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Abstract

Three computational problems to be solved for visually guided reaching movements, trajectory formation, coordinate transformation, and calculation of motor commands, are all ill-posed in redundant biological motor control systems. Two different theories, unidirectional and bi-directional, have been developed to account for how the brain solves them. In the unidirectional theory, the three problems are solved sequentially and step by step. In each calculation, the higher-level in the hierarchy resolves ill-posedness at that level without reference to what happens at the lower-level in the hierarchy. The representative models developed in the unidirectional theory framework are minimum-jerk model and virtual trajectory control hypothesis. The bi-directional theory retains the same hierarchical structure, but the three computational problems are solved simultaneously rather than sequentially while using both upward and downward information flows between different levels in the hierarchy. The upward and downward information flows are achieved by the internal forward and inverse models of the controlled object and the environment, respectively. The representative models developed in the bi-directional-theory framework are minimum-torque-change model and feedforward control using an inverse dynamics model. The two theories disagree on many points, some of which can be tested by a combination of carefully controlled experiments and computer simulations. This paper first summarizes comparisons between the two theories and introduces recent experimental and simulation data which address their differences.

1 Unidirectional versus Bi-directional Theory

The problem of controlling goal-directed limb movements can be partitioned conceptually into a set of information-processing sub processes; trajectory planning, coordinate transformation from extracorporal space to intrinsic body coordinates and motor command

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generation. These sub processes are required to translate the spatial characteristics of the target or goal of the movement into an appropriate pattern of muscle activation. Over the past decade, computational studies of motor control have become much more advanced as a result of concentrating on these three computational problems. Many of the models can be broadly classified into one of the two contrasting theories: unidirectional and bi-directional. In both the theories, hierarchical structure of information representations and the three problems are assumed to be as shown in Fig. 1. The fundamental difference between the two theories is direction of information flows allowed for solving the three computational problems.

In the unidirectional theory, information flows only downward from the higher level to the lower level. As a result, the higher level computational problem is solved without any reference to the lower level computational problems. For example, trajectory planning is solved without using any knowledge about coordinate transformation or motor command generation. Thus, the three problems are solved sequentially step by step (Table 1). That is, first the trajectory planning problem is solved to compute the desired trajectory in the extrinsic space (in many cases, task-oriented visual coordinates). Then, the coordinate transformation problem is solved to obtain the desired trajectory in the intrinsic space (joint angles, muscle lengths etc.) from the trajectory in the extrinsic space. Finally, the necessary motor commands for the desired trajectory in the intrinsic space are calculated by a controller.

On the other hand, in the bi-directional theory, upward information flows as well as downward flows are allowed and actually essential to solve the three computational problems in a reasonably short time (Table 1). As a result, the higher level computational problem is solved while taking account of events which happen at the lower levels. For example, trajectory planning is executed while taking account of the smoothness of motor command (Fig. 1). Thus, the three problems should be solved simultaneously rather than sequentially (Table 1).

This section briefly summarizes comparisons between the unidirectional theory and the bi-directional theory according to the order of items listed in Table 1. Some of the topics will be discussed in detail in the following sections. References to them will also be given here.

One of the most fundamental differences between the two theories concerns the spaces in which the trajectory is first planned. Consequently, at present there is a controversy about the coordinate system, extrinsic (kinematic) or intrinsic (dynamic), in which trajectories are planned. In the unidirectional theory, the trajectory is assumed to be planned solely in the extrinsic space (usually task-oriented visual coordinates), while all the kinematic and dynamic factors at the lower levels are neglected. On the other hand, in the bi-directional theory the trajectory is planned in both the intrinsic (body coordinates) and extrinsic space. Goals of movements such as the end point of reaching are given in the extrinsic space while necessary constraints to select a unique trajectory (i.e, to resolve the ill-posedness) are given in the intrinsic space. Thus, the two spaces are used simultaneously for trajectory planning.

The above explanation to the controversy might be too simple and slightly misguided.

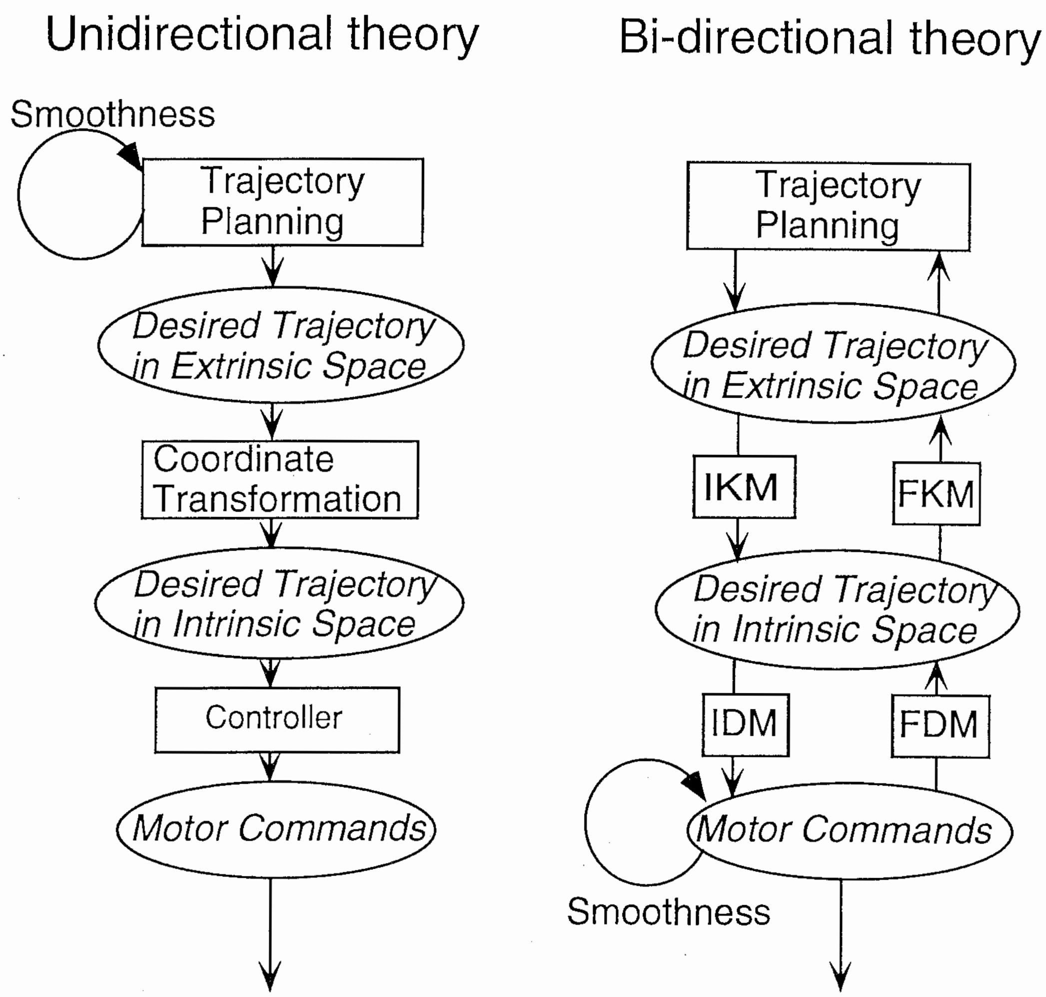

Figure 1: Hierarchical arrangement of computational problems and internal representations of visually-guided arm movements. The left side shows a block diagram of the unidirectional theory, and the right side a block diagram of the bi-directional theory.

Table 1: Comparison of the unidirectional and bi-directional theories for goal-directed arm movements

Theory	Unidirectional	Bi-directional
How to solve three computational problems	Sequential	Simultaneous
Spaces where trajectory is planned	Extrinsic space (task-oriented visual coordinates)	Intrinsic space (body coordinates) & Extrinsic space
Optimization principle (Example)	Kinematic (Minimum-jerk)	Dynamic (Minimum-torque-change)
Control	Virtual trajectory control	Inverse dynamics model
Internal models of motor apparatus and environment	Not necessary	Forward dynamics model & Inverse dynamics model
Motor learning	——	Acquisition of internal models
Curved path	· Incomplete control · Visual misperception · Virtual trajectory	Optimal (planned) trajectory itself is curved
Stiffness during movement	High stiffness	Low stiffness
Altered visual environments	· Invariant in extrinsic space · Variant in intrinsic space	· Invariant in intrinsic space · Variant in extrinsic space
Force field adaptation (new dynamic environment)	No adaptation	Adaptation
Trajectory under translation, rotation, reflection	Invariant	Variant

The difference between the uni-directional theory and bi-directional theory surely is not simply whether or not there is only planning in extrinsic space; somehow those high-level plans must be passed down to a system that deals with forces and motor commands, in which case there must be a lower-level planner (or controller). Actually as an illustrative example, we can imagine a uni-directional strategy in which first the minimum-jerk model in Cartesian coordinates specifies the path in extrinsic space, then the minimum-torque-change model transforms this desired trajectory into joint angle motions, and finally the minimum-motor-command-change model determines the necessary motor neuron firings from the desired joint angle motions. In this extreme case, motor planning (or in a wider sense, trajectory planning) is done at all of the three different levels but the information flow is uni-directional. The lower level planner obeys the commands (path constraints or desired joint angle motions) from the higher level strictly, and the higher level planner ignores the lower level planner. Thus, the distinction between the uni-directional and bi-directional theories is neither directly coupled to kinematic versus dynamic optimization models nor extrinsic versus intrinsic trajectory planning. The essential difference between the two theories is whether different level motor planners and controllers are arranged in a purely hierarchical manner (uni-directional) or whether they talk to each other (bi-directional) to determine motor behaviors.

However, in most of the biologically plausible models which have been studied, the optimization principles for trajectory planning developed by the two theories are markedly different, which are inseparably coupled to the spaces for the first trajectory planning. In the unidirectional theory, because the planning process does not take the lower levels into account, the optimization principle has to be kinematic at the highest level and all of the dynamic factors are therefore neglected at this first planning stage. One representative example is the minimum-jerk model defined in Cartesian coordinates. On the other hand, in the bi-directional theory, it is possible to use principles on the optimization of dynamics which takes lower levels into account. One representative example is the minimum-torque-change model.

With regards to motor command generation (control), several different schemes are possible under the unidirectional theory. If one takes the purest position of the unidirectional theory where upward information flows are not even used for motor learning on a longer time scale, the virtual trajectory control hypothesis (Bizzi, Accornero, Chapple and Hogan, 1984; Hogan 1984; Flash 1987) is one possible strategy. The virtual trajectory control hypothesis will be discussed in Section 4.3 as a possible reason for observed curved paths.

In the bi-directional theory, feedforward control is executed by an inverse dynamics model of the motor apparatus.

If one takes the purest position in the unidirectional theory which combines kinematic path planning with the virtual trajectory control hypothesis, the brain does not need to utilize any internal model of the motor apparatus or environment in trajectory planning and control.

On the other hand, both the forward dynamics model and the inverse dynamics model are necessary for fast computation of trajectory planning under the bi-directional theory

(Wada and Kawato, 1993). In general, inverse models are necessary for fast computation, while forward models are necessary to resolve ill-posedness, or in more intuitive terms, to improve adaptability of behaviors. These two kinds of models correspond to downward and upward information flows respectively (Fig. 1). These internal models should be learned and stored somewhere in the brain. I believe that this acquisition of internal models of the motor apparatus and the environment forms a major part of early-stage motor learning. A biologically plausible learning scheme to acquire the inverse dynamics model and some experimental evidence that internal models reside in the cerebellum were previously proposed (Kawato, Furukawa, Suzuki, 1987; Kawato and Gomi, 1992; Shidara, Kawano, Gomi, Kawato, 1993).

