CHAPTER 17

The Organization of Human Arm Trajectory Control

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17.1 Introduction

Traditionally, studies of human and animal movements have focused on systems composed of a single muscle, or a single joint. However, most natural human actions such as reaching, walking, writing, etc., require coordination among a large number of muscles and joints. Although the excess degrees of freedom problem, also known as Bernstein's problem (Bernstein, 1967), arises even in the context of single-joint movements, it becomes especially complicated to resolve in the multi-joint case.

In the strict kinematic sense, degrees of freedom are "the least number of independent coordinates required to specify the position of the system elements without violating any kinematic constraints" (Saltzman, 1979). To describe the location and orientation of the hand in space, six independent coordinates are required. However, to uniquely characterize the configuration of the upper arm, at least seven coordinates are necessary. Given the kinematic redundancy of the human arm, the inverse kinematics problem, i.e., finding what joint angles correspond to a given hand location and orientation in space, does not have a unique solution. This is but one example of a large number of ill-posed problems that arise in the control of arm posture and movement. A problem is well-posed when a solution exists, is unique, and depends continuously on the input information (Tikhonov and Arsenin, 1977). Ill-posed problems fail to satisfy one or more of these criteria. Most motor problems are ill-posed in the sense that the kinematic solution to the problem is not unique. Since most limb segments are operated upon by a much larger number of muscles than are strictly necessary from mechanical considerations, the problem of torque distribution among redundant muscles in another example of an ill-posed problem.

A third and perhaps more fundamental ill-posed problem arises at the task level. Any behavioral goal can be acheived in many different ways. Thus, for example, a cup of coffee might be reached while moving the hand along many different paths. Likewise, in drawing an ellipse, or writing the letter *z*, we may generate the same geometrical form, while using each time a totally different law of motion for the time course of pen position along the path. Again, how does the brain determine in what way to perform a given motor task in order to achieve the desired behavioral goals?

The excess degrees of freedom problem, therefore, poses a real challenge to any motor control theory. How does the motor system select specific solutions to any of these ill-posed problems? How does the system manage to handle the large number of controlled parameters available at all levels of sensorimotor representation? The two solutions that were offered to this problem were: ***a)*** the motor system is hierarchically organized; ***b)*** the system makes use of coordinative constraints.

Instead of trying to directly bridge the gap between the behavioral goals of any motor act and the neural input to muscles needed to achieve this goal, this gap is progressively narrowed down by using a hierarchy of motor control levels (Bernstein, 1967; Gelfand et al., 1971; Saltzman, 1979). Higher levels translate the motor problem

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into terms that are more suitable for the lower level to handle, all the way down to the muscles. Associated with this idea is the concept of internal representations of motor actions (e.g., Bernstein, 1967; Saltzman, 1979; Keele, 1981). Many papers dealing with the problem of motor organization have stressed the need to distinguish between long-term and short-term, or working representation of action (for a review see Saltzman, 1979). While the working plan was postulated to be quite specific and to depend on the current task demands and the current state of the musculoskeletal system and of the environment, the long-term representation was postulated to be more abstract and to relate to the general features of any motor action. Two considerations led to this hypothesis. One is the limitation on the memory storage capacity of the system. The other is derived from the similarities that exist between the characteristics of movements produced by different effectors (e.g., handwriting produced by wrist and finger movements or by upper limb movements while writing on a blackboard). Since it would have been extremely inefficient for the system to store all possible variations of any single movement, it was argued that there should exist more abstract and general representations of movement. The actual performance of every motor act was therefore claimed to incorporate both abstract information derived from long-term memory, and particular information about the current task demands and the physical state of the environment and of the musculoskeletal system.

It was also argued that in order to simplify motor control, it is essential to reduce the number of controlled parameters and the amount of information needed to be analyzed in the performance of any motor act (Gelfand et al., 1971). Coordinative constraints, or the so-called basic motion synergies, were claimed to play an important role in establishing such working conditions for the higher motor levels. Gelfand et al. (1971) have defined synergies as "those classes of movements that have similar kinematic characteristics, coinciding active muscle groups and conducting types of afferentation." Such synergies, then, form the basic alphabet from which more complicated motor acts can be generated.

