# Are arm trajectories planned in kinematic or dynamic coordinates? An adaptation study

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## Abstract

There are several invariant features of point-to-point human arm movements: trajectories tend to be straight, smooth and have bell-shaped velocity profiles. One approach to accounting for these data is via optimization theory; a movement is specified implicitly as the optimum of a cost function, e.g. integrated jerk or torque change. Optimization models of trajectory planning, as well as models not phrased in the optimization framework, generally fall into two main groups—those specified in kinematic coordinates and those specified in dynamic coordinates. To distinguish between these two possibilities we have studied the effects of artificial visual feedback on planar two-joint arm movements. During self-paced point-to-point arm movements the visual feedback of hand position was altered so as to increase the perceived curvature of the movement. The perturbation was zero at both ends of the movement and reached a maximum at the midpoint of the movement. Cost functions specified by hand coordinate kinematics predict adaptation to increased curvature so as to reduce the visual curvature, while dynamically specified cost functions predict no adaptation in the underlying trajectory planner, provided the final goal of the movement can still be achieved. We also studied the effects of reducing the perceived curvature in transverse movements, which are normally slightly curved. Adaptation should be seen in this condition only if the desired trajectory is both specified in kinematic coordinates and actually curved.

Increasing the perceived curvature of normally straight sagittal movements led to significant ($p < 0.001$) corrective adaptation in the curvature of the actual hand movement; the hand movement became curved, thereby reducing the visually perceived curvature. Increasing the curvature of the normally curved transverse movements produced a significant ($p < 0.01$) corrective adaptation; the hand movement became straighter, thereby again reducing the visually perceived curvature. When the curvature of naturally curved transverse movements was reduced there was no significant adaptation ($p > 0.05$). The results of the curvature increasing study suggest that trajectories are planned in visually-based kinematic coordinates. The results of the curvature reducing study suggest that the desired trajectory is straight in visual space. These results are incompatible with purely dynamic-based models such as the minimum torque change model. We suggest that spatial perception—as mediated by vision—plays a fundamental role in trajectory planning.

## Introduction

Invariant features at the behavioral level provide hints as to the internal representation of movements in the central nervous system (Bernstein 1967). In this paper we focus on the invariant features of the hand trajectories seen in human point-to-point arm movements[1]. When a subject is asked to reach towards a stationary target there are an infinite number of possible trajectories that can be chosen. However, many studies have shown invariances in human arm movements; subjects tend to move their hand along a straight path with a single-peaked, bell-shaped velocity profile (Bernstein 1967; Kelso et al. 1979; Morasso 1981; Abend et al. 1982; Atkeson and Hollerbach 1985; Flash and Hogan 1985; Uno et al. 1989). These features are independent of the hand's initial and final position within the workspace. In contrast, the joint angular position and velocity profiles show considerable variation depending on the hand's initial and final position within the workspace (Morasso 1981).

Humans, therefore, do not use the full repertoire of possible trajectories but produce movements with certain invariant properties, suggesting a tendency to select one trajectory from the many available. One way to select a unique trajectory is to place additional constraints on the task thereby reducing its effective degrees of freedom. Concepts from the field of optimal control have been dominant in attempts to use constraints to explain the invariant features of arm movements. In optimal control a cost function is chosen in order to evaluate quantitatively the performance of the system under control (Bryson and Ho 1975). The *cost function* is usually defined as the integral of an instantaneous cost over a certain time interval, and the aim is to minimize the value of this cost function. In engineering the goal is to design an appropriate cost function for the given task. In trying to use optimal control theory to explain the invariances seen in human trajectory formation, the task is that of reverse-engineering—trying to find the cost function that produces the observed trajectories. The optimal control approach also provides a parsimonious account of trajectory formation; given the arm's initial and final position, velocity, and acceleration (the initial and final state of the arm) and given the movement duration, the trajectory is determined uniquely.

Early studies of trajectory formation considered cost functions such as minimum energy, minimum torque and minimum acceleration (Nelson 1983). Hasan (1986) has suggested that the cost function is the integrated "effort" of movement, where effort is defined as the product of muscle stiffness and the square of the derivative of the equilibrium point position. Thus there is a trade-off between low stiffness with large equilibrium point discursion and high stiffness with small equilibrium point discursion. Although simulations show good agreement between predicted and actual one-joint movements it is not clear whether this model would be able to reproduce multi-joint movements. At present only two cost functions are able to account for the majority of the multi-joint data—cost functions based on Cartesian jerk and on the first derivative of torque. In this paper we abstract away from these particular cost functions and attempt to assess whether trajectories are planned with respect to kinematic or dynamic coordinates. By *kinematics* we mean the geometrical and time-based properties of motion; the variables of interest are the positions (e.g. joint angles

[1]The *trajectory* refers to the path and speed of the movement where the *path* is the sequence of positions through which the hand passes.

or hand Cartesian coordinates) and their corresponding velocities, accelerations and higher derivatives. *Dynamics* refers to the forces required to produce motion and is therefore intimately linked to the properties of the arm such as its mass, inertia and stiffness; the variables of interest include joint torques, forces acting on the hand, and muscle commands. Although trajectory planning may be specified in terms of purely dynamic coordinates the boundary conditions (i.e. start and end points[2]) must be specified in kinematic coordinates appropriate to the task. Before outlining the experiments we have used to distinguish between kinematic and dynamic-based trajectory planning, we will first describe in some detail the main proponent cost function from each category: kinematic-based minimum jerk and dynamic-based minimum torque change.

The minimum jerk model, originally proposed by Hogan (1984) for one-joint and Flash and Hogan (1985) for multi-joint movements, states that the cost to be minimized is the first derivative of Cartesian hand acceleration or 'jerk' and is therefore based on kinematics. Thus for planar movements the cost function is

$$C_J = \frac{1}{2}\int_0^T \left( \left(\frac{d^3x}{dt^3}\right)^2 + \left(\frac{d^3y}{dt^3}\right)^2 \right) dt.$$

where $T$ is the duration of the movement and $(x,y)$ is the hand's position at time $t$. Minimization of this cost function yields a reference trajectory[3] with positions $x$ and $y$ which are fifth-order polynomials in time.

The trajectories predicted by the minimum jerk model are straight lines with bell-shaped velocity profiles. The minimum jerk model takes no account of the arm's dynamics, thus the velocity profile of the predicted trajectories are invariant under rotation and translation of start and end points of the movement. Moreover the velocity profiles scale linearly with distance and duration. Once the trajectory is determined in Cartesian space other processes must be invoked to translate the desired hand trajectory into joint coordinates and finally into motor torques.

An alternative approach to trajectory formation, the minimum torque change model, has been proposed by Uno, Kawato & Suzuki (1989). The minimum torque change model differs from the minimum jerk model in that the reference trajectories are dependent on the dynamics of the arm. For a planar two-joint arm the cost function proposed by Uno et al. (1989) is of the following form:

$$C_T = \frac{1}{2}\int_0^T \left( \left(\frac{d\tau_1}{dt}\right)^2 + \left(\frac{d\tau_2}{dt}\right)^2 \right) dt$$

where $T$ is the duration of the movement and $\tau_1$ and $\tau_2$ are the shoulder and elbow torques respectively at time $t$. Unlike minimum jerk this cost function is not amenable to analytic solution but can be solved by iterative algorithms. As Uno et al. (1989) point out the cost functions $C_J$ and $C_T$ are closely related because acceleration is proportional to torque at zero speed.

