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RAPID PUBLICATION

Trajectory Adaptation to a Nonlinear Visuomotor Transformation: Evidence of Motion Planning in Visually Perceived Space

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SUMMARY AND CONCLUSIONS

1. Although reaching movements are characterized by hand paths that tend to follow roughly straight lines in Cartesian space, a fundamental issue is whether this reflects constraints associated with perception or movement production.

2. To address this issue, we examined two-joint planar reaching movements in which we manipulated the mapping between actual and visually perceived motion. In particular, we used a nonlinear transformation such that straight line hand paths in Cartesian space would result in curved paths in perceived space and vice versa.

3. Under these conditions, subjects learned to make straight line paths in perceived space even though the paths of the hand in Cartesian space were markedly curved. In contrast, when the motion was perceived in Cartesian space (i.e., in the absence of a nonlinear distortion), straight line hand paths were observed.

4. These findings suggest that visually guided reaching movements are planned in a perceptual frame of reference. Reaching movements in the horizontal plane are adapted so as to produce straight lines in visually perceived space.

INTRODUCTION

One of the most striking features of point-to-point arm movements is that the motion of the hand tends to follow an approximately straight line in Cartesian space regardless of the locations of the start and end points and movement speed (e.g., Hollerbach and Flash 1982; Kaminski and Gentile 1986; Morasso 1981; Soechting and Lacquaniti 1981). Although there are some exceptions (Atkeson and Hollerbach 1985; Lacquaniti et al. 1986), roughly straight line hand paths characterize a large class of movements and are even observed, after adaptation, when moving against unusual loads (Shadmehr and Mussa-Ivaldi 1994). These findings have led to the suggestion that arm movements are planned in terms of motion of the hand in Cartesian space. Moreover, recent neurophysiological data are consistent with the view that the CNS plans motions in terms of the direction of the hand (for reviews see Georgopoulos 1991; Soechting and Flanders 1992).

Although the CNS appears to prefer moving the hand in straight lines, a fundamental issue is whether the constraints underlying the generation of these movements are perceptual or motoric in nature. In other words, does the CNS produce straight lines because they are perceived to be straight or because of constraints acting on movement production. Several theories of motion planning propose that movements are organized to minimize cost functions associated with movement kinematics (Flash and Hogan 1985) or dynamics (Uno et al. 1989) and thus emphasize production. However, recent data from Wolpert and colleagues suggest that motion planning may be influenced by perceptual factors. Wolpert et al. (1995) have recently shown that when the curvature of the perceived hand path is gradually increased (over many trials) via altered visual feedback, subjects adapt their actual movements in order to preserve straight line paths in visually perceived space. (Interestingly, subjects were unaware of the manipulation.) Moreover, Wolpert et al. (1994) have suggested that the hand paths observed in transverse movements in the horizontal plane may be slightly curved because they are visually perceived as straight lines. Although these results suggest that planning is influenced by perception, conflicting results have recently been reported by Kawato and colleagues. In particular, Imamizu et al. (1994) have reported that hand paths in actual space are unaffected by a nonlinear distortion of visually perceived space, and Osu et al. (1994) have shown that transverse movements are slightly curved even under conditions in which they are perceived to be curved. Thus the issue of whether motion planning is shaped by perceptual or production constraints is very much unresolved.

In this study we tested the hypothesis that arm movements are planned in a perceptual frame of reference by having subjects move in a visually perceived space that is highly nonlinearly related to Cartesian space (hand space). In particular, we examined visually guided movements in which the positions of the limb and targets were represented in a joint space defined by the angles at the shoulder and elbow (see Fig. 1*A*). For comparison, we also examined visually guided movements in which the positions of the limb and targets were represented in Cartesian hand space. Because joint space is nonlinearly related to hand space, straight line motion paths in joint space will, in general, be associated with curved paths in hand space and vice versa (see Fig. 1*B*). If motion planning takes place in a perceptual frame of reference, we would expect to observe straight paths in joint space (and highly curved hand paths) when moving to targets visually perceived in joint space. On the other hand, if motion planning is carried out in actual space, we would expect to observe straight hand paths (and highly curved paths in joint space) regardless of the space in which the targets are visually perceived. It should be stressed that, although joint space was used in the present study, in principle other spaces (e.g., polar coordinates) that are nonlinearly related to hand space could have been used to test the current hypothesis.