As explained in the next section, point-to-point arm trajectories are roughly straight in front of the body. However, some trajectories such as lateral (transverse) motions are markedly curved. In the unidirectional theory, the curvature of these paths is ascribed to one or several of the following reasons because the kinematically planned trajectory has no rational reason to be curved (that is, it must strictly be straight). These three reasons were first clearly pointed out by Wolpert, Ghahramani and Jordan (1993,1994) and examined by them. The first is that although the planned and desired trajectory is straight, because of incomplete control capability of the central nervous system, the realized trajectory becomes a little curved. The second is that although humans perceive a straight path, realized trajectories are curved because of distortion in their visual systems. The third is that although the virtual trajectory is planned to be straight, the actual trajectory is the outcome of interactions of the nonlinear dynamical properties of the arm and the visco-elastic properties of muscles, thus it is a little curved (Flash 1987). On the other hand, in the bi-directional theory, the optimal trajectory itself is curved (Uno, Kawato and Suzuki, 1989). Section 4 reviews experimental data obtained in our laboratory which disproves the above three possible reasons ascribed by the unidirectional theory (Osu, Uno, Koike and Kawato, 1994; Katayama and Kawato, 1993; Kawato, Gomi, Katayama and Koike, 1993; Koike and Kawato, 1993).

In order that the planned virtual trajectory be straight and the resulting actual trajectory be slightly curved, the arm should be stiffer during movement than during posture control (Flash, 1987). On the other hand, in the bi-directional theory, low stiffness values during movement can be assumed. Recent experiments directly estimated dynamic stiffness values during movement and reported low values (Bennett, Hollerbach, Xu and Hunter, 1992; Bennett, 1993; Gomi, Koike and Kawato, 1992; Gomi and Kawato, 1995). These experimental data will also be introduced in Section 4.3.

The lower-most three items in Table 1 indicate experimental tests of predictions made by the two theories. First, if visual perception of the hand position is systematically altered for example by artificial coordinate transformation between the measured hand position and the cursor position displayed on the CRT, the two theories make dramatically different predictions. In the unidirectional theory, because the trajectory is planned in the task-oriented visual coordinates it is not influenced by any operation below the extrinsic space. Thus, the prediction is that the trajectory is invariant in extrinsic space while it is variant in intrinsic space. On the other hand, because the objective function in the bi-directional theory is given in the intrinsic space, once the target point to be reached is transformed into the intrinsic space, the trajectory should be planned in exactly the same way. Thus, the trajectory is invariant in intrinsic space and hence variant in extrinsic space. This experimental paradigm was first proposed by Uno and tested by an undergraduate student at the University of Tokyo (1989 unpublished bachelor thesis). It was cited by Kawato (1992). Wolpert, Ghahramani and Jordan (1993) drew conclusions favorable to the unidirectional theory based on their own experimental data. This paper points out that their conclusion is inappropriate in the light of their own data. It also introduces experimental data which supports the bi-directional theory obtained in our lab (Uno, Imamizu and Kawato, 1994).

Force field adaptation is another useful way to discriminate between the predictions of the two theories. Examples of force fields are elastic, viscous or inertia fields. Because in the unidirectional theory, the trajectory is planned regardless of dynamics, it is not adapted to the new force field. Thus, once the controller finds out how to achieve the original planned trajectory, the realized trajectory should be identical to the planned one under the normal condition. On the other hand, in the bi-directional theory, the planned trajectory is altered by an external force field. This experimental examination of the theories was first adopted by Uno, Kawato and Suzuki (1989) and supported the bi-directional theory. Flash and Gurevich (1992) and Shadmehr and Mussa-Ivaldi (1993) used the same force field adaptation paradigm and drew different conclusions from ours. Section 6 shows that either because the training was not sufficient or because the effect of the force-field on the trajectory shape was too small, they were not able to properly examine the two theories.

Finally, in the unidirectional theory, even if the starting, via and target points are transformed either by translation, rotation, or reflection, the same trajectory is predicted. However, in the bi-directional theory, different trajectories are predicted under such conditions. Uno, Kawato and Suzuki (1989) already confirmed that the latter prediction is correct.

The next section briefly describes well known invariant features of multi-joint arm trajectories. These characteristics must be reproduced by any candidate for a computational model of trajectory planning and control.

2 Invariant Features of a Multi-Joint Arm Trajectory

One interesting feature of human multi-joint arm movements is that the hand paths between two points are roughly straight, and the hand-speed profiles are bell-shaped (Kelso, Southard and Goodman, 1979; Morasso, 1981; Abend, Bizzi and Morasso, 1982; Atkeson and Hollerbach, 1985; Flash and Hogan, 1985; Uno, Kawato and Suzuki, 1989).

We re-examined human multi-joint arm movements using the OPTOTRAK (Northern Digital Inc.) position measurement system. Subjects (3 males aged 28-39) were asked to move their hands from one point to another using elbow and shoulder joint rotations while their wrists were braced. Arm movement was constrained in the horizontal plane at the shoulder level. We tested the following three methods for constraining the movement in the horizontal plane. (1) Hanging the elbow by a long strap from the ceiling. (2) Attach a cuff made of a low friction material to the wrist. The table was covered by a low friction

Teflon sheet. (3) Subjects were asked to hold their arms above the table about 5 cm to 10 cm before, during and after the movement. The three different methods gave essentially the same results, but the third one gave the smoothest and most comfortable movement execution. Thus, we report here the results obtained under the third condition. The path data shown in Fig. 2 has already been published in Japanese (Koike and Kawato, 1994) but the velocity and acceleration data shown in Fig. 3 have not. Similar but more noisy data using the long strap (above method (1)) were previously published (Kawato, Gomi, Katayama and Koike, 1993).

Durations for movement were not given; instead, subjects could select their own comfortable duration, which ranged from 500 to 750 ms depending on the distances moved. Figure 2 shows hand paths for five different movements (T1$\Longrightarrow$T3, T2$\Longrightarrow$T6, T3$\Longrightarrow$T6, T4$\Longrightarrow$T1, T4$\Longrightarrow$T6) taken from one subject. The hand position was sampled at 400 Hz and each point in Fig. 2 corresponds to one sampled position. Paths generated under 10 trials for each movement were overwritten. The positions of the initial and target points were the same as those used in Uno et al. (1989). The origin of Fig. 2 is the shoulder position, the X-axis is toward the right and the positive direction of the Y-axis is forward away from the body. One can see that the trajectories are usually roughly straight but that they are significantly curved for some movements (e.g. T2$\Longrightarrow$T6). The observation that transverse paths are significantly curved but radial paths (paths away from the frontal plane of the body) are considerably straighter played an important role in discriminating different computational theories.

We also calculated hand tangential velocities and accelerations. Figures 3A and B show them for the movement from T2 to T6 shown in Fig. 2. Note that velocity and acceleration profiles of other movements are very similar (see Fig. 3 of Uno et al. 1989 for velocity profiles for different paths). A second-order Butterworth filter with a cutoff frequency of 10 Hz was used to make numerical calculations of the velocity from the position data. The same filter was again used to obtain the acceleration from the velocity.

The shape of the velocity profile agrees with previous studies and is characterized by a single peak and bell-shaped profile. The acceleration profile is more noisy because of numerical differentiation, but reveals very important characteristics which can be used to reject some computational models for trajectory planning and control. When the hand is in a static state either before or after the movement, the acceleration is zero. During the movement, it is of course not zero except at the time of peak velocity as can be seen from Fig. 3B. It should be emphasized that the acceleration gradually increased from zero at the beginning of the movement, and also that it gradually increased (decreased in magnitude) to zero at the end of the movement (conceptually depicted in the right column of Fig. 3C). It was not discontinuous at the beginning or end of the movement. Consequently, optimization models such as minimum acceleration or minimum torque which predict the discontinuity of acceleration at the beginning and end of movement are rejected.

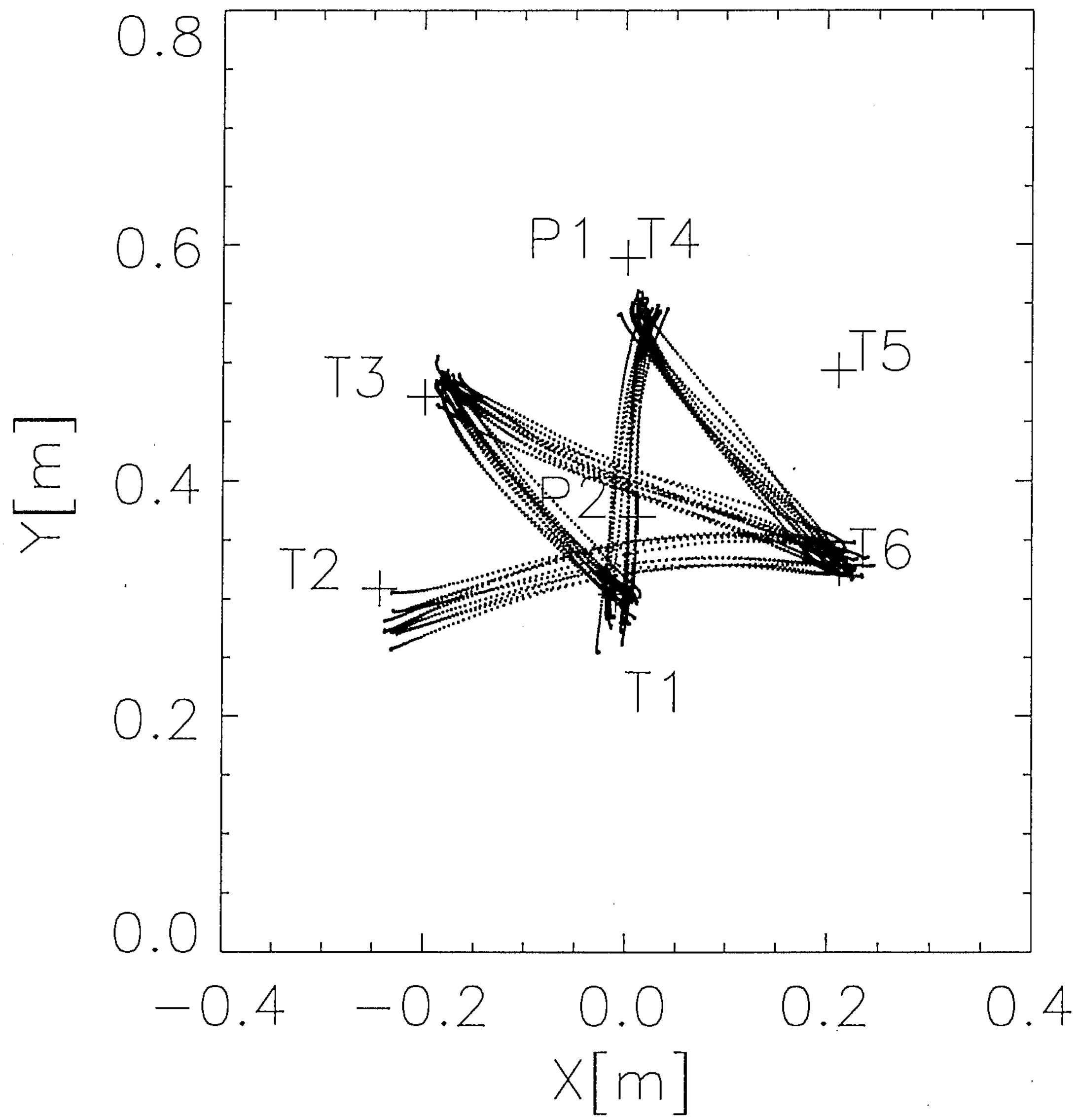

Figure 2: Hand paths for five different discrete point-to-point movements (T3$\Longrightarrow$T6, T2$\Longrightarrow$T6, T1$\Longrightarrow$T3, T4$\Longrightarrow$T1, T4$\Longrightarrow$T6) measured with the OPTOTRAK position measurement system (Koike and Kawato, 1994).