[2]We will use *end point* to refer to the final position of a movement rather than the endpoint of the human arm i.e. the hand.

[3]The *reference trajectory* is the optimal trajectory given the cost function. The actual achieved trajectory need not be the reference trajectory due to factors such as incomplete control and joint limitations.

Minimum torque change, like minimum jerk, predicts bell-shaped velocity profiles, but also predicts that the form of the trajectories should vary across the arm's workspace. Uno et al. (1989) showed that there is a reasonably good correspondence between the predictions of the minimum torque change model and actual hand trajectories. They also showed that the minimum torque change model predicts the curved trajectories seen when subjects are instructed to make movements while a spring is attached to their hand, a finding which they argued is inconsistent with the minimum jerk model. However, two recent studies on the effects of dynamic environments on movements have shown that, over the course of several practice trials, subjects adapt their movements resulting in a straightening of the hand paths (Gurevich 1993; Shadmehr and Mussa-Ivaldi 1994).

The minimum torque change model, unlike the minimum jerk model, does not require a separate controller to transform desired positions into torques as the trajectory planning and torque production proceed in one step. The minimum jerk and minimum torque change models, therefore, propose cost functions which are specified in different coordinate systems, kinematic and dynamic respectively. The two models also provide alternative explanations for the natural curvature seen in human arm movements. The minimum jerk model suggests that the reference trajectory is a straight line but that the control process leads to the production of curved paths, whereas the minimum torque change model suggests that the curvature is a direct result of the minimization of the integrated torque change.

We have sought to determine, using an adaptation paradigm, whether trajectories are planned in kinematic or dynamic coordinates. Although we have illustrated the kinematic vs. dynamic hypotheses with reference to the minimum jerk and minimum torque change models our experiments were designed to test in which coordinate system trajectories are planned, rather than which particular cost-function within a coordinate system best models the data.

Since Helmholtz's (1867/1925) pioneering work on prismatic adaptation many studies have investigated adaptation to a variety of forms of altered visual feedback (for a review see Welch 1986). In this study we have used altered visual feedback to change the visually perceived kinematics of the movement in order to study the trajectory planner. By judicious choice of the perturbation we can test between the hypotheses that trajectories are planned in kinematic or dynamic coordinates. This is shown in the schematic in Figure 1, in which we illustrate how a visual perturbation leads to two different predictions depending on the two hypotheses. The top of the figure shows the kinematic profile (KP) for a natural movement between two targets (dotted line), along with the corresponding dynamic profile (DP). The two profiles embody the kinematic and dynamic aspects of the movement. We chose to alter the visual feedback of the hand in such a way that the perturbation was zero at both ends of the movement and reached a maximum at the midpoint of the movement—such a kinematic perturbation is shown in the upper KP (solid line). It is interesting to note that this perturbation is, in some sense, a kinematic equivalent of the dynamic perturbation used by Lackner & DiZio (1993). In their experiment subjects made arm movements while sitting at the center of a rotating room—this only affects the Coriolis force acting on the arm. As the Coriolis force is velocity dependent the perturbation was only active during the movement but not, as in our experiment, while the subject was at rest. In our experiment we used a perturbation which ensured that the target could be reached by moving as if there were no perturbation, thus an identical torque profile (upper DP) still achieves the target.

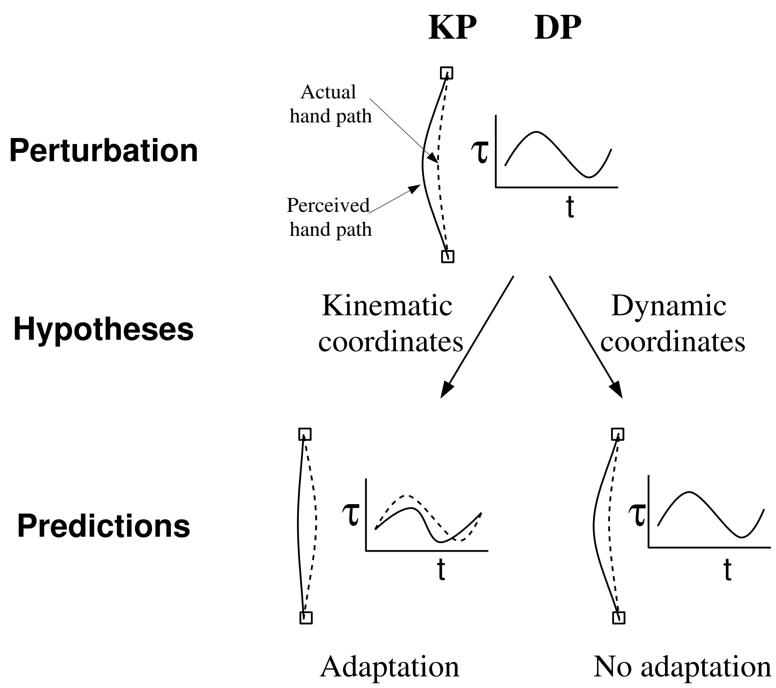


Figure 1. A schematic showing the different predictions made by the kinematic and dynamic hypotheses after a visual perturbation. In the upper part, the natural hand path is shown between two targets (dotted line)—this represents the kinematic profile (KP) of the movement. The corresponding torque plot ($\tau$) is also shown which represents the dynamic profile (DP) of the movement. The solid line in the KP shows the perturbed visual feedback of hand position (i.e. the visually perceived hand path); note that there is no perturbation at the beginning or end of the movement. The lower figures show the predicted movements under the kinematic and dynamic hypotheses. As before, the dotted lines represent the actual hand paths and the solid lines the perceived paths. The left hand schematic shows adaptation under the kinematic hypothesis—the actual hand path changes (with an appropriate change in the dynamic profile) so that the perceived path matches the previous natural path. The right side shows the predictions under the dynamic hypothesis—no adaptation is seen as the dynamic profile is optimal and the target is achieved.

Kinematic and dynamic-based hypotheses make quite different predictions with regard to the effects on trajectory planning of such an altered visual feedback—while the former tries to preserve kinematic invariances (KP), the latter maintains the dynamics invariant (DP). If the trajectory planner is based on kinematic coordinates and the perturbation takes the perceived trajectory away from the reference trajectory, the actual hand trajectory should adapt to bring the perceived trajectory closer to the reference trajectory. In other words, if the trajectory is planned in kinematic coordinates we might expect subjects to adapt their planner so as to restore the perceived kinematics of the movement (Figure 1 lower left). In this case the torque profile must change to as to produce this altered hand path. However, dynamic-based hypotheses permit visually-curved movements, provided that the target is reached and the cost function (captured by the form of the DP) is minimized. Therefore, for dynamic-based models we would expect the hand to continue to take its normal trajectory as the task can still be achieved using the optimal dynamic profile. Adaptation to such a visual perturbation would, therefore, imply that trajectories are not planned solely in dynamic coordinates and would suggest that the trajectory had been perturbed away from the reference trajectory.