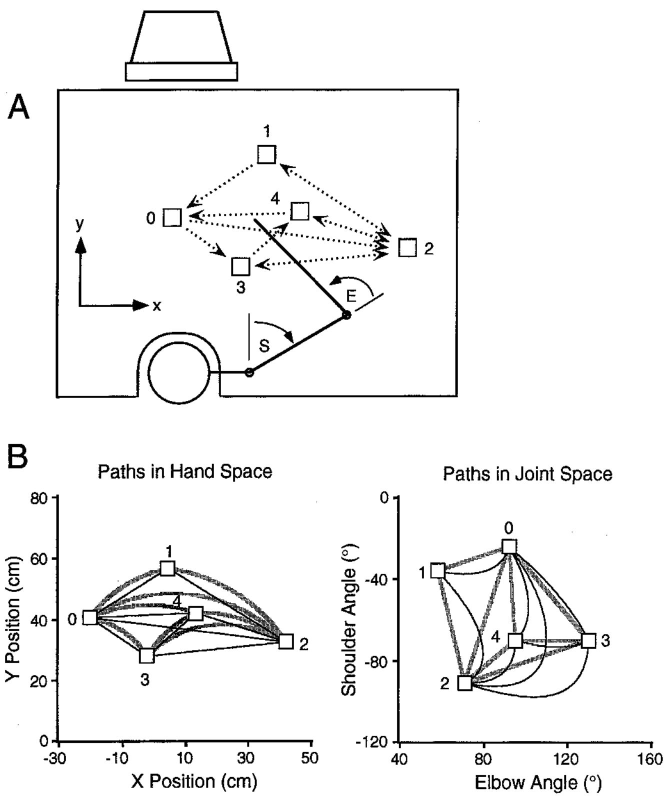

FIG. 1. *A*: top view schematic of the experimental setup showing the locations of the 5 targets. The subject viewed a computer monitor that displayed targets and a cursor representing the position of the moving limb in either hand (*x*, *y*) space or joint (*E*, *S*) space. Dashed arrows illustrate the 11 movements (target pairs) tested. *B*: locations of the targets in hand and joint space, as they appeared on the monitor. Thin traces represent paths in hand and joint space given straight line paths in hand space; thick traces represent hand and joint space paths given straight lines in joint space. The shoulder represents the origin in hand space; the origin in joint space corresponds to the point at which the arm is fully extended in front of the subject.

METHODS

Six healthy female subjects between 18 and 44 yr of age participated in this study after giving informed consent. The subject sat at a table with the upper and lower arms supported by two lightweight "air sleds" that glided over the surface on a cushion of air. The wrist was immobilized with a splint. The *x,y*-position of the hand was recorded with an electromagnetic transmitter (Ascension Technology), and the angles at the shoulder and elbow were computed with the use of inverse kinematics.

The subject viewed a computer monitor that displayed a start and an end target and a cursor representing the position of the moving arm in real time (1/60-s lag). Vision of the actual arm was blocked. The positions of the limb and targets were visually presented in either joint space or hand space. In joint space, the positions of the limb and targets were defined by the angles at the shoulder (ordinate) and elbow (abscissa). In hand space, the targets and the position of the arm were represented in terms of the *x,y*-coordinates of the hand.

Each subject performed 180 trials in visually perceived hand space followed by 660 trials in visually perceived joint space. The start and end targets were displayed at the beginning of each trial and were visible throughout. The end target from one trial served as the start target for the next trial. The subject was instructed to make a single, quick movement to the end target as soon as it appeared, but no instructions about the form of the trajectory were given. Before the first trial in each space, the subject was given several minutes to explore the space while receiving visual feedback of the position of the limb. They were told that the cursor would move in relation to the motion of the hand or joints. (In pilot work we obtained similar results when subjects were given no information about the task. However, we felt that learning might be facilitated if some information was provided.)