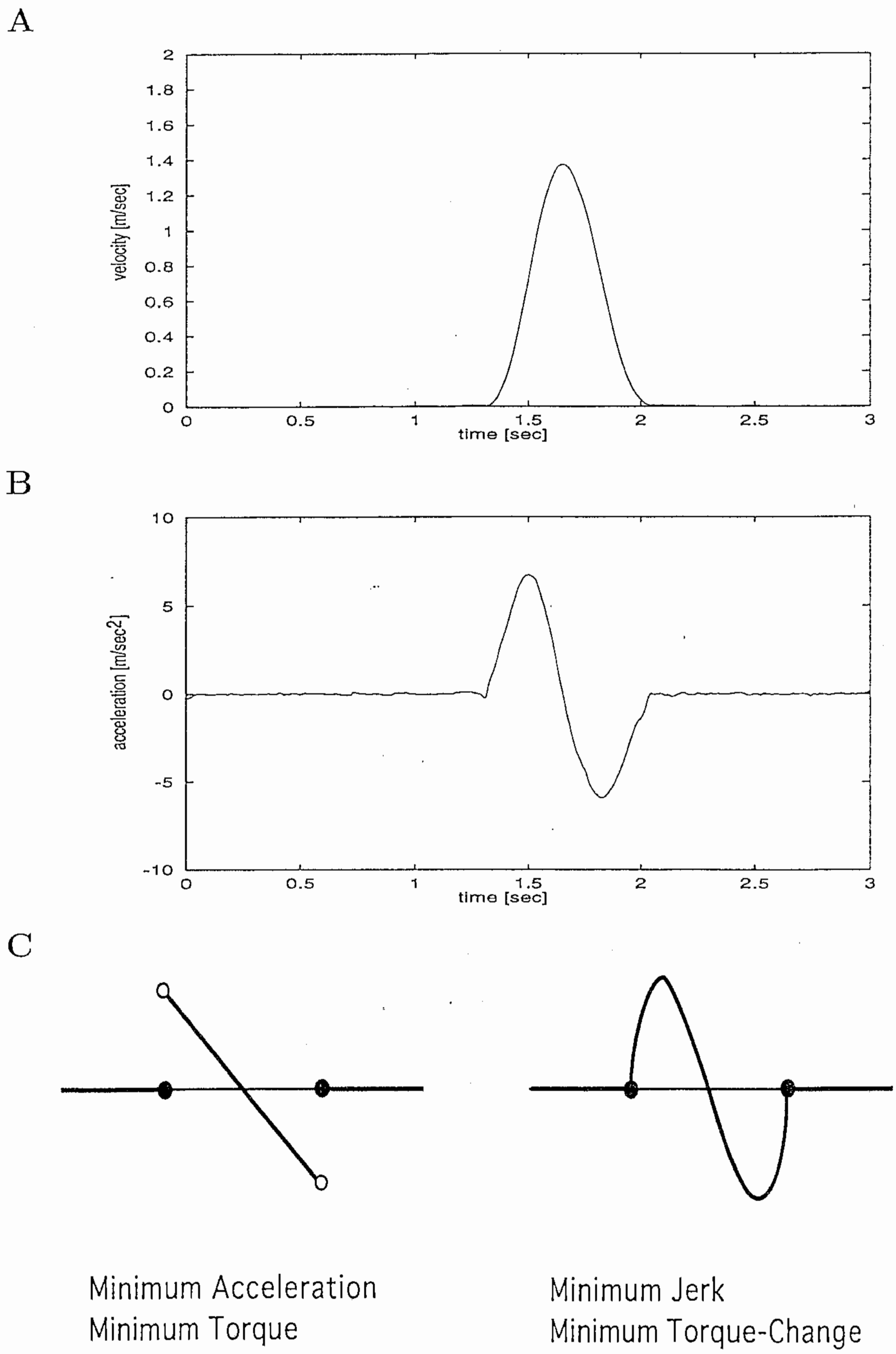

Figure 3: Velocity and acceleration profiles for T2 to T6 movement in Fig. 2. **A** The velocity profile. **B** The acceleration time course. **C** Theoretical predictions of the acceleration profile made by the minimum-acceleration model and minimum-torque model (left) and by the minimum-jerk model and the minimum-torque-change model (right).

3 Kinematic versus Dynamic Optimization Models for Trajectory Planning

This section first introduces several optimization models that have been experimentally confirmed. In particular, it shows that optimization at a given space can solve the ill-posed motor control problem at that level (Figure 4). The minimum-jerk model defined at the task space can resolve the ill-posed trajectory formation problem. The minimum-torque-change model defined at the intrinsic body coordinates can resolve the ill-posed inverse kinematics problem. The minimum-muscle-tension-change model defined at the muscle level can resolve the ill-posed inverse dynamics problem. And finally, the minimum-motor-command-change model defined in the central nervous system can resolve indeterminate motor control problems. The first model is classified into the unidirectional theory while the other three are all examples of the bi-directional theory. As mentioned in section 1, depending on which of these models is used, there is a controversy about the coordinate system in which trajectories are first planned. The first model proposes the extrinsic space whereas the latter three propose the intrinsic space.

3.1 Minimum-jerk model

In order to account for the kinematic features of human multi-joint arm movements such as those explained in the previous section, Flash and Hogan (1985) proposed a mathematical model, the minimum-jerk model, which assumes that the trajectory followed by a subject's arm tends to minimize the square of the movement jerk (rate of change in acceleration), integrated over the entire movement:

$$C_J = 1/2 \int_0^{t_f} \{(\frac{d^3X}{dt^3})^2 + (\frac{d^3Y}{dt^3})^2\} dt. \tag{1}$$

Here, (X, Y) are the Cartesian coordinates of the hand, and t_f is the movement duration. Flash and Hogan (1985) showed that the unique trajectory predicted by this equation agreed closely with data on movements made in front of the body. Let us explain this in a little more detail.

By using the Euler-Poisson equation, it can be mathematically shown that the optimal solution of the minimum-jerk model for each coordinate axis has the form of a 5-th order polynomial in time. The predicted trajectory for a discrete point-to-point movement is a straight line because the temporal dependence of X and Y is identical. The trajectory is also characterized by a perfectly symmetrical bell-shaped speed profile. Thus, the prediction is in qualitative agreement with the data shown in Fig's. 2 and 3.

The minimum-jerk model was the first optimization model to be experimentally confirmed; this was epoch making for biological optimization theories. The minimum-jerk model is based solely on the kinematics of movement, independent of the dynamics of the musculoskeletal system. It is successful only when formulated in terms of the motion of the hand in extracorporeal space, and fails when defined in terms of, for example, the joint angles. This is because the minimum-jerk model predicts straight trajectories

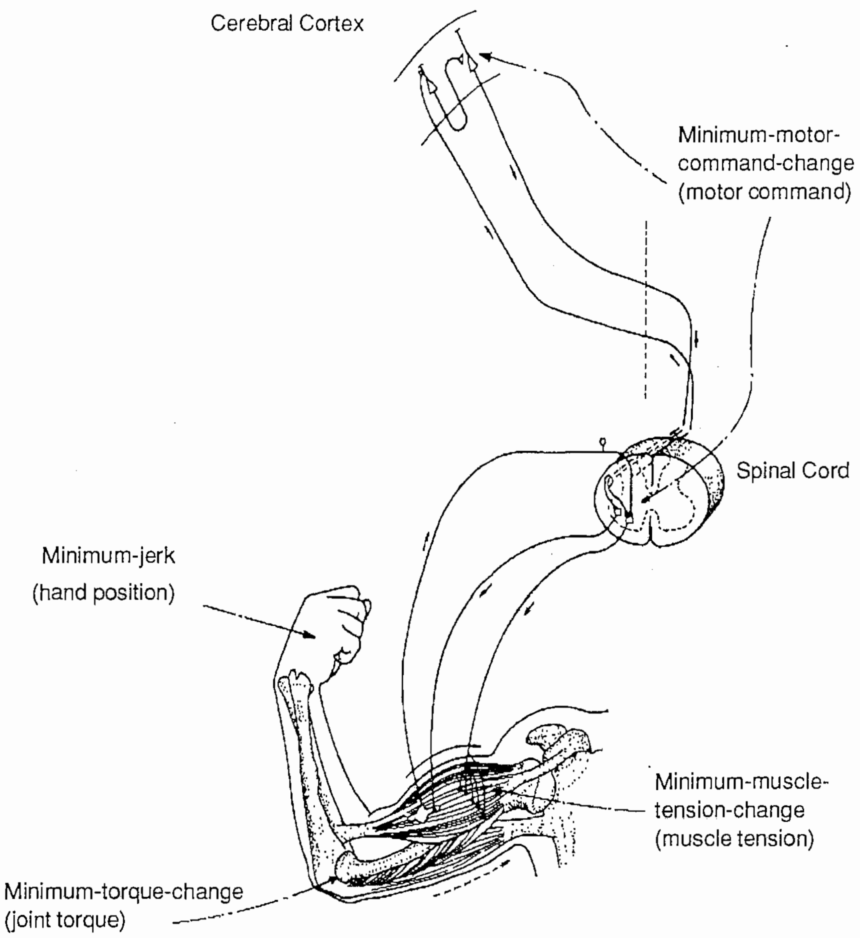

Figure 4: Schematic diagram illustrating components involved in visually-guided reaching movements and different spaces where different variables are represented. Four different spaces are used to represent movement conditions, movement trajectories, and motor commands. The positions of the target or obstacles are represented in 3-dimensional Cartesian space (extrinsic space). The hand position in this coordinate system can be measured by the visual system. During movements, joint torques are generated from muscle tensions. Muscle activation levels are controlled by the nervous system. The minimum-jerk model is defined at the Cartesian coordinates of the hand position, and can solve the trajectory formation problem. The minimum-torque-change model is defined at the joint torque coordinates, and can solve the trajectory formation problem, the inverse kinematics problem, and the inverse dynamics problem up to the joint torque. The minimum-muscle-tension-change model is defined at the muscle tension coordinates, and solves the above three problems up to the muscle tension. The minimum-motor-command-change model is defined in the motor command coordinates of the central nervous system, and can solve the above three problems up to the motor commands in the brain. It is possible to impose a smoothness constraint on motor commands at different levels such as a motor neuron firing in the spinal cord, or a pyramidal tract neuron firing in the cerebral motor cortex.

in the space where the objective function is defined. The minimum-jerk model defined in joint angle space predicts straight paths in the joint angle space but these are overly curved in Cartesian space when compared with the experimentally observed data. Thus, the minimum-jerk model implies that the trajectory is first planned in extrinsic space.

3.2 Minimum-torque-change model

The minimum-jerk model is simple and beautiful, but the uniqueness of the solution seems too strong in the sense that the model predicts a unique trajectory regardless of various conditions which may be present in the environment or in the motor task itself.

If a major objective of motor control is merely to decrease the degrees-of-freedom in the system, this can be easily achieved by introducing very strong couplings between all independent variables so that the system behaves in a stereotyped, single-fixed-action pattern. However, this is not at all desirable. The solutions adopted by the motor-control network should be flexible and should adapt to various environmental conditions; otherwise, humans would not have the capacity for *motor equivalence* or *equi-finality* - the ability to achieve the same physical objective in more than one way. However, because the minimum-jerk model is a kinematic model, it can not adapt planned trajectories in extrinsic space to different dynamic aspects involved in the motor task, environment and the motor apparatus, such as the inertial characteristics of manipulated objects, force field or physical parameters of the arm.