We have studied both sagittal and transverse movements[4] in a condition in which the visually perceived curvature of the subject's trajectories was increased (groups 1 & 2). For this perturbation, kinematic-based hypotheses predict that the subject may adapt so as to produce trajectories having the desired kinematics while dynamic-based hypotheses predict no adaptation. After a period of exposure to perturbed feedback, arm movements were recorded in the absence of visual feedback to assess any adaptive effects on the trajectory planner. As transverse movements show a natural curvature we also sought to test (group 3) the hypothesis that the reference trajectory is planned in kinematic space and curved—a possibility distinct from both the minimum jerk and minimum torque change models. We therefore reduced the perceived curvature of these naturally curved transverse movements. Adaptation should only be expected if the reference trajectory is indeed curved and the cost function specified in kinematic space. We have also investigated the loss of adaptation on the removal of the visual perturbation (group 4) as well as longer term effects of the perturbation on fast, paced movements (group 5).

Many previous studies have investigated the effects of altered visual feedback on trajectories. These studies have used either optical devices such as prisms (e.g. Jakobson & Goodale 1989) or visual feedback on a computer monitor separate from actual hand position (e.g. Cunningham 1989). We could not easily use an optical system, such as a prism, to perturb the visual feedback of the actual arm as it was necessary for the perturbation to be zero at the start and end of the movement; no simple optical device has this property. On the other hand, the use of a computer monitor requires the subjects to make an additional coordinate transformation to link their hand position to the cursor spot. Using a Video Graphics Array (VGA) projector and mirror setup we obviated the need for any coordinate transformation between cursor and hand position; the virtual image of the cursor was at the same position, in three-dimensional space, as the hand. Using this setup we were also able to introduce state dependent perturbations. As Held et al. (1966) have shown, also using a virtual image setup, the use of a luminous spot to represent hand position is sufficient to elicit prismatic adaptation provided that the cursor spot and hand movements are highly correlated.

## Methods

Twenty-four naive normal right handed students, who gave their informed consent prior to their inclusion, participated in this study. The subjects were randomly allocated to one of five groups (six each in groups 1, 2 & 3, two in group 4 and four in group 5). We will first describe the methodology for the first three groups which formed the main experiment and then highlight the differences in the paradigms for group 4, which was designed to

[4]We use *sagittal* to refer to movements made towards or away from the body—specifically along the line of intersection of the horizontal and sagittal planes. We use *transverse* to refer to movement made across the body. See Figure 3a.

assess the decay of adaptation, and group 5, which was designed to assess adaptation in fast movements over an increased number of trials.

The subjects were familiarized with the equipment and then performed two sessions of arm movements—a control and a visual perturbation session. The data was analyzed to determine whether the subjects had adapted their trajectory planner over the course of the perturbation session when compared to the control session.

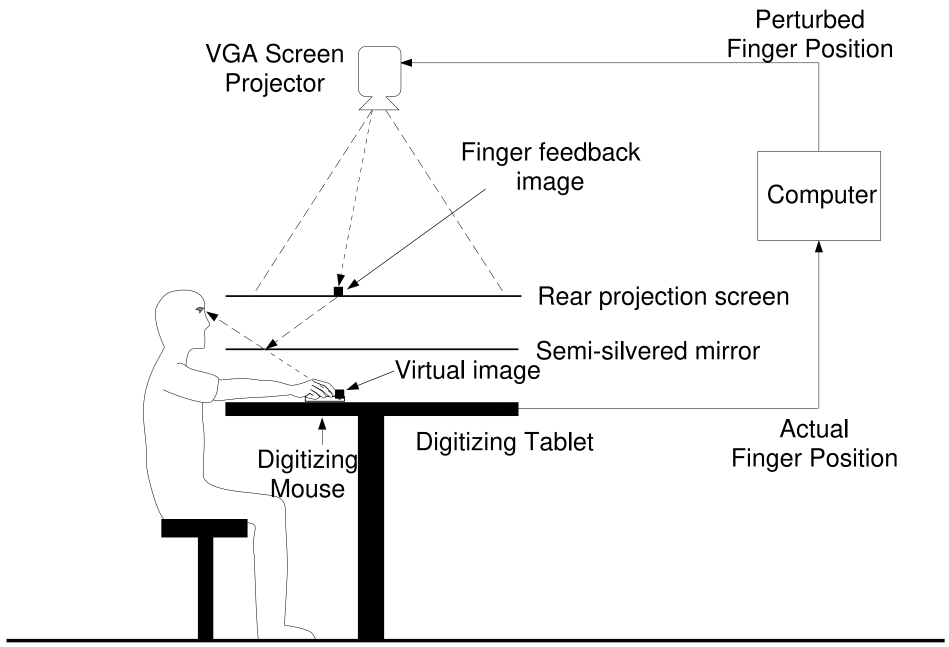


Figure 2. Experimental apparatus for measuring arm trajectories in the horizontal plane under artificial visual feedback. The position of the hand was captured on-line by a computer which calculated the perturbed hand position. This feedback of hand position was projected onto a screen as a white filled square. Looking down at the mirror, the subject saw the virtual image of the cursor spot in the plane of his hand.

## Arm movement recording

Subjects sat at a large horizontal digitizing tablet (Figure 2) with their head supported by a chin and forehead rest. The subjects held a digitizing mouse with their finger tip mounted on its cross hairs. The mouse could be moved along the surface of the digitizing tablet (Super L II series, GTCO, MD). The subjects had no direct view of their arm which was covered by a screen. The digitizing tablet's coordinates were sampled at 185 Hz by a PC as $(x, y)$ coordinate pairs; the accuracy of the board was 0.25 mm.

## Target and hand position feedback

The targets and feedback of hand position (as defined by the index finger tip location which was fixed relative to the palm) were presented as virtual images in the plane of the digitizing tablet (and therefore in the plane of the hand). This was achieved by projecting a VGA screen (640 x 480 pixels) with an LCD projector (Sayett Media Show) onto a horizontal rear projection screen suspended 26 cm above the tablet (Figure 2). One pixel measured 1.2 x 1.2 mm on the screen. A horizontal front-reflecting semi-silvered mirror was placed face up 13 cm above the tablet. The subjects viewed the reflected image of the rear projection screen by looking down at the mirror. By matching the screen-mirror distance to the mirror-tablet distance all projected images appeared to be in the plane of the hand (when viewed in the mirror) independent of head position. To reduce corrective movements we represented the targets as large (5.5 cm) hollow squares and the finger position was displayed as a 7 mm filled white square (cursor spot). The position of the finger was used on-line to update the position of this cursor spot at 60 Hz.