RESULTS

The main results of this study are illustrated in Fig. 2. The *top two panels* show paths in hand and joint space for movements visually perceived in hand space. Each path represents a single movement, and paths between different targets pairs are color coded. The figure shows data from one subject (*S5*); however, similar results were obtained in all six subjects. As expected, when moving to targets perceived in hand space, the paths of the hand follow roughly straight lines and the corresponding paths in joint space tend to be highly curved. [Note that a number of studies (e.g., Ghez et al. 1993) have shown that when subjects view the *x,y*-position of the hand and targets on a vertical screen in front of them, they generate trajectories that are similar to those observed when the hand and targets are viewed directly.] Because of the arm's geometry, some movements (e.g., between *targets 0* and *3*) can have paths that are roughly straight in both hand and joint space.

The *bottom panels* of Fig. 2 show paths in hand and joint space for movements to the same targets but visually perceived in joint space. These paths are from the last 165 movement trials; i.e., after some 500 trials during which the subject adapted to joint space. (Initially, movements in joint space were slow and included numerous corrective movements before the end target was attained. However, in all subjects, single, smooth movements began to emerge after ~200 trials and, after ~400 trials, subjects consistently produced smooth, quick movements.) As can be seen in the figure, when moving in visually perceived joint space, the paths in joint space follow approximately straight lines, whereas the paths in hand space tend to be markedly curved. Thus, whereas movements in visually perceived hand space are characterized by straight hand paths, movements in visually perceived joint space feature straight joint paths. In other words, arm reaching movements in the horizontal plane appear to be planned so as to generate straight line paths in visually perceived space.

Comparison of the joint (or hand) paths observed when moving in visually perceived hand space and joint space illustrates that the frame of reference in which the positions of the targets and moving limb are perceived can have a powerful effect on the organization of movement. For example, consider the paths in joint space for movements from *target 0* to *target 2* (yellow curves). When moving in visually perceived hand space, the joint paths are highly curved, and there is a reversal in the direction of elbow motion (from extension to flexion). By comparison, when moving in visually perceived joint space, nearly straight line joint paths are observed, and both joint angles change monotonically. A similar pattern of results is observed for movements between other target pairs.

To quantify path curvature, we computed a linearity ratio a/b, where b is the straight line distance from the start