Based on the idea that movement optimization must be related to movement dynamics, Uno, Kawato and Suzuki (1989) proposed the following alternative quadratic measure of performance:

$$C_\tau = 1/2 \int_0^{t_f} \sum_{i=1}^{m} (\frac{d\tau_i}{dt})^2 dt, \tag{2}$$

where, τ_i is the torque fed to the ith of m actuators. Here, the performance measure (objective function) is the sum of the square of the rate of change of the torque, integrated over the entire movement. One can see that C_τ (Equation 2) is related to C_J (Equation 1) because the rate of change of torque is locally proportional to the jerk. In particular, if the controlled object is a point mass, then the force is equal to the product of the mass and the acceleration. Thus, the minimum-jerk (rate of change of acceleration) is identical to the minimum-force-change (minimum-torque-change). For a multi-joint, nonlinear-controlled object, the two criteria are different. In particular, it must be emphasized that C_τ depends critically on the dynamics of the musculoskeletal system, not just on the kinematics.

For movements between pairs of targets in front of the body, predictions made by both these models have agreed closely with experimental data. However, movement trajectories predicted by the minimum-torque-change model (Equation 2) are quite different from those predicted by the minimum-jerk model (Equation 1) in four other behavioral situations. In one situation, past data already support the minimum-torque-change model (Atkeson and Hollerbach, 1985). The other three situations were not examined. However, when Uno, Kawato and Suzuki (1989) dealt with them they found that predictions of the minimum-torque-change model matched the data better than did those of the minimum-jerk model.

The first result by Uno, Kawato and Suzuki (1989) concerned what happened when the starting point of an arm was to the side of the body and the end point was in front. Here the movement path was curved under the minimum-torque-change model, but always straight under the minimum-jerk model. The hand paths of sixteen human subjects were all curved, supporting the minimum-torque-change model (Uno, Kawato, Suzuki, 1989). This specific movement was utilized again by Osu, Uno, Koike and Kawato (1994) to examine the origin of the curvature, and will be introduced in Section 4.

The second result found by Uno, Kawato and Suzuki (1989) concerned movements between two points while resisting a spring, one end of which was attached to the hand while the other was fixed. This is exactly the first examination of the force field adaptation listed in Table 1. Here, the minimum-jerk model always predicted a straight movement path regardless of external forces. The minimum-torque-change model predicted a curved path and an asymmetrical speed profile for the movement with the spring. The latter predictions again agreed closely with the data, further supporting the minimum-torque-change model.

Third, Uno, Kawato and Suzuki (1989) examined vertical movement affected by gravity. The minimum-jerk model always predicted a straight path between two points. The minimum-torque-change model predicted curved paths for large up and down movements, but essentially straight paths for small fore and aft movements. The speed profiles were bell-shaped for both movements. This outcome agrees closely with the data of Atkeson and Hollerbach (1985), as one would expect from the minimum-torque-change model.

Finally, the most compelling evidence obtained by Uno, Kawato and Suzuki (1989) concerned a pair of via-point movements (Fig. 5). These movements involved two subcases, with identical starting and end points, but with mirror-image via-points. This corresponds to the lower most item listed in Table 1. Because of objective function C_J's invariance under translation, rotation, and roll, the minimum-jerk model predicted identical movement paths with respect to roll as well as identical speed profiles for the two subcases. On the other hand, the minimum-torque-change model predicted two different paths. For the concave path, the speed profile should have two peaks. However, for the convex path, the speed profile should have only one peak. These latter predictions agree closely with the data obtained by Uno, Kawato and Suzuki (1989).

Summarizing these comparisons, it can be seen that the trajectory derived from the minimum-jerk model is determined only by the geometric relationship between the initial, final, and intermediate points on the movement trajectory. The trajectory derived from the minimum-torque-change model depends not only on the relationship between these three points but also on the arm posture (in other words, the location of the shoulder relative to the three points), and on external forces. Empirical data suggest that the latter dependence is in fact the case. Wann, Nimmo-Smith and Wing (1988) also found that the minimum-jerk model fails due to its lack of information on movement dynamics.

3.3 Physical parameter values of the arm

Flash (1990) recently criticized the minimum-torque-change model based on her own simulation of the minimum-torque-change trajectory. Her criticism concerned the link-inertia moment values assumed in Uno, Kawato and Suzuki (1989). Let subscript 1 denote physical parameter values of the upper arm (link 1), and subscript 2 denote those of the forearm (link 2). The values assumed in Uno, Kawato and Suzuki (1989) are as follows and are summarized in Table 2: mass M_1=0.9[kg], M_2=1.1[kg]; length L_1=0.25[m], L_2=0.35[m]; center of mass from joint S_1=0.11[m], S_2=0.15[m]; inertia moment around joint I_1=0.065[kg m^2], I_2=0.100[kg m^2]; coefficient of viscosity around joint b_1=0.08[kg m^2/s], b_2=0.08[kg m^2/s]. Although our simulations used the moment value I_2 experimentally obtained by Cannon and Zahalak (1982), it was about double a reasonable value based on the other physical parameters of the links: mass, length, and center of mass used in the simulation. When a reasonable, smaller inertia moment value was assumed while keeping the other parameter values constant, the hand path for point-to-point movement in front of the body was too concavely curved compared with the human data (Fig. 17.6 pp. 293, Flash,1990 for T3$\Longrightarrow$T6 movement). When Uno simulated minimum torque-change trajectories with parameters I_1=0.0201[kg m^2], I_2=0.0453[kg m^2] , which were less than half of the above values, and with other parameters which were the same as those in Table 2, the predicted hand paths were too concave and too curved to the left compared with the human data.

Table 2: Parameter values assumed in Uno, Kawato and Suzuki (1989) for examining the minimum-torque-change model

		link 1 (upper arm)	link 2 (forearm)
L_i	[m]	0.25	0.35
S_i	[m]	0.11	0.15
M_i	[kg]	0.9	1.1
I_i	[kgm^2]	0.065	0.100
b_i	[kg m^2/s]	0.08	0.08

The other uncertain parameter values in the above simulations were the viscosity values during movements because 0.08 was cited from a monkey study (Hogan, 1984) and no direct measurement was made for viscosity during human movements at that time. Recently, Bennett et al. (1992) directly estimated stiffness and viscosity values of the elbow joint during cyclic movements. They reported that the damping ratio defined as $\xi = b_2/\sqrt{4K_2I_2}$ during movement varied between 0.2 and 0.6 over one movement cycle. Here K_2 is stiffness of the elbow joint and I_2 was 0.072 [kgm^2] including the apparatus inertia of 0.032 [kgm^2]. Then, Bennett (1993) estimated dynamic stiffness values during targeted elbow joint movements at speeds ranging from slow to very fast. In Fig.

6 of Bennett (1993), mean stiffness during movement was plotted as a function of the mean background torque magnitude (mean absolute value of net muscle torque during unperturbed movement). This paper is concerned with two-joint movements. The elbow joint stiffness and viscosity during multi-joint movements was estimated by calculating the mean background torque magnitude at the elbow as defined by Bennett (1993). Koike (personal communication, 1994) calculated this using the data and the method described in Koike and Kawato (1994). The resulting values [Nm] are as follows: 0.306 (T3$\Longrightarrow$T6), 0.341 (T2$\Longrightarrow$T6), 0.022 (T1$\Longrightarrow$T3), 0.141 (T4$\Longrightarrow$T1), 0.187 (T4$\Longrightarrow$T6), 0.266 (T6$\Longrightarrow$T3), 0.307 (T6$\Longrightarrow$T2), 0.047 (T3$\Longrightarrow$T1), 0.099 (T1$\Longrightarrow$T4), 0.202 (T6$\Longrightarrow$T4). The mean is 0.19 and the range is 0.022 to 0.34. By using Fig. 6 of Bennett (1993), the mean dynamic stiffness K_2 for these 10 two-joint movements can be estimated as 3 [Nm/rad] with a range of 2 [Nm/rad] to 4 [Nm/rad]. Viscosity value can be estimated from the damping ratio ξ of Bennett et al. (1992) using the following equation: $b_2 = \xi 2\sqrt{K_2 0.072}$, which gives an average of 0.37 [Nms/rad] and a range of 0.15 to 0.64. Because vigorous EMG activities in elbow related muscles were observed even when the mean background torque magnitude was small in (T1$\Longrightarrow$T3) and (T3$\Longrightarrow$T1) movements, the lower bound was apparently underestimated. It can be safely concluded that the average viscosity is around 0.4 and that the variation ranges from 0.2 to 0.8. Incidentally, the viscosity value changed from 0 to 0.7 with an average of around 0.3 to 0.4 in elbow joint cyclic movement examined by Bennett et al. (1992).

Accordingly, the current best estimation of parameter values is summarized in Table 3. Uno and Kawato (1994) recently found that, for this set of parameter values, the minimum-torque-change model predicts trajectories which are quite similar to those given by human data. Thus, it can be concluded that the minimum-torque-change model is still a very attractive model which can reproduce human-movement data with realistic inertia moment values and measured viscosity values. Flash (1990) apparently used an underestimated value for the dynamic viscosity (0) in her simulation of the minimum-torque-change model. If the viscosity parameter is assumed to be twice as large b=0.8[kg m^2/s], predicted paths are only a little too convex (curved away form the body), and if it is assumed to be twice as small b=0.2[kg m^2/s], trajectories are a little too concave (curved towards the body). Thus, predictions are sensitive to the viscosity values. However, this sensitivity is not considered to be a weak point of the minimum-torque-change model. It only suggests that dynamic viscosity values can still not reliably be estimated during multi-joint arm movements.

In summary, accidentally chosen inertia moment values that were too large and viscosity values that were too small gave human-like trajectories (Uno, Kawato and Suzuki, 1989). A combination of the correct inertia moment values and viscosity values that were too small gave concavely curved trajectories (Flash, 1990). The best current estimate of moment values and viscosity values reproduces human data quite well (Uno and Kawato, 1994). If the viscosity values are twice as large as these, the paths are convexly curved while if they are twice as small, the paths are concavely curved.

Finally, Table 4 shows the link physical parameter values recently estimated by Koike and Kawato(1994) from 3-D shape measurements of a subject arm using a Cyberware

Table 3: The current best estimate of parameter values based on measurements of dynamic stiffness and viscosity by Bennett et al. (1992) and Bennett (1993)

		link 1 (upper arm)	link 2 (forearm)
L_i	[m]	0.25	0.35
S_i	[m]	0.12	0.15
M_i	[kg]	0.9	1.1
I_i	[kgm^2]	0.0201	0.0453
b_i	[kg m^2/s]	0.4	0.4

Laser Range Scanner. Please note that the values in Tables 3 and 4 are quite similar.

Table 4: Link parameter values estimated by Koike and Kawato (1994) from 3-D shape measurements of a human arm using a Cyberware Laser Range Scanner

		link 1 (upper arm)	link 2 (forearm)
L_i	[m]	0.256	0.315
S_i	[m]	0.104	0.165
M_i	[kg]	1.02	1.16
I_i	[kgm^2]	0.0167	0.0474

3.4 Minimum muscle-tension-change model

Musculoskeletal systems possess muscle-tension sensors (Golgi tendon organs) as well as muscle-length and velocity sensors (muscle spindles) but no direct joint-torque sensors; joint capsule mechanoreceptor afferents are not sensitive to intermediate joint angles, but are sensitive to extremes of joint angles (Kandel, Schwartz and Jessell, 1991). Considering these physiological constraints, Uno, Suzuki and Kawato (1989) proposed a minimum-muscle-tension-change model, in which the following objective function is minimized:

$$C_F = 1/2 \int_0^{t_f} \sum_{i=1}^{n} (\frac{dF_i}{dt})^2 dt, \tag{3}$$

where, F_i is the muscle tension generated by the ith of n muscles. Generally, the number of muscles n is much larger than the number of joints m. Here, the performance measure (objective function) is the sum of the square of the rate of change of the muscle tension, integrated over the entire movement. One can see that C_F (Equation 3) is related to C_τ (Equation 2) because the joint torque is the summation of muscle forces weighted by their moment arms for the joint. If the joint torque were to be generated by only one muscle and if its moment arm were to be constant regardless of the joint angle and the same for all different muscles, then the minimum-muscle-tension-change model would be identical to the minimum-torque-change model. However, of course, joint torque is generated by a number of muscles, their moment arms are different and moment arms do depend on joint angles. Thus, the minimum-muscle-tension-change model is different from the minimum-torque-change model.