## Calibration

Prior to each experiment the position of the digitizing mouse cross-hairs relative to projected pixel position was calibrated over a grid of 16 points on the tablet. By illuminating the semi-silvered mirror from below the virtual image and the cross-hairs of the digitizing mouse could be lined up by eye. A quadratic regression fit of $x$ and $y$ pixel position to $x$ and $y$ hand position was performed and this was then used on-line to position the targets and cursor spot. The correlation of the fit was always greater than 0.99. Cross-validation sets gave an average calibration error of 1.5 mm.

## Experimental Design

The subjects were asked to reach "naturally" between the targets—no instructions were given as to the movement path. In all the experiments there were two stationary targets which were alternately illuminated. The subject's task was to move his arm so as to place the hand cursor spot within the illuminated target. When the cursor spot was within the target and stationary the target was extinguished and an audible beep signaled that the subject should move to the other target which became illuminated. Apart from placing the cursor spot within the target there were no accuracy or time constraints.

Each session consisted of 100 movements with a 30 second rest period after 50 movements. The first 80 movements were performed with the cursor spot continuously displayed. The last 20 movements of each session were performed with the cursor spot extinguished during the movement. During these movements without visual feedback the cursor spot was only illuminated once the subject's hand was stationary to allow the subject to come onto target if necessary.

The first group of subjects were required to make sagittal movements towards and away from their body (Figure 3a). The target positions were at (0,20) and (0,50) cm relative to a point midway between the subjects' eyes. The second and third group of subjects were required to make transverse movements between targets positioned at (–10,40) and (30,40) cm.

Each subject performed two consecutive sessions; a control and an altered feedback session. The order of the control and altered feedback sessions were balanced within each group. In the control session the cursor spot accurately indicated the position of the hand. In the altered feedback session the relationship between hand position and cursor spot

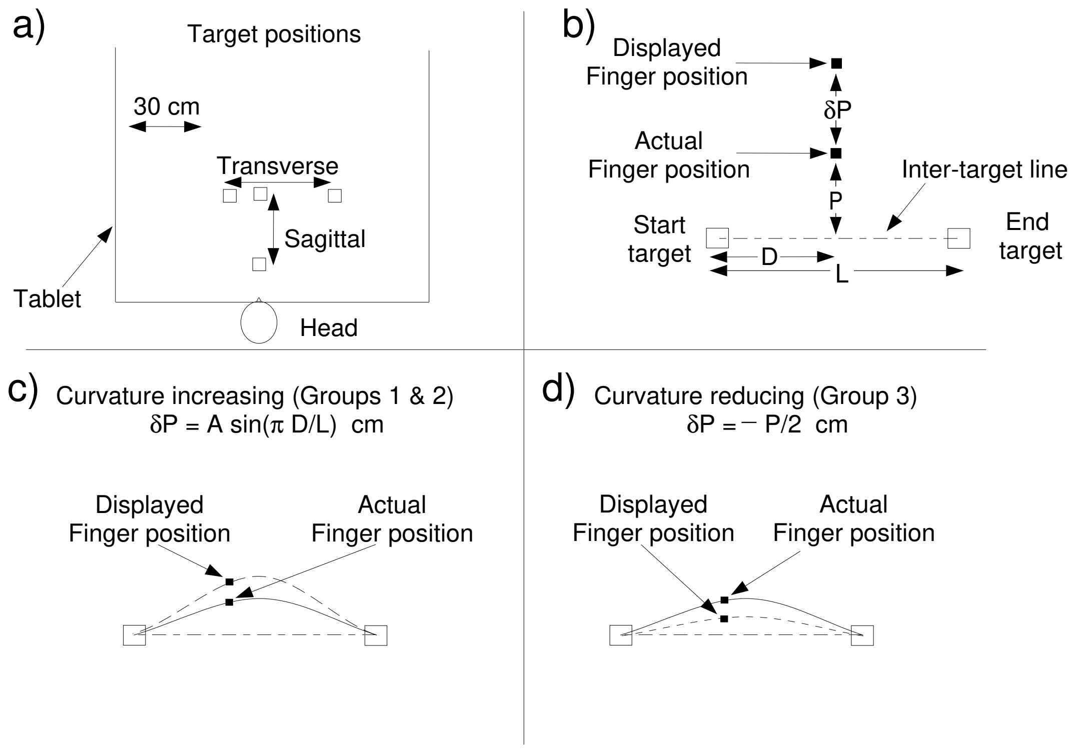


Figure 3. a) The position of the targets relative to the head is shown from a plan view. b) A plan view of the start and end target, hand position and virtual feedback of hand position are shown. The parameters required to calculate $\delta P$ on-line are also shown. c) Perturbation used for groups 1 and 2 in which a half-sinusoid was added to the path. The actual and visually altered hand positions at a moment in time are shown along with the path they follow. Note that the subject only saw the moving cursor spot. d) The perturbation for group 3, which halved the perpendicular distance to straighten the path, is shown in the same format as c). Note that in b), c) and d) the $y$ dimension has been exaggerated for clarity.

position was perturbed. Two separate perturbations were used—one to increase and one to decrease the perceived trajectory curvature. The displacement of the virtual hand feedback to the actual hand position was always made in the direction perpendicular to the inter-target line (Figure 3b). The perpendicular displacement $\delta P$ at any instant could depend on two parameters which were calculated on-line—the distance of the hand *along* the inter-target line ($D$) and the distance of the hand *to* the inter-target line ($P$).

Groups 1 and 2 received altered feedback which increased the perceived curvature of their movements. The perturbation $\delta P$ depended only on the distance along the inter-target line; $\delta P = A\sin(\pi D/L)$ where $L$ denotes the inter-target distance. This had the effect of adding a half-sinusoid to the path (Figure 3c). To prevent conscious detection of the perturbation the amplitude of the sinusoid, $A$, started at zero (no perturbation) and was increased linearly from movement 20 to reach a maximum of 4.0 cm at movement 40, at which point it was held constant for the rest of the session. The perturbation applied was leftwards for the group 1 sagittal movements and away from the body for the group 2 transverse movements.

Group 3 received feedback which decreased the perceived curvature of their movements. The perturbation $\delta P$ introduced on trial 20 depended only on the hand to inter-target line distance; $\delta P = -P/2$. This had the effect of halving the distance of the perceived hand feedback to inter-target line and thereby reduced the perceived curvature (Figure 3d). This perturbation was not attempted on a sagittal movement group as sagittal movements tend to be straight and there is, therefore, little scope to reduce the curvature of these movements.

The effects of removing the perturbation were assessed in the group 4 subjects. These subjects participated in a study similar to the group 1 perturbation session, except that the visual feedback was always present and the perturbation was turned off in one step on trial 100 and the session continued for an additional 100 trials.

Group 5 was used to assess both the effects on adaptation of fast, paced movements and of increased number of movements. These subjects were paced with a tone metronome at 650 ms intervals for 1400 sagittal movements in batches of 60, with a rest period after each batch. A curvature increasing perturbation was introduced on trial 60 and was increased linearly until trial 200 and then held constant at 3.0 cm for the remainder of the experiment. The last ten movements of each batch were made with no visual feedback to assess adaptation.

