory adaptation to a nonlinear visuomotor transformation: evidence of motion planning in visually perceived space. *J Neurophysiol* 74:2174–2178
- Flanders M, Helms-Tillery SI, Soechting JF (1992) Early stages in a sensorimotor transformation. *Behav Brain Sci* 15:309–362
- Flash T, Hogan N (1985) The coordination of arm movements: an experimentally confirmed mathematical model. *J Neurosci* 5:1688–1730
- Flash T, Hogan N (1987) The control of hand equilibrium trajectories in multi-joint arm movements. *Biol Cybern* 57:257–274
- Foley JM (1980) Binocular distance perception. *Psychol Rev* 87:411–434
- Gandevia S, McCloskey DI, Burke D (1992) Kinaesthetic signals and muscle contraction. *Trends Neurosci* 15:62–65
- Georgopoulos AP, Kalaska JF, Caminiti R, Massey JT (1982) On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex. *J Neurosci* 2:1527–1537
- Haggard PN, Hutchison K, Stein J (1995) Patterns of coordinated multi-joint movement. *Exp Brain Res* 107:254–266
- Imamizu H, Uno Y, Kawato M (1994) Learning and trajectory planning in kinematic alteration of joint angles. *Soc Neurosci Abstr* 20:576
- Kalaska JF, Crammond DJ (1992) Cerebral cortical mechanisms of reaching movements. *Science* 255:1517–260
- Kalaska JF, Crammond DJ (1995) Deciding not to GO: neural correlates of response selection in a GO/NOGO task in primate premotor and parietal cortex. *Cereb Cortex* 5:410–428
- Kalaska JF, Caminiti R, Georgopoulos AP (1983) Cortical mechanisms related to the direction of two-dimensional arm movements: relations in parietal area 5 and comparison with motor cortex. *Exp Brain Res* 51:247–260
- Kalaska JF, Cohen DA, Hyde ML, Prud'homme M (1989) A comparison of movement direction-related versus load direction-related activity in primate motor cortex, using a two-dimensional reaching task. *J Neurosci* 9:2080–2102.
- Lackner JR, Dizio P (1994) Rapid adaptation to Coriolis force perturbations of arm trajectory. *J Neurophysiol* 72:1–15
- Lacquaniti F, Guigon E, Bianchi L, Ferraina S, Caminiti R (1995) Representing spatial information for limb movement: role of area 5 in the monkey. *Cereb Cortex* 5:39–409
- Miall RC, Haggard PN (1995) The curvature of human arm movements in the absence of visual experience. *Exp Brain Res* 103:421–428
- Morasso P (1981) Spatial control of arm movements. *Exp Brain Res* 42:223–227
- Otten E (1987) Concepts and models of functional architecture in skeletal muscle. *Exerc Sport Sci Rev* 16:89–137
- Scott SH, Kalaska JF (1997) Reaching movements with similar hand paths but different arm orientations. I. Activity of individual cells in motor cortex. *J Neurophysiol* 77:826–852
- Scott SH, Loeb GE (1994) The computation of position sense from spindles in mono- and multiarticular muscles. *J Neurosci* 14:7529–7540
- Scott SH, Sergio LE, Kalaska JF (1997) Reaching movements with similar hand paths but different arm orientations. II. Activity of individual cells in dorsal premotor and parietal area 5 cortex. *J Neurophysiol* 78:2413–2426
- Sergio LE, Kalaska JF (1998) Changes in the temporal pattern of primary motor cortex activity in a directional isometric force versus limb movement task. *J Neurophysiol* (in press)
- Shadmehr R, Brashers-Krug T (1997) Functional stages in the formation of human long-term motor memory. *J Neurosci* 17:409–419
- Shadmehr R, Mussa-Ivaldi FA (1994) Adaptive representation of dynamics during learning of a motor task. *J Neurosci* 14:3208–3224
- Shen L, Alexander GE (1997a) Neural correlates of a spatial sensory-to-motor transformation in primary motor cortex. *J Neurophysiol* 77:1171–1194
- Shen L, Alexander GE (1997b) Preferential representation of instructed target location versus limb trajectory in dorsal premotor area. *J Neurophysiol* 77:1195–1212
- Snedecor GW, Cochran WG (1980) *Statistical methods*. 7th edn. Iowa State University Press, Ames
- Soechting JF, Flanders M (1991) Deducing central algorithms of arm movement control from kinematics. In: Humphrey DR, Freund HJ (eds) *Motor control: concepts and Issues*. John Wiley and Sons, NY, pp 293–306
- Suzuki M, Yamazaki Y, Mizuno N, Matsunami K (1997) Trajectory formation of the center-of-mass of the arm during reaching movements. *Neuroscience* 76:597–610
- Turner RS, Owens JW, Anderson ME (1995) Directional variation of spatial and temporal characteristics of limb movements made by monkeys in a two-dimensional work space. *J Neurophysiol* 74:684–697
- Uno Y, Kawato M, Suzuki R (1989) Formulation and control of optimal trajectory in human multijoint arm movement. *Biol Cybern* 61:89–101
- Wolpert DM, Ghahramani Z, Jordan MI (1994) Perceptual distortion contributes to the curvature of human arm movements. *Exp Brain Res* 98:153–156
- Wolpert DM, Ghahramani Z, Jordan MI (1995) Are arm trajectories planned in kinematic or dynamic coordinates? An adaptation study. *Exp Brain Res* 103:460–470
- Young RP, Scott SH, Loeb GE (1993) Distal muscles of the cat hindlimb. I. Multi-axis moment arms at the ankle joint. *Exp Brain Res* 96:141–151