Using the minimum-muscle-tension-change model requires a more sophisticated model of the arm than the minimum-torque-change model. Not only the link dynamics but also the muscle geometry should be taken into account for the dynamic modeling of the arm. Specifically, it is necessary to first determine which muscles effectively contribute to the considered movements, then to estimate the moment arms of these muscles, which generally change with varying postures. This sounds like a formidable task, and it is actually very laborious, but it can be done perfectly independent of the measurement of movement trajectories. Thus, although the minimum-muscle-tension model possesses more parameters (related muscles and their moment arms) than the minimum-torque-change model, it by no means guarantees a better fit to the observed trajectories because the muscle parameters are estimated from literature of biomechanical studies or dissection experiments, and are perfectly independent of the observed trajectories.

Uno, Suzuki and Kawato (1989) simulated discrete point-to-point trajectories (Fig. 2) based on the minimum-muscle-tension-change model. They used a two-link manipulator with six muscles (elbow flexor and extensor, shoulder flexor and extensor, and double-joint flexor and extensor) as a model of the human arm. It was found that the minimum-muscle-tension-change model can reproduce human trajectory data for a wide range of dynamic parameter values of the arm.

3.5 Minimum-motor-command-change model

This evolution of the minimum-torque-change model to the minimum-muscle-tension-change model can be interpreted as a proximal shift of the space where the smoothness constraint is given (see Fig. 4): from more extrinsic space (joint torques) to more intrinsic space (muscle tensions). Because of several theoretical and computational reasons given below, this proximal shift seems to be further extended so that the smoothness constraint is defined in the intrinsic space even for the brain.

I proposed the minimum-motor-command-change model (Kawato, 1992) where the following criterion is minimized:

$$C_M = 1/2 \int_0^{t_f} \sum_{i=1}^{n} (\frac{dM_i}{dt})^2 dt, \tag{4}$$

where M_i is the ith motor command out of n commands. Several definitions of motor commands are possible. At the lowest level, we could define the i-th muscle motor command by the instantaneous frequency of nerve pulses arriving at the i-th muscle. At the spinal cord level, the firing frequency of each alpha motoneuron could be denoted by M_i.

In this case summation in the above equation is taken over all motor neurons related to the investigated movements. Thus, both the rapid change in individual firing rate and rapid recruitment are penalized. At an even higher level, firing frequencies of corticomotoneuronal neurons in the cerebral motor cortex could be represented by M_i.

In order to understand the theoretical reasons for the preference of the minimum-motor-command-change model, it is necessary to recall that all three computational problems involved in visually-guided reaching movements (trajectory planning, coordinates transformation, motor-command generation) encounter computational difficulty: the redundancy problem. The above optimization principles were proposed to resolve the ill-posedness of one or some of these problems. It is very important to realize that if the smoothness criterion of some optimization model is defined at a specific space, then the model can only solve ill-posed computational problems that are defined at or above that level (Figure 4). The minimum-jerk model defined at the task space can thus resolve only the ill-posed trajectory formation problem. Because the minimum-torque-change model specifies the smoothness criterion at the joint-torque coordinates, it can determine unique torque waveforms when the target position is specified. Because joint angles and the corresponding Cartesian coordinates are uniquely determined from the torque waveforms, both the ill-posed inverse kinematics problem (coordinates transformation from visual to joint space), which is formulated between the joint space and the visual space, and the trajectory formation problem are said to be simultaneously solved by the minimum-torque-change model. Similarly, the minimum-muscle-tension-change model, which specifies the smoothness criterion at the muscle level, can resolve the ill-posed inverse dynamics problem (the problem of determining muscle tensions from desirable joint motions) as well as the inverse kinematics problem and trajectory formation problem. And finally, the minimum-motor-command-change model which specifies the smoothness criterion in the central nervous system can resolve excess degrees of freedom at that motor command level as well as all of the above three problems (trajectory formation, inverse kinematics and inverse dynamics).

The following gives three reasons for extending the minimum-muscle-tension-change model to the minimum-motor-command-change model. First, in order to solve the ill-posed problem posed by the enormous excess degrees-of-freedom in the central nervous system (larger numbers of motor or cortico-motoneuronal neurons than the number of muscles), it is necessary to use the smoothness principle in the state space of the central nervous system (i.e. firing frequency of neurons).

Second, in view of the nature of the neural network hardware which executes trajectory planning and control, it can be said that the origin of the smoothness resides in the central nervous system rather than in the periphery. Thus, it would seem more plausible to impose the smoothness constraint at the central nervous system level rather than at the peripheral level.

Finally, Uno and Kawato (1994), in response to Flash's (1990) criticism of the link inertia parameter values used in Uno et al. (1989), found that the minimum torque-change model can reproduce human data well if measured dynamic viscosity values (Bennett, Hollerbach, Xu and Hunter, 1992) in combination with correct inertia parameter values are used in the simulation. But if zero viscosity values are assumed as in Flash (1990), the predicted hand paths are too concavely curved from the body compared with the human data. Because the musculoskeletal system's viscosity properties arise mainly from muscle velocity-tension relationships and spinal reflex characteristics, the measured viscosity coefficients used can not be interpreted as a visco-elastic component of the dynamical properties of the arm. Thus, if we are really talking about the torque which is actually generated at the joint, there is only a little viscosity in the controlled object. Consequently, the "torque" in this simulation should be interpreted as the motor command arriving at the muscles determining muscle-generated torques. In this sense, the original minimum-torque-change model should be renamed the minimum-*commanded*-torque-change model.

4 Curved Paths

Observed curved paths in point-to-point arm movements, at first sight, would seem to support the dynamic optimization theory (e.g., the minimum-torque-change model) rather than the kinematic optimization model (e.g., the minimum-jerk model). As mentioned in section 3.2, for movements whose starting point is an outstretched arm to the side of the body and whose end point is in front of the body, the hand paths were significantly and convexly curved. One can also see that the trajectory from T2 to T6 in Fig. 2 is detectably and convexly curved.

Dynamic optimization models such as the minimum-torque-change model, the minimum-muscle-tension-change model and the minimum-motor-command-change model always predict roughly straight but gently curved paths and never predict perfectly straight paths. On the other hand, kinematic optimization models such as the minimum-jerk model predict perfectly straight paths for point-to-point movements. This is because invariance of objective function under translation, rotation or reflection is the consequence of any kinematic model with symmetry, and thus curved paths can not be unique optimal solutions. If a curved path were the unique optimal solution, the symmetrically reflected curved path with respect to the line connecting the starting and end points should have exactly the same objective function value, and thus should become another unique optimal solution. This is a contradiction. Thus, the optimal trajectory in a kinematic optimization model with symmetry, which is a very natural assumption, must be strictly straight. This strong property would appear to contradict the actual data mentioned above unless some explanation is given to salvage the unidirectional theory.

Wolpert, Ghahramani and Jordan (1994) listed the following three possible ways to explain the observed curvature in the unidirectional theory framework (see also Table 1).

1. The first possibility is that the reference trajectory is straight but that imperfections in the control system lead to a curvature which is dependent on the dynamics of the arm. The reference trajectories produced by the minimum jerk model are straight lines in space. Models such as minimum jerk, in which only the kinematic aspects of the movement are determined, require a controller that produces motor torques

to follow the reference trajectory. Imperfections in these controllers could lead to curved trajectories.

2. The second possibility is that the curvature seen is due to visual misperception. Under this hypothesis, subjects try to make visually-straight movements but misperception of the curved nature of the path followed by the hand leads to perceived straight-line motion when the hand is, in fact, making a curved movement.

3. The third possibility is that the central nervous system, rather than directly computing torque, specifies the trajectory in terms of an intermediate representation, such as a series of equilibrium positions (Flash, 1987) or desired muscle lengths. The actual trajectory produced then depends on the dynamics of the arm. This possibility differs from imperfect control in that it is this intermediate representation, rather than the outcome, which is matched to the reference trajectory.

The following subsections discuss these three possible explanations while referring to recent experimental data and theoretical studies.

4.1 Incomplete control and visual misperception

Wolpert, Ghahramani and Jordan (1994) found a significant correlation between curvature perceived as straight and the curvature of actual arm movements. They suggested that subjects try to make straight-line movements, but that actual movements are curved because visual misperception makes the movements appear to be straighter than they really are. This explanation is quite interesting and also seems to be closely related to the well known *horopter*. That is, rods on the horizontal plane which appear to lie parallel to the fronto-parallel plane are convex to the body at a far distance and are concave to the body at a near distance (Foley, 1980). However, the correlation between visual misperception and movement curvature itself can not tell whether there exists a causal relationship.

In order to examine the visual misperception as well as the first incomplete control as explanations of curvature, Osu, Uno, Koike and Kawato (1994) conducted two experiments. In the first, subjects were asked to move their right hand from the starting point where their arm was at the side of their body to the end point in front of their body. These movements are very similar to the first experimental data discussed in section 3.2, that is, T7$\Longrightarrow$T8 movements in Fig. 4 of Uno, Kawato and Suzuki (1989). The following four types of instructions were given to the subjects.

1. Move your hand from the starting point to the end point.

2. Move your hand from the starting point to the end point along the curved path drawn on a table which is actually the average path in the above first paradigm.

3. Move your hand straight from the starting point to the end point.

4. Move your hand along a straight path drawn on a table from the starting point to the end point.

The above four instructions were used to define a set of four corresponding experimental conditions that were given in the following order: 1→2→3→4→3 →2→1.

Under all of these conditions, the subjects were required to reach the target within a specified period of time. The first beep sound cued the initiation of movement and the second beep indicated the end of movement. The interval between the two sounds was 900 msec and the actual movement duration was from 850 to 950 msec.

Figure 5 shows the averaged hand paths and their standard deviation for each test block and one subject. The upper plot shows movements without a visual reference (instructions 1 and 3). In the upper plot, from the top are movement spontaneously generated (instruction 1), instructed straight trajectory before learning (instruction 3 before instruction 4), and instructed straight trajectory after learning (instruction 3 after instruction 4). The lower plot shows movements (top is instruction 2 and bottom is instruction 4) with visual references which are denoted by solid curves. The experimental procedures, relevant statistics about the data and detailed results will be presented elsewhere (Osu, Uno, Koike and Kawato, submitted).

In 1, normal trajectories generated under the most natural condition were measured. Instruction 2 was used to examine the effect of imposing path constraints; no significant difference between instructions 1 and 2 was observed. Instruction 3 was used to test the first and second explanations for curvature. The difference between instructions 3 and 4 was whether or not to give visual guidance about the straight path, thus the visual misperception effect could be examined by comparing trajectories made under 3 and 4. It was found that subjects generated much straighter trajectories under condition 3 than they did under condition 1. The difference was not only statistically significant but also very marked. This simply disproved the incomplete control hypothesis.

Trajectories made under 4 were only a little bit straighter than those made under 3. This slight difference could be ascribed to the visual misperception effect or, in our preferred interpretation, imperfect ability to internally generate a straight path. The fact that subjects were able to generate almost straight paths under 3 indicates that visual misperception, even if it has some causal relationship to movement curvature, does not have a large effect.