## Data Analysis

We first describe the analysis of the data from groups 1, 2 & 3 before highlighting the differences for groups 4 & 5. We analyzed the last 20 trials of each session, which were performed without visual feedback. Comparisons were made between the control and the post-perturbation movements. As these movements are made in the absence of visual feedback, any differences between them are due to changes in the trajectory planner resulting from the perturbation. These changes are analogous to the post-exposure aftereffects seen in prism adaptation; in both cases the effect is measured once the perturbation has been removed—in the prism case by removing the prism and in our case by removing the visual feedback.

The paths were first scaled and rotated so as to align the start and end point of the movements. This was necessary to ensure that movement curvature could be assessed independently of inaccuracy resulting from the absence of visual feedback. The trajectories were then spatially resampled and mean paths with standard errors were calculated. This involved linearly interpolating the actual paths to find the perpendicular distances to the inter-target line at 100 evenly spaced points along the inter-target line. The resampled paths were averaged over each group for each session and direction of movement. The mean $\pm 1$ standard error path for the control and post-perturbation sessions were plotted. As our measure of curvature we used the averaged midpoint deviation—the perpendicular distance of the hand to the inter-target line at the midpoint of the movement.

Movement times were also calculated by defining the start and the end of the movement with a 10 cm $s^{-1}$ velocity threshold. The movement times were averaged within each group for the control and post-perturbation sessions.

For both group 4 subjects the movement curvature for each movement was calculated and plotted against movement number. A local linear smoother, loess (Cleveland 1979), was used to fit the mean $\pm 1$ standard error to the data.

The trials made in the absence of visual feedback were analyzed in the group 5 subjects. For each batch the mean curvature with 95% confidence limits, averaged across the four subjects, was calculated and plotted against movement number.

## Results

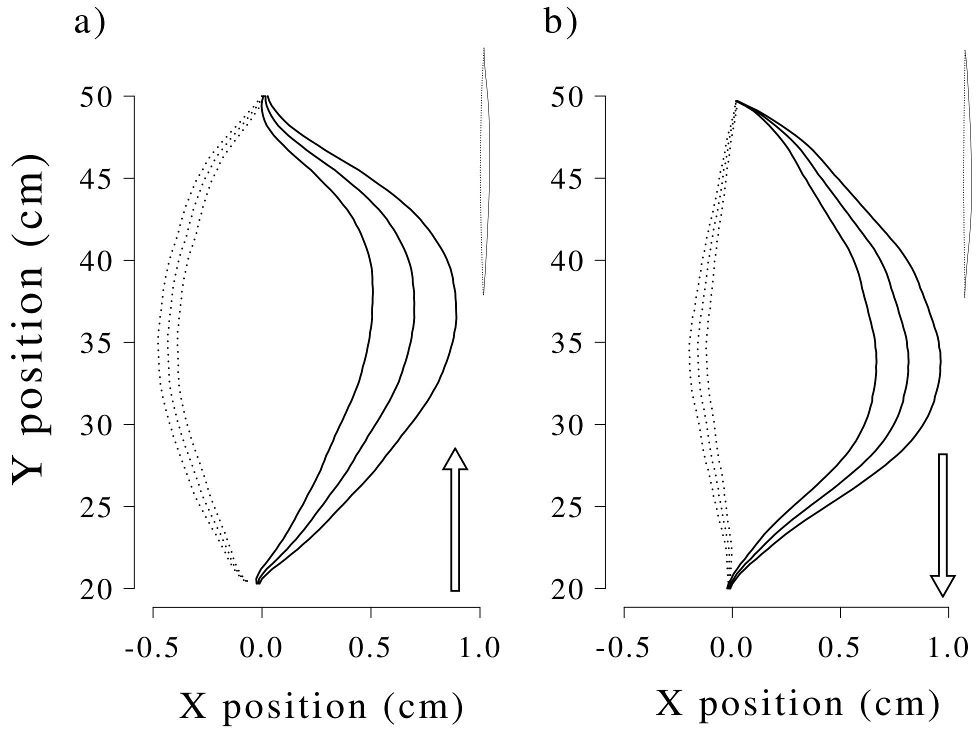


Figure 4. Group 1 control (dotted lines) and post-perturbation (solid lines) mean $\pm 1$ standard error paths for a) outward and b) inward sagittal movements. The perturbation (not shown) was a hemi-sinusoid in the negative $x$ direction. The $x$ axis has been enlarged to show detail. The insets show the mean paths on a veridical scale. The $x$,$y$ coordinates are measured relative to the head position. The arrows show the direction of the movement.

The subjects in group 1 produced control sagittal movements which were approximately straight (Figure 4). Although significantly different from zero ($p < 0.001$) the average midpoint deviations were less than 5 mm to the left for the controls (Table 1). Increasing the perceived curvature with the addition of a half-sinusoid increased the perceived mid-point deviation leftward by 40 mm. The post-perturbation changes in the average mid-point deviations were significant at the $p < 0.001$ level (Table 1). The subjects showed an average adaptation of 11.1 mm for outward and 9.6 mm for inward movement thereby compensating for about 25% of the midpoint perturbation.

The subjects in group 2 produced control transverse movements which were significantly ($p < 0.001$) curved outwards, away from the body (Figure 5). The average control midpoint deviations were 14.0 mm for leftward and 14.8 mm for rightward movements. Increasing the

| Group | ΔCurv. | Sign | Control | Post-pert. | Change | $p$ |
|---|---|---|---|---|---|---|
| 1. Sagittal | increase | −ve | | | | |
| outwards | | | $-4.3 \pm 0.44$ | $6.8 \pm 1.91$ | $11.1 \pm 1.96$ | $< 0.001$ |
| inwards | | | $-1.6 \pm 0.39$ | $8.0 \pm 1.46$ | $9.6 \pm 1.51$ | $< 0.001$ |
| 2. Transverse | increase | +ve | | | | |
| leftwards | | | $14.0 \pm 1.62$ | $6.7 \pm 2.07$ | $-7.3 \pm 2.62$ | $< 0.01$ |
| rightwards | | | $14.8 \pm 1.29$ | $7.6 \pm 1.66$ | $-7.2 \pm 2.10$ | $< 0.001$ |
| 3. Transverse | decrease | | | | | |
| leftwards | | | $23.4 \pm 1.73$ | $24.9 \pm 1.44$ | $1.5 \pm 2.25$ | $> 0.05$ |
| rightwards | | | $27.3 \pm 1.61$ | $25.4 \pm 1.56$ | $-1.9 \pm 2.24$ | $> 0.05$ |

Table 1. Averaged midpoint deviations (mm) and standard errors for each group and direction of movement. The control and post-perturbation deviations are shown along with the change between them and the significance as measured by a $t$-test. The second column shows the change in curvature induced by the altered feedback and the third column shows the direction of the increase in curvature.

perceived curvature with the addition of a half-sinusoid increased the perceived midpoint deviation outwards by 40 mm. The post-perturbation changes in the average midpoint deviation were significant at the $p < 0.01$ level (Table 1). The subjects showed an average adaptation of −7.3 mm for leftward and −7.2 mm for rightward movements, representing about 18% of the midpoint perturbation.