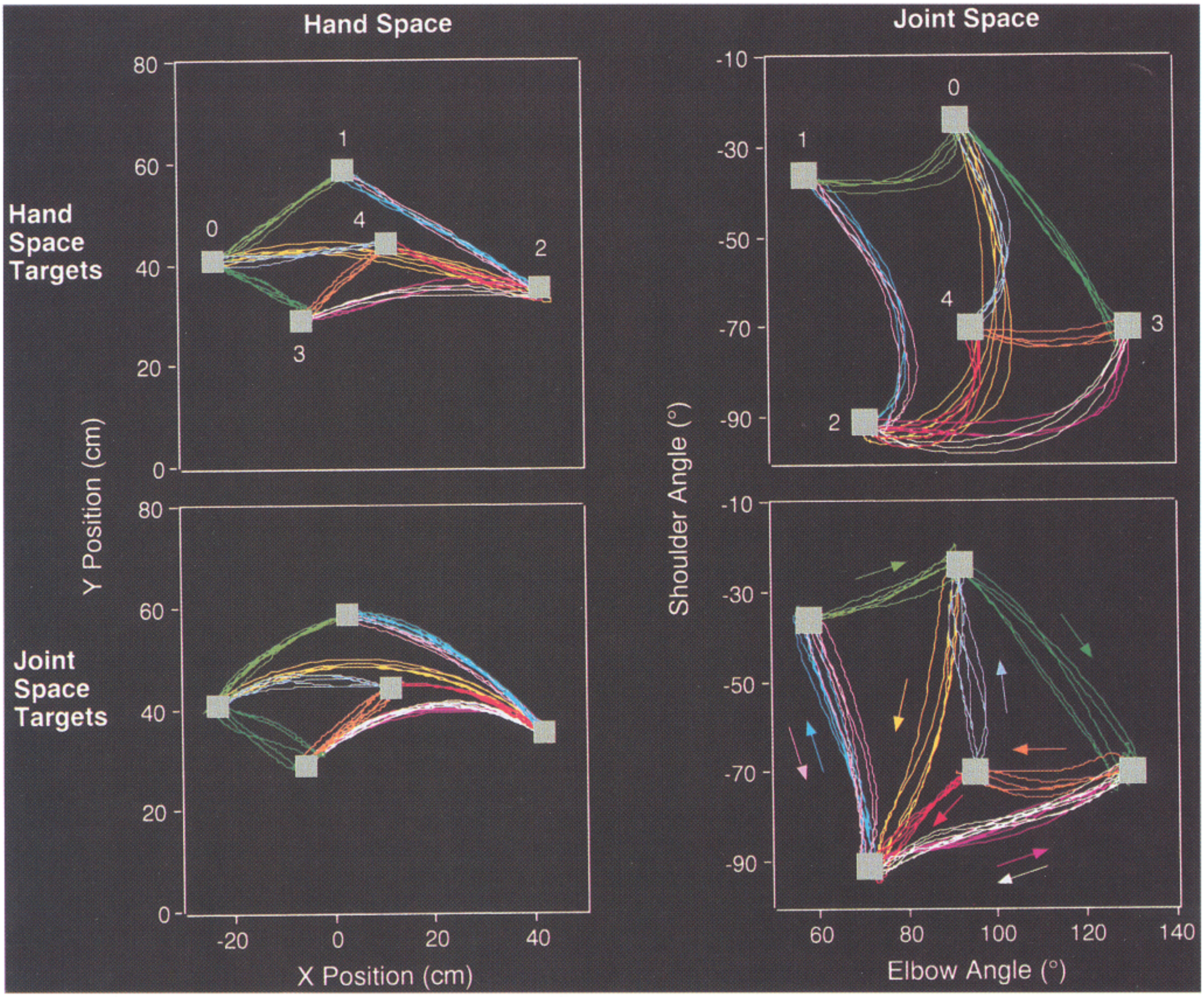

FIG. 2. Motion paths represented in hand (*left*) and joint (*right*) space for movements between targets perceived in either hand space (*top*) or joint space (*bottom*). In both cases, movements are organized so as to produce straight line motions paths in perceived space. Large targets were used to reduce error corrections. The targets in hand space (4.5 cm^2) and joint space ($6^{\circ 2}$) were equated in terms of their size on the monitor.

position to the end position and *a* is the maximum normal distance from the actual path to this straight line (Atkeson and Hollerbach 1985). (This measure increases with curvature; a straight line path would have a value of zero.) This ratio was computed for both the hand space paths (hand linearity ratio) and joint space paths (joint linearity ratio). Average hand and joint linearity ratios, collapsed across target pairs and trials, are presented for each subject in Fig. 3. For all six subjects, the hand linearity ratio was greater when moving in visually perceived joint space than when moving in visually perceived hand space, whereas the joint linearity ratio was greater when moving in visually perceived hand space than when moving in visually perceived joint space. To test the reliability of these differences, we calculated mean ratios for each target pair (based on the last 10 trials) for each subject and target space yielding 132 observations. A repeated measures analysis of variance (ANOVA) revealed that the hand linearity ratio was significantly smaller when moving in visually perceived hand space than when moving in visually perceived joint space [$F(1,5) = 101.6$; $P < 0.001$] and that the joint linearity ratio was significantly smaller when moving in visually perceived joint space than when moving in visually perceived hand space [$F(1,5) = 78.8$; $P < 0.001$].

Average movement times for motions between hand and joint space targets are also shown in Fig. 3 for each subject. Movements to targets visually perceived in joint space were only a little slower (<200 ms on average) than movements to targets visually perceived in hand space. It should be stressed that the paths in visually perceived joint space were straight right from the start of the movement (as illustrated in the *bottom right panel* of Fig. 2), before there was time for trajectory modifications based on visual feedback. This indicates that the straight lines paths observed in visually perceived joint space were planned in advance. Although not the focus of the present paper, it is worth noting that we did not observe negative aftereffects when subjects returned (at the end of the experimental