Osu et al. (1994) then examined point-to-point movements constrained in the fronto-parallel plane within 3-D space. The instructions given to subjects were like those in 1 and 3 in Experiment 1. It was further required that the movement paths be contained in the fronto-parallel plane about the eye-level. The reason for this requirement was that no strong visual distortion effect such as *horopter* is known to exist within this plane (Indow and Watanabe, 1988). Under instruction 1, subjects generated a significantly upward convex path in the fronto-parallel plane and showed a slight curvature (outward convexity) in the horizontal plane when the 3-D path was projected onto these two planes. On the other hand, under instruction 3, trajectories projected onto the fronto-parallel plane were significantly and markedly straighter than those projected in 1. The same conclusions can be drawn from this experiment as were drawn form the above experiment. Furthermore, because visual distortion was not expected in the fronto-parallel plane the observed movement curvatures in 1 could not be ascribed to visual misperception.

Furthermore, Osu, Uno, Koike and Kawato (1994) conducted Experiment 3 while

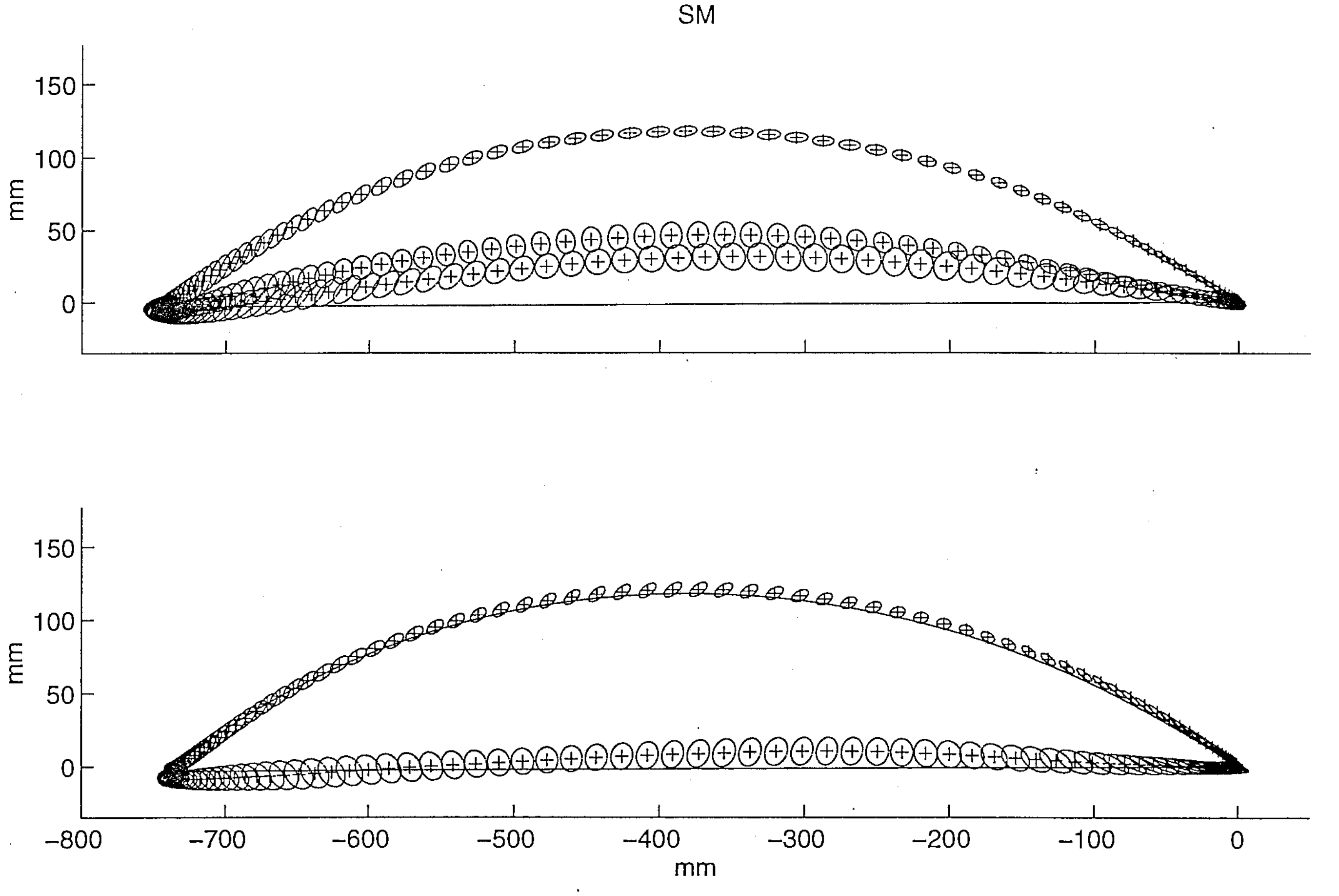

Figure 5: Averaged hand paths and standard deviation under different instructions for one subject. The point (0,0) denotes the initial position of the movements. The cross denotes the average X-Y positions normalized and re-sampled at 80 Hz. The orientation of the long axis of ellipses surrounding crosses denotes the direction of the principal component of the position variation at that time. The radius of ellipses denotes the standard deviation of the position at that time. The solid line in the upper plot denotes a start-to-goal straight line.

recording EMG activities from six related muscles in order to directly evaluate several possible objective functions. They compared various objective functions for the spontaneously curved trajectories made under (1) in Experiment 1, and straight trajectories made under (3) in Experiment 1. The minimum-jerk objective function was lower under condition (3) than it was under condition (1), while the minimum-motor-command-change objective function, which was calculated from EMG using the network of Koike and Kawato (1994), was lower under condition (1) than it was under condition (3). The smaller minimum-jerk objective function for straighter trajectories under (3) strongly rejects the minimum-jerk model without any reservation. Subjects can generate straighter trajectories whose minimum-jerk criterion is lower than it is under (1) if they intend to do so. Thus, if the minimum-jerk criterion is really the objective function which the central nervous system tries to minimize, then at least for the control condition under instruction (1) subjects must by no means generate curved trajectories whose minimum-jerk criterion is higher.

On the other hand, the latter half of the experimental results do not lead to any unequivocal conclusion. If some criterion functions are lower for spontaneously curved trajectories than they are for instructed straighter trajectories, it does not necessarily mean that this is the objective function which the central nervous system tries to minimize. All that can be said is that such an objective function survives the experimental test.

Another source of evidence supporting the major role of link dynamics in observed curvature comes from comparing of curvatures within the horizontal plane (e.g. Fig. 2) and within the vertical plane (Atkeson and Hollerbach, 1985). For movements shown in Fig. 2, only shoulder and elbow extension and flexion were involved. Transverse movements were curved but radial movements were relatively straighter. Atkeson and Hollerbach (1985) also examined movements in which only the elbow and shoulder flexion and extension were involved. They found that up and down movement paths are outwardly convex while fore and aft movement paths are relatively straight. If we rotate the vertical plane 90 degrees around the anterior-posterior axis passing thorough the shoulder joint, it exactly matches the horizontal plane at the shoulder level. This rotation can actually be achieved by 90 degrees shoulder abduction. Then, fore and aft movements in the vertical plane correspond to radial movements in the horizontal plane, and up and down movements in the vertical plane correspond to transverse movements in the horizontal plane. This conceptual yet interesting coincidence of observed curvatures by 90 degrees shoulder abduction makes perfect sense if the curvature difference associated with different paths comes from dynamic interactions between the forearm and upper arm. Here, for this discussion we neglected the effect of gravity on path shapes based on a previous computer simulation (Uno et al., 1989), and additionally adopted the theoretical argument given by Eq. 12 in section 6. Note that the same visual misperception effect was not expected for the up and down movements in the vertical plane and the corresponding 90 degrees rotated transverse movements in the horizontal plane.

4.2 Virtual trajectory control hypothesis

Flash (1987) explained slight curvatures observed in point-to-point paths in front of the body by combining the minimum-jerk-model with the virtual trajectory control hypothesis (Bizzi et al., 1984, Hogan, 1984). That is, the virtual trajectory, and not the real trajectory, was assumed to be planned as the minimum-jerk trajectory. Although the virtual trajectory is straight, the real trajectory is slightly curved because of imperfect control by the virtual trajectory control. However, the stiffness values assumed in Flash's simulation (1987) could be controversial. Bennett et al. (1992), Bennett (1993), Gomi, Koike and Kawato (1992) and Gomi and Kawato (1995) found that dynamic stiffness during movement was much less than was assumed by Flash (1987). Then, based on these measured values of stiffness during movement, Katayama and Kawato (1993) showed that to reproduce roughly straight hand paths the virtual trajectory must be wildly curved. The differences between Flash's and Katayama's simulations can be readily understood if one recalls that the required joint torques are generated as the product of mechanical stiffness and the difference between the virtual and real trajectories under the virtual trajectory control hypothesis. If physical parameters such as the moment of inertia, mass, and link length are given, and the desired hand trajectory is fixed, the required joint torques can be uniquely determined from the inverse dynamics equation. When the stiffness is large, the difference between the virtual and real trajectories is small, but if the stiffness is small, this difference becomes large. Human multi-joint hand paths are roughly straight for point-to-point movements. Consequently, in Flash's simulation where relatively high stiffness was assumed, the virtual trajectory could be close to the real trajectory; that is, it could be a simple straight trajectory. In Katayama's simulation, however, where relatively low stiffness was assumed, the virtual trajectory was very different from the real trajectory and was wildly curved. Conversely, if the virtual trajectory is planned as the minimum-jerk trajectory, real trajectories are overly curved and do not get close enough to the target point if the dynamic stiffness values measured during movement are used (Katayama and Kawato, 1993). Thus, if we consider the low mechanical stiffness values recently measured during movement (Bennett et al., 1992, Gomi, Koike and Kawato, 1992, Gomi and Kawato, 1995), it would seem difficult to reproduce slightly curved hand paths by combining the virtual trajectory control hypothesis with the minimum-jerk model (see Kawato, Gomi, Katayama and Koike, 1993 for review).

Furthermore, Koike and Kawato (1993,1995) provided experimental data which supports the low stiffness values and complicated virtual trajectory shapes using a completely different and independent methodology. They constructed a forward dynamic neural network model which can estimate dynamic joint torques from 10 surface EMG signals by using intensive training based on a vast amount of physiological data collected during multi-joint arm movements as well as posture control. The trained network is very accurate in reproducing the isometric as well as the dynamic torques and also the trajectories. It contains muscle-nonlinear properties such as the length-tension curve and the velocity-tension curve. The network can be readily used to calculate virtual trajectories without any further assumption about the musculo-skeletal system and its controller. The predicted virtual trajectories for slow movements are close to the actual trajectories but those for medium speed movements are considerably different from the actual trajectories. The predicted complicated virtual trajectories are very different from the minimum-jerk trajectory.

There exist at least three different levels of propositions developed under the same name of equilibrium point control hypothesis.

(1) The dynamics of the musculo-skeletal system including spinal reflex loops is characterized by spring like properties. That is, if the supra-spinal motor command is constant during posture control, the state of the above dynamics converges to a stable attractor which is defined as the equilibrium of several nonlinear springs. Even during movement, the positional (elastic) force is dominant in the above dynamics when the acceleration and the velocity are small compared with some positional perturbation.

(2) The motor commands descending from the brain down to the spinal cord are represented as the equilibrium position or some quantity which has direct connection with the equilibrium (e.g. muscle activation threshold lambda).

(3) The virtual trajectory could be straight and having single-peaked velocity in reproducing human multi-joint arm data, thus inverse dynamics problem and/or neural internal models can be avoided.

The third is the most radical proposition while the first seems trivially true if we consider only musculo-skeletal system without neural feedback loops.