The subjects in group 3, like those in group 2, showed outwardly curved control transverse movements (Figure 6). The average midpoint curvatures were 23.4 mm for leftward and 27.3 mm for rightward movements. These subjects' perceived curvature was halved thereby reducing the perceived average midpoint deviation by 11.5 mm for leftward and by 13.6 mm for rightward movements. The post-perturbation changes in averaged midpoint deviations were not significant at the 5% level.

The group 1 subjects' movement durations increased from $1061 \pm 43$ms (control) to $1186 \pm 33$ms (post-perturbation). This increase in movement duration of $125 \pm 54$ms was significant at the 5% level. The group 2 subjects' movement durations increased from $929 \pm 34$ms to $1114 \pm 39$ms. The increase in movement duration of $185 \pm 52$ was significant at the $p < 0.001$ level. The group 3 subjects' movement durations decreased from $828 \pm 21$ms to $811 \pm 25$ms. The decrease in movement duration of $17 \pm 33$ms was not significant at the 5% level.

The adaptation plots for the group 4 subjects are shown in Figure 7. Both subjects showed adaptation to the perturbation. When the perturbation was removed on trial 100 both subjects demonstrated a gradual decline back to the normal curvature although subject 1 had not fully returned to the pre-perturbation curvature after 100 unperturbed movements.

The average adaptation plots for the group 5 paced subjects is shown in Figure 8. The average adaptation was 0.78 cm (26%) by 1400 movements. All subjects individually showed a significant change between pre-perturbation and the last batch ($p < 0.05$)—two had a general linear increase in curvature whereas the other two showed a more erratic increase.

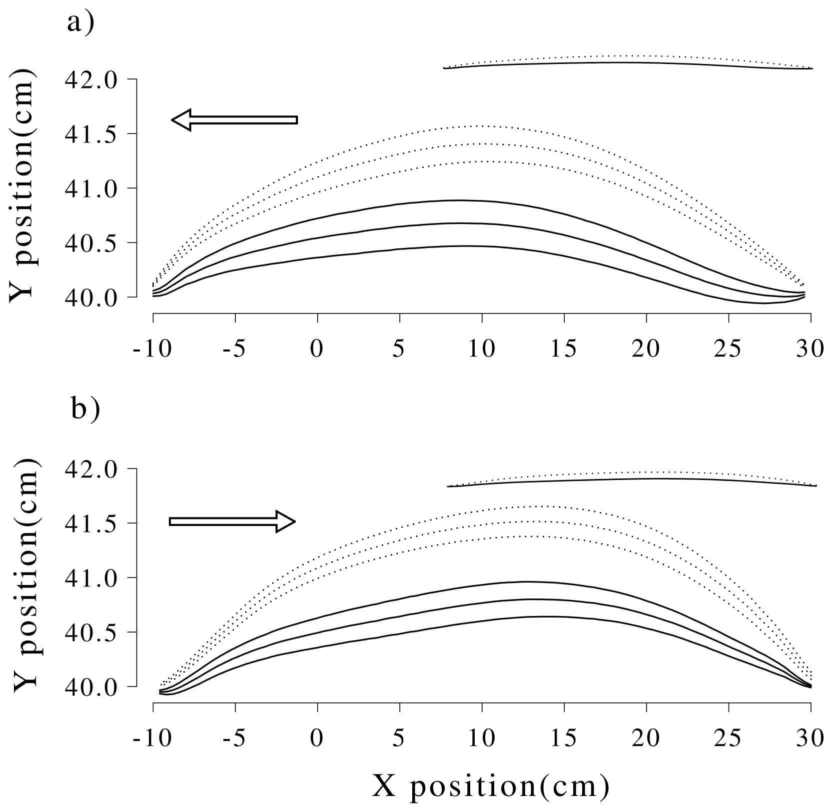


Figure 5. Group 2 control (dotted lines) and post-perturbation (solid lines) mean $\pm 1$ standard error paths for a) leftward and b) rightward movements. The perturbation (not shown) was a hemi-sinusoid outwards in the positive $y$ direction. The $y$ axis has been enlarged to show detail.

# Discussion

In this paper we have investigated adaptation of the trajectory planner to changes in the perceived curvature of reaching movements. Subjects in groups 1 and 2 showed significant adaptation in their actual hand trajectories under conditions in which the perceived curvature of movement was increased. The adaptation was partial, about 25% for sagittal and 18% for transverse movements. When the curvature of the transverse movements of the group 3 subjects was decreased no significant adaptation was seen. However, it must be noted that since these transverse movements are only gently curved the actual size of the visual perturbation for this group was about 25% that of groups 1 & 2. Both the time course of adaptation and of the decay of adaptation were similar, as shown by the group 4 study.

Analysis of movement times in groups 1 & 2 shows a significant increase with adaptation. While it may be possible to explain this increase for the group 1 subjects whose post-perturbation paths were longer, it is not possible to similarly explain the increased movement times for the group 2 subjects as they produced shorter post-perturbation paths. To control for the possible effect of this change in duration we studied paced movements in the group 5 subjects. These subjects, who were paced to produce 650 ms movements, also

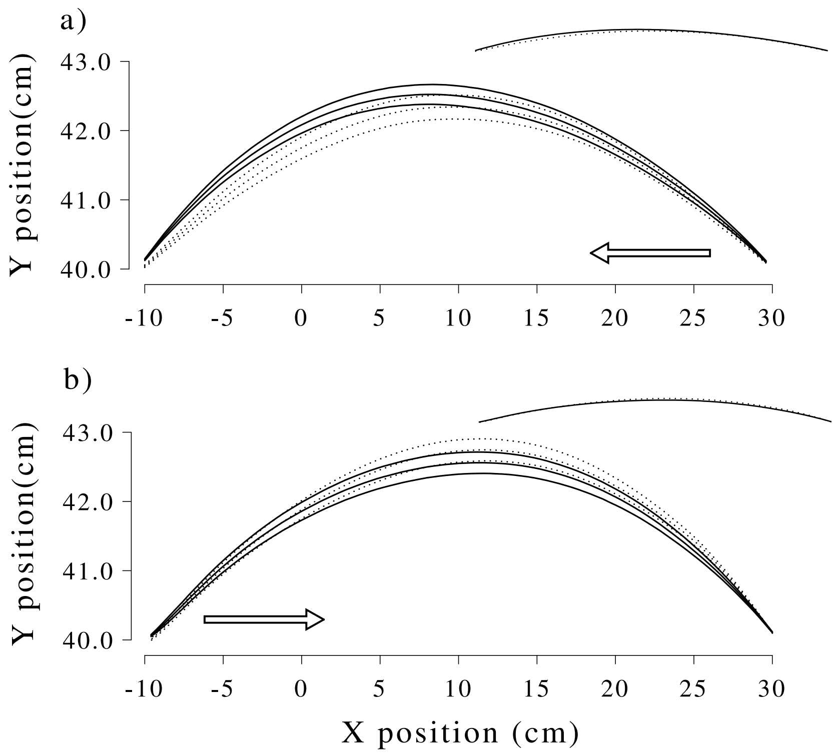


Figure 6. Group 3 control (dotted lines) and post-perturbation (solid lines) mean $\pm 1$ standard error paths for a) leftward and b) rightward movements. The perturbation (not shown) halved the curvature. The $y$ axis has been enlarged to show detail.

showed significant adaptation, although the rate of adaptation was somewhat decreased compared to the self paced groups.