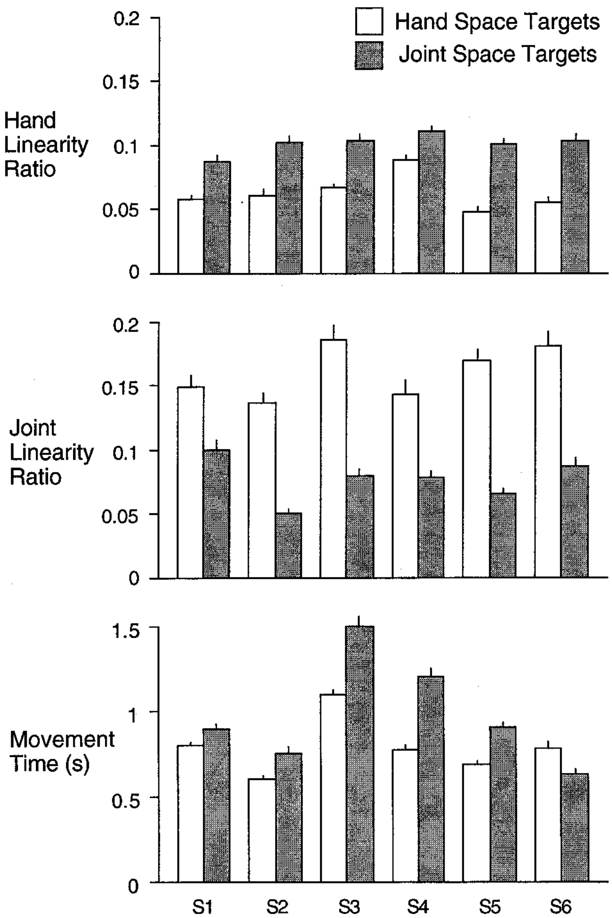

FIG. 3. Means and standard errors of the hand and joint linearity ratios and movement time, averaged across target pairs and trials, for movements to hand space targets (□) and joint space targets (▩) for each of 6 subjects.

session) to visually perceived hand space after moving in visually perceived joint space. Within one or two trials in perceived hand space, all subjects generated roughly straight line hand paths.

DISCUSSION

The present results provide strong evidence in support of the hypothesis that the CNS plans visually guided reaching movements in a perceptual (i.e., visual) frame of reference (Wolpert et al. 1994, 1995). Initial support for this hypothesis came from the results of Wolpert et al. (1995) described above. In their study, subjects produced motions between two targets and were unaware of the visuomotor transformation. Moreover, the transformation only affected the curvature of the motion, not the location of the endpoints. In contrast, we examined movements between targets located throughout the work space, and subjects were clearly aware of the visuomotor transformation that affected both the curvature of the path and the endpoint locations. Thus the present results considerably strengthen the argument that planning occurs in visually perceived space.

The results reported here suggest that constraints on motion planning are primarily perceptual in nature and do not support theories of trajectory formation based on the minimization of cost functions associated with movement production. It may be noted that, whereas the minimum-jerk hypothesis (Flash and Hogan 1985) could be adapted to perceived motion, the same cannot be said for the minimum torque-change hypothesis (Uno et al. 1989).

Our findings contrast with the results of Imamizu et al. (1994) showing that the path of the hand is largely unaffected by nonlinear distortions of visually perceived space. However, in the Imamizu et al. study, only a couple of targets pairs were used, and it is possible that subjects simply remembered the position of the hand for each perceived target and then moved between remembered positions (as they would in the absence of vision). In the present study we used 5 targets and 11 target pairs precisely to prevent subjects from adopting this strategy. However, it is also possible that the effect of perceived space on movement planning is sensitive to the nature of the visuomotor transformation employed.

A number of researchers have suggested that arm reaching movements are organized at the joint level (e.g., Flanagan and Ostry 1990; Hollerbach and Atkeson 1985; Kaminski and Gentile 1986). Thus it is possible that subjects learned to generate straight lines in visually perceived joint space because this space represents a natural frame of reference. We feel that this is unlikely and that similar results could have been obtained with the use of other nonlinear visuomotor transformations. However, the sensitivity of motion planning to parameters of the visuomotor transformation awaits further study.

The process of reaching to a visual target involves a sensorimotor transformation of the frame of reference in which the target is perceived into an intrinsic frame of reference in which movement parameters are planned (Flanders et al. 1992). Our results indicate that this transformation can be adapted so as to produce straight lines paths in visually perceived space. In future work, we plan to examine the kinds of visual information underlying trajectory generation and learning by removing visual feedback of the limb (i.e., cursor) and/or targets during the movement.

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