Our previous studies seriously questioned the third-level proposition. On the other hand, I am not against the second-level proposition. I am neutral about the second level because I think that we do not have any good experimental data which prove or disprove any representational model at the second level. Many experimental data which support only the first level were referred as if supporting the second or the third level. I think the first-level proposition is true and is very important advancement of our understanding of motor control.

Many articles have been written about the equilibrium control hypothesis while emphasizing its computational advantage (namely level (3)) in the past 10 years. I think still many of motor control researchers believe in (3) (for example several papers in Journal of Motor Behavior special issue in 1993) with or without knowing recent criticism by us described above.

5 Altered Visual Environments

5.1 Logic underlying kinematic transformation test

As shown in Table 1, trajectories generated in altered visual environments can be used to discriminate between the unidirectional and bi-directional theories. An undergraduate student supervised by Uno at the University of Tokyo (1989) used nonlinear coordinate transformation between the hand position on a two-dimensional position digitizer and on the CRT coordinates where the end point, the starting point, and the hand position are displayed. Because of the nonlinear transformation, a straight line on the CRT corresponds to a curved line on the digitizer, and *vice versa*. Here, subjects generated roughly straight hand paths on the digitizer (i.e., curved paths on the CRT), conforming to the minimum torque-change trajectories. This study was cited in page 844 of Kawato (1992).

Let me explain in more detail how these interpretations are drawn from the two theories. Let $X = (x, y)$, $P = (p, q)$ and $\Theta = (\theta_1, \theta_2, \cdots, \theta_m)$ denote the hand position on the CRT, the hand position on a board or a table, and the joint angles of the arm, respectively. Here, m is the number of joints related to the arm movements which are being considered. Generally, functional relationships exist between the three coordinates as follows:

$$\begin{aligned} X &= f(P), \\ P &= g(\Theta). \end{aligned} \tag{5}$$

In usual cases of experimentation or the use of a computer mouse to move a cursor on a CRT, the first equation becomes very simple, and is just a magnification or contraction if the origins of the CRT plane and the hand plane are appropriately chosen:

$$X = \lambda P. \tag{6}$$

Here, λ is a positive scalar. We are interested in the case where f is a nonlinear function which causes a straight path on a CRT to become curved on the hand plane and *vice versa*. Let us assume that the subjects learned this nonlinear mapping from repeated trials of point-to-point movement on a CRT screen where the starting point X_S, the target point X_T as well as the hand cursor $X = f(P) = f\{g(\Theta)\}$ are presented.

Let us assume first as per the unidirectional theory that subjects plan their trajectories in the task-oriented visual coordinates, in this case on the CRT screen. Given this assumption, a straight trajectory should be observed connecting the starting and target points $X(t) = \phi(t)(X_T - X_S) + X_S$ on the CRT screen. Here, $\phi(t)$ is a scalar function of time t which is zero at $t = 0$ and 1 at $t = t_{end}$. The corresponding trajectory on the hand plane can be obtained using the inverse of f as follows:

$$P(t) = f^{-1}\{\phi(t)(X_T - X_S) + X_S\}. \tag{7}$$

This path in the hand space is curved since the inverse of nonlinear function f distorts the straight line into a curve.

Next, as per the bi-directional theory, let us assume that the trajectory is planned in the intrinsic body space such as the joint torques, muscle tensions or the motor commands. It must be emphasized that not only the internal model of the inverse mapping f^{-1}, but also the internal model of the forward mapping f are essential for calculation of the optimal trajectory in the intrinsic space (see Fig. 1), especially when f is a many to one mapping as usual. This is because it is necessary to use the forward model of nonlinear transformation to predict the trajectory and its end point on the CRT screen from tentative motor commands and adaptively modify them. This is in sharp contrast to the unidirectional theory where inverse mapping only is sufficient. This is another example of where only downward information flows are necessary in the unidirectional theory and both downward (inverse model) and upward (forward model) information flows are necessary in the bi-directional theory. If two kinds of internal models are acquired through training, trajectory planning and control can be done in a very simple manner. The starting and target points on the CRT screen are first transformed into the corresponding starting and target points on the hand plane by the inverse mapping model:

$$\begin{aligned} P_S &= f^{-1}(X_S), \\ P_T &= f^{-1}(X_T). \end{aligned} \tag{8}$$

Then using these intermediate representations in the hand space, calculation and control of the optimal trajectory can be done in exactly the same manner as it is done under the normal condition where CRT does not exist and the two points P_S and P_T are given directly on the hand plane. If the two points are in front of the body, it is known that dynamic optimization models predict roughly straight hand paths in the hand plane:

$$P(t) \simeq \gamma(t)(P_T - P_S) + P_S. \tag{9}$$

Here, $\gamma(t)$ is a scalar function of time t which is zero at $t = 0$ and 1 at $t = t_{end}$. The corresponding trajectory on the CRT screen can be obtained using f as follows:

$$X(t) \simeq f\{\gamma(t)(P_T - P_S) + P_S\}. \tag{10}$$

Thus, the path on the CRT plane is markedly curved while the path on the hand plane is roughly straight. The above computational procedure is described as if in the brain information flows only downward between the CRT screen level and the hand plane level, and the rest of the calculation is done solely below the hand plane representation. This probably does not happen in the brain and it is believed that the forward internal model of f is continuously used for trajectory planning and control. The above explanation is simply meant to show that the planned paths are roughly straight on the hand plane.

5.2 Adaptation in altered visual environments

Wolpert, Ghahramani and Jordan (1993) followed the experimental design of Uno (1989) and used only a part of the above logic. They examined shapes of paths only in the hand plane and never examined them in the extrinsic space. This partial data analysis seems to be one of the reasons for their biased conclusion. Their experimental paradigm is very close to Uno's but different in several important aspects. First, although they also used a digitizing tablet to measure the hand position, they used an LCD projector to present the finger positions as virtual images on the plane of the digitizing tablet instead of using a simple CRT screen. Second, the magnitude of visual distortion started at zero (no perturbation) and was increased linearly from movement 20 to reach a maximum of 4 cm at movement 40 at which point it was held constant for the remaining 60 movements. In

Uno's experiment, nonlinear coordinate transformation was given from the beginning of the experiment and the subjects knew of its existence.

In Experiment 1, when they increased the perceived curvature of normally straight sagittal movements by 40 mm, subjects showed significant ($p < 0.001$) corrective adaptation in the curvature of their actual hand movement with an average magnitude of adaptation of 10 mm. In Experiment 2, increasing the curvature of the normally curved transverse movements by 40 mm produced a significant ($p < 0.01$) corrective adaptation with a magnitude of 7 mm. Here, the hand movement became straighter, thereby reducing the visually perceived curvature. In Experiment 3, when the curvature of naturally curved transverse movements was reduced by about 12 mm there was no significant adaptation ($p > 0.05$), with less than 2 mm of change.

Only 25 %, 17 % and -2 % of the imposed distortion of curvature was compensated for by adaptation of subjects in Experiment 1, 2 and 3, respectively. As described above and also in Table 1, the unidirectional theory (e.g., the minimum-jerk model) predicts 100 % adaptation in the hand space for all these experiments so that no (0 %) change is observed on the LCD screen. On the other hand, the bi-directional theory (e.g., the minimum-torque-change model) predicts 0 % adaptation resulting in no change in the hand space and 100 % change on the LCD screen. Experimental data shows 25 %, 17 % and -2 % adaptation in the hand space and hence 75 %, 83 % and 102 % change on the LCD screen. Is it not therefore reasonable to say that this result is close to the prediction of the bi-directional theory? Should it be concluded that both theories are wrong because both predictions (100 % and 0 % or 0 % and 100 %) are different from the experimental data? Or, should it be concluded that the truth is in between the two theories with a score of 4 to 1 (Experiment 1), 5 to 1 (Experiment 2) or ∞ to -2 (Experiment 3) in favor of the bi-directional theory over the unidirectional theory? To say the very least we were very surprised by the following conclusion drawn by them: "The results of the curvature-increasing study suggest that trajectories are planned in extrinsic visual space and the results of the curvature-reducing study suggest that the desired trajectory is indeed straight in visual space. These results are incompatible with models such as minimum-torque-change and suggest a critical role for visual perception in trajectory formation". To be fair they might also have said that these results are more significantly incompatible with models such as minimum-jerk and suggest a quantitatively more critical role for internal variables such as muscle tension in trajectory formation. Because the manuscript contains no data for trajectories seen on the LCD screen where curvature was much more marked than it was on the hand plane, it misleads readers.

Besides how to interpret their data with regards to discriminating between the two theories, we are also very much interested in the cause of the observed small adaptations in Experiments 1 and 2. We believe that Experiment 3 supports the bi-directional theory and disproves the unidirectional theory unequivocally. For Experiments 1 and 2, the authors interpreted the adaptation as being partial because the number of movements was only 60. This implies that as subjects experienced more movements, adaptation increased from 25 % to 100 %. We interpreted the partial adaptation in the completely opposite way. Because the subjects could not experience enough trials, they could not acquire the internal forward model of the nonlinear transformation. As a result, they could not use the bi-directional scheme, and were forced to rely on some *ad hoc* strategy where partial adaptation was observed. For example, it would be interesting to know how much subjects feel obliged to conserve the usual straightness of hand paths on the screen in the absence of information about what happens when they do this. In other words, how much of the straightness of the path is implicitly included in the task instruction? We predict that if subjects experience a sufficient number of trials, the adaptation or disturbance in our interpretation would be reduced from 25 % to 0 %.

5.3 Intensive training experiment under kinematic transformation

Uno, Imamizu and Kawato (1994) conducted a new experiment which was an extension of the previous experiments of Uno (1989). Subjects moved their right hands (shoulder and elbow) at the level of the shoulder. Their wrists were secured by a cuff. The hand, elbow and shoulder positions were measured with the OPTOTRAK position measurement system. Then, the shoulder joint angle θ_1 and the elbow joint angle θ_2 were calculated from these data. Direct vision of the hand was not allowed, and the hand cursor, the starting point and the target point were presented on a 33 inch CRT located vertically in front of the subject. Here, a simple linear transformation in joint angles was introduced which actually corresponds to a strongly nonlinear transformation between the hand plane and the CRT screen. Let $X = (x, y)$ and $P = (p, q)$ denote the hand cursor position on the CRT screen and the hand position on a table at the shoulder level as in Equation 5. Then, the nonlinear coordinate transformation from the measured joint angles to the CRT screen is given as follows:

$$
\begin{aligned}
\theta_1^* &= a(\theta_1 - \theta_1^0) + \theta_1^0, \\
\theta_2^* &= b(\theta_2 - \theta_2^0) + \theta_2^0, \\
P &= g(\theta_1, \theta_2), \\
X &= g(\theta_1^*, \theta_2^*), \\
X &= f(P).
\end{aligned} \tag{11}
$$

It is important to note that the nonlinear transformation f is actually determined by the first four equations. Although the transformation in the body coordinates which is defined by the first two equations gives a simple reduction or magnification of joint angles around a fixed point (θ_1^0, θ_2^0), its corresponding transformation f is highly nonlinear with only one fixed point $g(\theta_1^0, \theta_2^0)$. In previous studies by Uno (1989) and Wolpert, Ghahramani and Jordan (1993) the positions of the starting and end points were invariant under the imposed transformation. Thus, in these previous studies, subjects could execute a reaching task even when they did not change their motor commands at all. We wanted to change this so that subjects had to learn inverse and forward internal models of imposed transformation to successfully execute the task. The introduced transformation satisfies this requirement.