We will argue that the adaptation between the control and post-perturbation sessions in groups 1 & 2 reflects a change in the underlying trajectory planner. The effects of altering the visual feedback and the concomitant changes in hand trajectory could be due to either conscious or automatic compensation. Only automatic compensation would suggest true adaptation of the trajectory planner. We designed our experiment so as to reduce the possibility that subjects could detect the perturbation. This was achieved by using small perturbations which were introduced gradually with the result that subjects did not report noticing anything unusual about the movement of the cursor. As the analyzed movements were made without visual feedback they represent the visually feedforward outcome of the trajectory planner. The aftereffects present in the absence of visual feedback therefore suggest that the effects seen represent automatic compensation rather than a conscious change. The subjects in group 4 demonstrated a decay in adaptation which was on the same timescale as adaptation. This suggests, again in analogy to the prism adaptation literature, that the change in the trajectory planner represents automatic rather than conscious processes.

The adaptation to an increase in curvature suggests that if the trajectory is determined by a cost function, this cost function is specified, at least in part, in kinematic coordinates and measured visually. This adaptation also implies that the reference trajectory may be visually straight, a hypothesis further supported by the lack of adaptation to the reduction

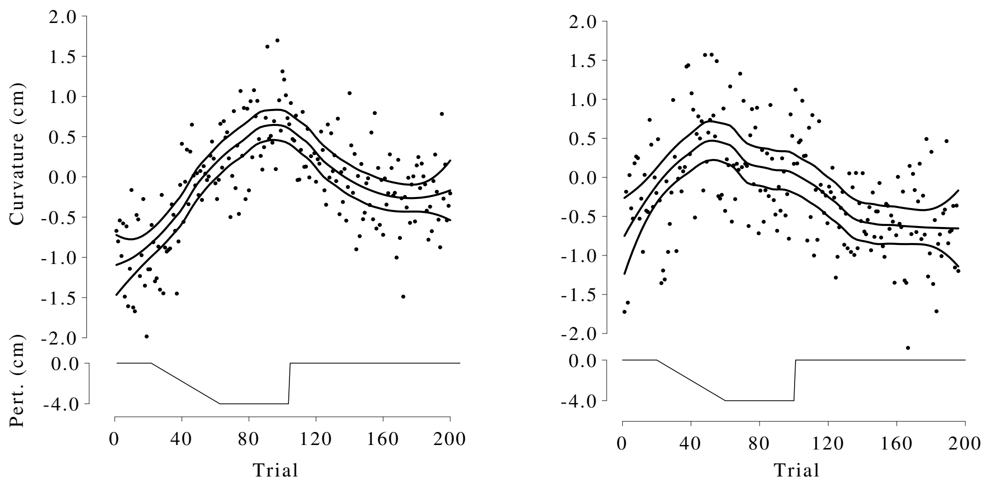


Figure 7. Group 4 adaptation plots show the movement curvature against movement number for the two subjects. Also shown is the perturbation applied against movement number. A loess has been used to fit the mean ±1 standard error to the data.

of curvature in group 3. These results suggest a kinematically specified cost function and hence are incompatible with purely dynamic cost functions such as minimum torque change.

The adaptation seen in all our groups was partial suggesting that there is a kinematic component to trajectory planning. We do not feel that partial adaptation supports a conclusion of a partially dynamic-based planner as there are at least three possible alternative causes for this partial adaptation. First, there are two sources which can be used to judge the kinematics of the movement; vision and proprioception. In our experiment only the visual inputs were altered while the proprioceptive inputs remained veridical. Ghez et al. (1990) have shown that deafferented patients demonstrate trajectories that differ in many respects from normal subjects, showing that proprioception is certainly necessary for normal trajectory production. Although in normal subjects vision tends to dominate in studies such as prism adaptation (for a review see Welch 1986), in our study the conflict between these two senses may limit adaptation. Second, it is well known from the prism adaptation literature that complete adaptation is rare (Welch 1986). Lastly, in this experiment we used a luminous dot to represent hand position rather than actual vision of the hand. Held et al. (1966) have shown that subjects adapt to a dot representing their hand in a prismatic adaptation paradigm. However, their subjects were still adapting after 30 minutes exposure and had only attained about 30% adaptation. This is generally slower than adaptation to prismatic displacement when the actual hand is viewed (Welch 1986), suggesting the visual relevance of the dot may be less than that of the hand. Therefore, had it been possible to perturb the actual feedback of the hand position greater adaptation might have been seen.

The results presented here suggest that the reference trajectory is a visually straight line between the start and end points. In general, our results would agree with any theory, whether stated within an optimal control framework or otherwise, which leads to a reference trajectory that is straight in visual space. Thus, although our results agree with the minimum visual jerk model, there are alternative models which could explain our findings. For example, Jordan, Flash & Arnon (1993) have suggested that the desired path is a straight line but that the bell-shaped velocity profile is an emergent feature of the control system

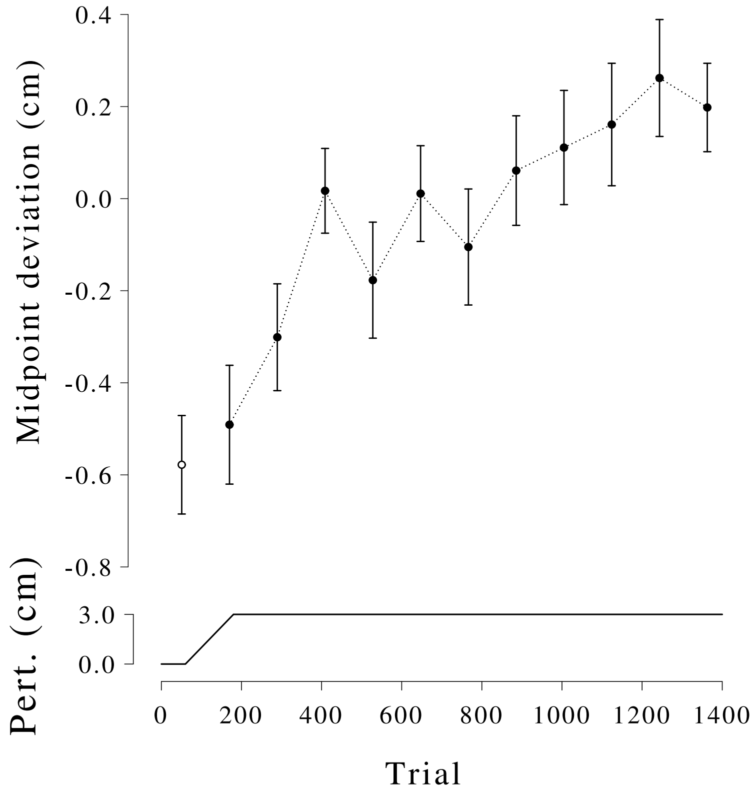


Figure 8. Group 5 ensemble data shows the binned average curvature with 95% confidence limits. Also shown is the perturbation applied against movement number.

and biomechanics. This is in sharp distinction to the minimum jerk model which suggests that the straight line path and bell-shaped velocity profile are intimately linked through the cost function. Both models predict adaptation to curvature increasing perturbations but make different predictions to velocity perturbations. If the velocity profile is perturbed while maintaining the curvature of the movement (by perturbing only tangentially to the inter-target line) the minimum jerk model predicts adaptation while the Jordan et al. (1993) model predicts no adaptation. A careful study of velocity perturbations could distinguish between these two models.

Although our results suggest that the cost function seems to imply straight-line planning in kinematic Cartesian space, Hollerbach & Atkeson (1987) point out that similar paths can be obtained by interpolation in joint space. They suggest that the start and end point of the movements are represented as joint angles obtained through inverse kinematics and that the trajectory is planned through staggered linear interpolation of these angles. However, our results show that the visually perceived kinematic coordinates of the hand are controlled throughout the movement rather than only at the start and end.

It is interesting to note that, while our results suggest a straight reference trajectory, all three groups showed control trajectories that were gently curved. Before we discuss the possible causes of this curvature we will briefly review two models of the controller (the process which produces motor torques given the reference trajectory, thereby realizing an actual trajectory) which bear on the form of the trajectories. A controller is required for models such as minimum jerk, in which only the kinematic aspects of the movement are determined, but is not required for the minimum torque change model, in which the torques are calculated directly during the optimization process. Two main control approaches have been advanced—internal dynamic modeling and equilibrium point control.

Internal dynamic modeling involves learning an inverse model of the arm dynamics. The inputs to the inverse model are the present state and the desired next state of the arm, and the output is the control signal (motor torques or muscle commands) needed to achieve the desired state. As the dynamics of the arm change due to growth, damage, fatigue and changes in external loading, the inverse model must be adaptable. Three main approaches for adaptation have been proposed in such inverse models—direct inverse modeling (Miller 1987; Kuperstein 1988), distal supervised learning (Jordan and Rumelhart 1992) and feedback-error-learning (Kawato 1990). The latter two models both rely on the ability to convert errors in the actual trajectory into changes in the motor command and are able to acquire an accurate inverse model even for redundant systems.

On the other hand, the equilibrium point or virtual trajectory control hypothesis is based on the idea that a set of muscle activations specifies a unique equilibrium end position for the effector (Bizzi et al. 1976; Hogan 1984). A movement between two points can then be thought of as changing from one set of muscle activations to another; the actual hand trajectory being dependent on the dynamics of the arm. This model was refined to suggest that, rather than choosing just the end points, a series of moving equilibrium points (a virtual trajectory) is chosen to produce the desired trajectory (Bizzi et al. 1984). Flash (1987) simulated multi-joint arm movements and concluded that human arm movements could be reproduced by using straight-line, minimum jerk virtual trajectories at high stiffness[5]. This hypothesis is attractive as the CNS only needs to produce a simple virtual trajectory which is sent to the periphery thereby avoiding the need for an explicit computation of the inverse dynamics.

Returning to the curvature seen in the control movements we note that there are at least four possible explanations. The first is that the reference trajectories are indeed curved. However, the lack of adaptation back towards a curved reference trajectory when the perceived curvature was decreased (group 3) implies that the reference trajectory is unlikely to be curved. The second possibility is that imperfections in the control system lead to curvature dependent on the dynamics of the arm. It is interesting to note, however, that in group 2 the effect of the perturbation leads to a decrease in curvature of the transverse movements. This demonstrates that for naturally curved transverse movements, subjects are certainly able to produce straighter paths but do not do so naturally. The third possibility is that the CNS, rather than directly controlling torques, specifies the trajectory in terms of an intermediate representation, such as a series of equilibrium positions (virtual trajectory, Flash 1987) or desired muscle lengths (Bullock and Grossberg 1988). The actual trajectory produced then depends on the dynamics of the arm. With regard to the virtual trajectory hypothesis, recent work by Katayama and Kawato (1992) has shown that the virtual trajectory needed to achieve arm movements comparable to those of humans would be far more complex than the actual trajectories. These controversial findings are

[5]Stiffness can be thought of as gain; with a high stiffness the virtual and real trajectories will be very similar (and simple) but with low stiffness a large virtual trajectory discursion is needed to produce the same arm movement.

based on experiments which show that hand stiffness falls considerably during arm movement (Bennett et al. 1992); the actual stiffnesses are, therefore, much smaller than those used by Flash in her simulations. Based on their findings Katayama & Kawato suggest that the planning of virtual trajectories is as difficult as setting up an internal dynamic model and therefore may not offer the simplicity initially expected. Finally, we suggest a fourth possibility—subjects try to make a visually straight movement but perceptual distortion leads to perceived straight-line motion when the hand is, in fact, making a curved movement.

Static curvature perception is often assessed using the apparent fronto-parallel plane task (AFPP; for review see Foley, 1980)). The subject views an array of vertical rods, in which the center rod is fixed, and the subject must set the other rods so that they all appear to lie in the fronto-parallel plane. These studies report that at far distances the subjects set the rods on a surface convex to them and at near distances they are set on a surface increasingly concave. Usually the apparent plane corresponds to the physical plane at only one viewing distance; the viewing distance of the human reaching workspace corresponds to the near distance of the AFPP task. We have shown here that subjects adapt their movement to experimentally induced curvature. We might, therefore, expect that, if the natural distortion inherent in the visual system increases the perceived movement curvature, natural movements may reflect curvature compensating for this perceptual distortion. To assess the effect of curvature misperception on trajectory planning we have examined the relationship between curvature perception and movement curvature for planar sagittal and transverse arm movements (Wolpert et al. 1994). We examined movement curvature using a similar paradigm to the one described in this paper and measured the average curvature for natural movements in the absence of visual feedback in a group of subjects. In the same subjects we used a force choice paradigm to assess visual perception of curvature along paths matched to the movement curvature session; this enabled us to estimate the curvature which subjects perceived as straight. We found, on a per subject and movement direction basis, a significant correlation between the natural curvature of movement and the curvature perceived as straight. For example, if a subject made transverse movements which were curved away from the body then they also perceived such movement to be straighter than they actually were—when shown a straight movement they would perceive the movement as being curved toward the body. We concluded that misperception of curvature contributes significantly to movement curvature, a result which strengthens the position of visual based kinematic trajectory planning.

In conclusion, the results of the curvature increasing study suggest that trajectories are planned in visually perceived kinematic coordinates and the results of the curvature reducing study suggest that the desired trajectory may be straight in visual space. These results are incompatible with purely dynamic optimization models such as minimum torque change. Finally, the results suggest a critical role for visual perception in trajectory formation.

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