The subjects were told about the nature of transformation. The instruction given to them was to achieve a target within a fixed duration signaled by two beeps. It was also stated that no requirement was imposed on path shape either on the CRT screen or on the hand plane. Four experiments were conducted for more than 10 subjects altogether. In Experiment 1, each subject learned to execute the transverse movements with two directions and the sagittal movements with two directions (four altogether). In Experiment 2, each subject learned to execute only the transverse movements with two directions. In Experiment 3, each subject learned to execute only the saggital movements with two directions. Only in Experiment 4 were the subjects not told about nonlinear transformation, and during the course of the experiment, the strength of distortion was increased incrementally. That is, a and b were slowly changed from 1.

Each subject experienced each kind of movement for 320 times which was more than in Wolpert, Ghahramani and Jordan (1993). At the end of the experiment, two kinds of control experiments were done. In the first one, each subject was asked to move their hand from the same starting X_S and end points X_T in the training session but with no distortion of joint angles. Here, f becomes an identity. Let X_{CRT} denote the trajectory on the CRT obtained in this first control experiment and $P_{CRT} = f^{-1}(X_{CRT})$ denote its imaginary corresponding trajectory in the hand space, assuming that nonlinear transformation rather than actual identity mapping between the CRT and the hand plane still exists. In the second control experiment, subjects were able to watch their hands directly, and the starting and end points were given directly on the table on which the hand actually moved around. These points were determined by mapping f inversely to the points on the CRT screen: $P_S = f^{-1}(X_S)$ and $P_T = f^{-1}(X_T)$. Let P_{hand} denote the trajectory in the hand space obtained in this second control experiment, and $X_{hand} = f(P_{hand})$ denote its imaginary corresponding trajectory on the CRT, assuming that the CRT and nonlinear transformation still exist in this second control experiment. Similarly, let X_{alt} denote the trajectory on the CRT obtained in the final session of the main training experiment, and $P_{alt} = f^{-1}(X_{alt})$ denote its corresponding trajectory in the hand space.

As apparent from the discussion in Section 5.1, if the unidirectional theory is correct : $X_{alt} = X_{CRT}$, $P_{alt} = P_{CRT}$, $X_{alt} \neq X_{hand}$, $P_{alt} \neq P_{hand}$ is observed. On the other hand, if the bi-directional theory is correct,

$X_{alt} \neq X_{CRT}$, $P_{alt} \neq P_{CRT}$, $X_{alt} = X_{hand}$, $P_{alt} = P_{hand}$ would be expected to be observed.

Throughout Experiments 1 to 4, for almost all cases with only a few exceptions, the latter case was observed with significant statistical differences from the former case. Actually there was no single case where the former prediction was validated. Furthermore, the exceptions were observed only when the subject could not attain end-point accuracy even after 320 training trials. Even in that case, the exhibited trajectories did not agree closely with the above former perdition of the unidirectional theory. Our conclusion is that the unidirectional theory is disproved by these carefully controlled kinematic transformation experiments. The experimental data are compatible with the predictions of the bi-directional theory in that subjects who accurately learned the imposed transformation.

It is important to emphasize that one must carefully prepare the experimental paradigm so that subjects can learn imposed visual transformation or artificial force field if one wants to make a fair comparison of the two theories using such altered environments. This is because no algorithm or hardware in the framework of the bi-directional theory can work if either the inverse or forward internal models of kinematic and dynamic transformation is not acquired. In this context, it is interesting to note that the frequency of insufficient learning and violation of predictions of the bi-directional theory was highest in Experiment 4 for all of the conditions. Experiment 4 is closest in its design to Wolpert, Ghahramani and Jordan (1993) and tends to prevent subjects from acquiring internal models.

Although the conclusions drawn from the above two studies were opposite, the two sets of experimental data were not that different. However, it should be emphasized that in Uno, Imamizu and Kawato (1994), (1) the training session was longer, (2) subjects were informed of the existence and characteristics of transformation, (3) subjects could not attain the goal unless they acquired the internal model of the transformation (subjects could not achieve the task with the same motor command as that used under the no transformation condition), (4) the location of the CRT screen was different from that of the hand position, (5) the transformation was turned on at full strength from the beginning of the training session except in Experiment 4, and finally but probably most importantly (6) the transformation was very simple at body coordinates and was relatively easily learned. All these differences helped and encouraged the subjects to acquire internal models of the imposed transformation. I understand that researchers use altered kinematic or dynamic environments to elucidate the mode of computation employed by the brain in the normal environment by examining how such computation is adapted to the new environment. The bi-directional theory requires that the central nervous system possess both forward and inverse internal models of kinematics and dynamics of the normal environment. Consequently, in order to fairly compare predictions of the two theories which are supposed to be operating in daily life by using the novel kinematic or dynamic environments, it is critical to provide sufficient information so that subjects can acquire internal models of the imposed environments.

6 Force-Field Adaptation

As described in Table 1 and in Section 3.2, trajectories under externally applied force fields can be used to discriminate between the uni-directional and bi-directional theory. The underlying logic is very simple. Because the kinematic optimization principle defined in extrinsic space does not take account of any dynamic effect of the external force field, the desired trajectory in that situation is exactly the same as it is under the normal condition. Thus, once the controller regains its capability to achieve the optimal trajectory after a short period of adaptation, the central nervous system achieves exactly the same shapes of trajectories as it did under the control condition without the force field. On the other hand, the dynamic optimization principle defined in intrinsic space takes account of the new dynamic environment imposed by the external force field. Thus it recalculates a different optimal trajectory from that calculated without the force field, once the central nervous system acquires the internal model of both the forward and inverse dynamics of the arm in combination with the environment. Thus, after a relatively longer duration of adaptation, different trajectories than the control trajectories are predicted. Although this logic underlying the force-field adaptation experiment is simple, it turns out that the practical design of proper experimental conditions actually needs careful consideration.

As briefly described in section 3.2, Uno, Kawato and Suzuki (1989) first used this paradigm to support the dynamic optimization principle. They used a strong rubber band attached to the subject's hand to induce an elastic force field. After about 50 trials, subjects produced significantly curved paths with asymmetrical speed profiles which were in good agreement with the prediction made by the minimum-torque-change model. Although we did not fully realize it at that time, this experimental paradigm satisfied two important prerequisites of the force field adaptation experiment which were necessary to test the two theories on fair ground. (1) The force field must be strong enough and sharply variable along a generated trajectory to induce large effects on optimal trajectory shapes which can be detected even in the presence of experimental variations. (2) The experimental setting must allow subjects to learn both the forward and inverse dynamics model of the arm under the external force field. In order to satisfy the second condition, first of all, the number of training trials must be sufficiently large. Second, it is probably better for subjects to directly see the mechanical apparatus that induces external force fields and to understand its actions and nature. Third, it is also helpful to inform subjects about the characteristics of the force field as well as its existence. Finally, if subjects have had previous experience with similar force fields, their experience should greatly facilitate the acquisition of internal models.

Unfortunately, these prerequisites were not satisfied in the experimental examinations of force fields by Flash and Gurevich (1991) and Shadmehr and Mussa-Ivaldi (1993). Both of them reported failure to observe significant changes in trajectory shapes in the force field. Uno and Kawato (1994) simulated the minimum-torque-change trajectory based on the numerical values of force field of Shadmehr and Mussa-Ivaldi (1993) and found that optimal trajectories under their force field are only slightly different from those without the force field. Thus, in experiments, it should be difficult to find any significant difference. In simulation, we succeeded in reproducing large distortions of the trajectories after the first exposure to the force field. Thus, our simulation result that the optimal trajectory is not so much affected although the first exposed trajectory is very much affected is quite counter intuitive. This is because of the combined effects of relatively small forces (0 to 6 N), the small movement distance of 10 cm, and most importantly a quasi-uniform force field along a single trajectory, which is peculiar to the used viscous force field. Details of this simulation study will be presented elsewhere.

It must be noted that any uniform force field, even if it is very strong, has no influence on the optimal trajectory of the minimum-motor-command change model because the time derivative of such a uniform field vanishes in the criterion as shown below.

$$C_M = 1/2 \int_0^{t_f} \sum_{i=1}^{n} \left(\frac{dM_i^{Comp}}{dt}\right)^2 dt$$

$$= 1/2 \int_0^{t_f} \sum_{i=1}^{n} (\frac{dM_i^{WO}}{dt} + \frac{dM_i^{Unif}}{dt})^2 dt$$
$$= 1/2 \int_0^{t_f} \sum_{i=1}^{n} (\frac{dM_i^{WO}}{dt})^2 dt, \qquad (12)$$

where M_i^{Comp} is the total motor command necessary for compensating the arm inherent dynamics and canceling the imposed force field. M_i^{WO} is the motor command in the normal condition without the force field. M_i^{Unif} is the motor command that compensates the applied uniform force field. It might be quite large but its time derivative vanishes.

The necessity of internal models for making fair comparisons was discussed at some length in the previous section, thus it will not be repeated here. However, it is very helpful to discriminate between inverse models and forward models to fully understand the nature of both the bi-directional theory and computations in the brain. For reaching under the force field, the most important objective of the task is to reach the target. The shape of the path is of secondary priority. The first objective of reaching the target can be achieved in a feedforward manner only if the inverse dynamics model is acquired, even though the forward dynamics model is not acquired. Calculation of the optimal trajectory, however, necessitates acquiring both models. Thus, in general, three phases of adaptation to the external force field under the bi-directional theory are anticipated. (1) In the first phase, neither the inverse dynamics model nor the forward dynamics model is acquired for the suddenly applied external force field. In this case, reaching the target can not be achieved solely by using feedforward control and large errors are observed at the end of the ballistic control phase. (2) In the second phase, the inverse dynamics model is acquired but the forward model is still not acquired. There is no strong prediction for the desired trajectory planned for this phase, but it is reasonable to assume that the same trajectory as is used under the normal condition is similarly used. For, in the absence of the forward model, the optimal trajectory under the force field can not be calculated. Thus, a similar trajectory should be observed in this second phase. (3) Finally, when both models are acquired, the optimal trajectory and thus the similar realized trajectory is different from what it is under the normal condition. Here, it is assumed that learning the forward model is more difficult and occurs after the learning of the inverse model, without experimental support. Our experiences in neural network training and vague philosophical reasoning about the ontogeny and phylogeny of the two kinds of internal models are behind this assumption. It is interesting to see that this assumption is opposite to that underlying the forward-inverse modeling approach of Jordan and Rumelhart (1992).

Regarding the discrepancy between Flash and Gurevich (1991) and Uno et al. (1989), possible reasons for the failure to detect significant changes in the former study might be (1) the fixed point of the spring was much too far from the trajectory and so the force direction did not sufficiently change (again quasi-uniform force field), (2) the force magnitude was not large enough, and/or (3) the training number of less than 15 was not large enough for acquisition of internal forward models.

In order to clarify various factors which affect the easiness of acquiring internal models, we will soon repeat our previous force-field adaptation experiments using a most advanced parallel-link, direct-drive , air-floating manipulator, which was specially designed for reliable measurement of dynamic impedance during multi-joint arm movements. If it is possible to demonstrate the three adaptation phases predicted above by the bi-directional theory, this could be the first indication of strong support for participation of the forward model in planning the dynamically optimum trajectory.

7 Discussion

The paper contrasted the two theories while referring to new experimental and simulation results. Computational neuroscience of visuo-motor coordination appears to be moving into a really exciting and productive period of advancement. There are now two contrasting theories from which concrete predictions can be made which can be tested by experiments. Several groups of researchers have started to examine these predictions to find more appropriate computational models. At present, it looks like it will be possible to objectively and fairly examine the two theories if careful experimental design and reliable computer simulations are prepared. Construction and destruction of theories based on the accumulation of critical experimental data is the correct and preferable way for hard science to advance. I believe that we are currently working in a happy period of computational neuroscience. Probably, the only caution to researchers involved in this dispute is to pay maximum efforts and care to making arguments, mathematical theories, experimental data and computer simulation results as transparent as possible so that outsiders to this dispute do not lose their interest in this most interesting, profound and popular topic.

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