This chapter focuses on the organizing principles that underlie the generation of multi-joint arm movements. In discussing these principles, we will refer to the view that the motor system is hierarchically organized by addressing the question of what possible aspects of movement generation are dealt with at the various levels of sensorimotor representation. Section 17.2 deals with the topic of trajectory planning and reviews evidence from behavioral and modelling studies which supports the notion that higher levels deal with more abstract aspects of movement generation. In particular, a theory of motor coordination which offers a solution to the task-level redundancy problem is presented. Section 17.3 deals with the problem of motor execution. It focusses on the role played by the mechanical properties of muscles in simplifying the motor control problems arising in multi-joint posture and movement. This section also summarizes evidence in support of the view that arm trajectory control is a step-by-step process, whereby higher levels deal with motion planning while lower levels deal with the more concrete aspects of motor execution. Section 17.4 deals with possible strategies for trajectory modification. An experimentally confirmed model is presented which suggests that the modification of aimed arm movements in response to sudden changes in target location might involve the superposition of basic trajectory primitives. Next, the principles discussed in the former sections are summarized and an integrative view of arm movement organization is presented. Finally, we conclude by discussing several recommendations for future research directions.

17.2 Trajectory Planning

In recent years, the planning and control of multi-joint movements in general, and arm movements in particular, has attracted the attention of an increasingly large number of studies. The objective of many of these studies was to identify common kinematic features or sterotyped patterns of muscle activations which characterize intact motor behavior, and based on these observations to form new ideas and hypotheses about movement organization.

Motor behavior is fundamentally multi-dimensional. Hence, movements can be alternatively represented at the muscle, joint or task levels. This raises the two following fundamental questions: In what space(s) or coordinate frame(s) does the brain represent movement?

What rules govern the selection of specific trajectories among the infinite number of possible ones? One effective way to investigate these issues is to experimentally observe human movements. By looking for patterns of invariance in the observed behavior, certain hypotheses concerning the underlying organizing principles can be formulated leading to quantitative and testable theories of motor control. In this context, distinguishing between movement path and trajectory may provide a better understanding of the problems involved in multi-joint movement generation. ***Path*** is defined as the geometrical curve that the hand follows in space, while the term ***trajectory*** refers also to the velocity of movement along the path.

Based on experimental observations, several investigators (e.g., Soechting and Lacquaniti, 1981; Hollerbach and Atkeson, 1987; Flanagan and Ostry, 1990) have suggested that trajectories are planned in joint variables while others have argued that simplicity of motor control (at least for higher-level *CNS* planning) is achieved by planning hand trajectories in extracorporeal space; joint rotations are then tailored to produce the desired hand movements (Bernstein, 1967). This view gained support from several behavioral and neurophysiological studies of human and monkey reaching movements (Abend et al., 1982; Georgopoulos et al., 1981; Morasso, 1981; Flash and Hogan, 1985; Georgopoulos, 1986). When moving the hand between pairs of targets in the horizontal plane, subjects tended to generate roughly straight hand paths with single-peaked, bell-shaped speed profiles; this behavior was independent of the part of the work-space in which the reaching movement was performed. Because these common invariant features were only evident in the extracorporeal coordinates of the hand and not in the movements of individual limb segments, these results provided strong indication that planning takes place in terms of hand motion through external space and not in terms of joint rotations (Morasso, 1981).

This conclusion was also generalized to more complex movements, where kinematic invariances were again only present in the hand and not in joint movements. When subjects were instructed to generate curved, or obstacle-avoidance movements, the single-peaked velocity profiles were not preserved. Although the hand paths appeared smooth, movement curvature was not uniform and the trajectories displayed two or more curvature maxima. The hand velocity profiles also had two or more peaks and the minima between adjacent velocity peaks temporally corresponded to the maxima in curvature (Abend et al., 1982). To account for the observed kinematic featuress of straight and curved hand trajectories a mathematical model of the organization of voluntary arm movements was formulated (Flash and Hogan, 1985). This model, which was based on dynamic optimization theory, enabled us to describe an assumed goal of this class of movements, by a relatively simple formula, and to derive from that formula detailed predictions of the kinematics of a large number of specific motions.

17.2.1 The Maximum-Smoothness Theory for Arm Movements

Natural movements are characteristically smooth and graceful. This observation can be expressed by a mathematically concise model of motor coordination by postulating that voluntary movements are made, at least in the absence of any other overriding concerns (such as the minimization of movement duration), to be as smooth as possible under the circumstances. Mean squared magnitude of hand jerk (rate of change of hand acceleration, or equivalently, the third derivative of position) integrated over movement time was used as a measure of smoothness (Hogan, 1984; Flash and Hogan, 1985). Using dynamic optimization theory, the unique trajectory (among the infinite number of possible ones) that minimizes this performance measure was determined. More precisely, the smoothest motion is acheived by the trajectory that minimizes the following objective function:

$$C_T = \frac{1}{2}\int_0^{t_f} \left(\frac{d^3 \boldsymbol{r}}{dt^3} \right)^2 dt \qquad (17.1)$$

where $\boldsymbol{r}(t)$ is the vector of hand position and t_f is the movement duration. Based on this definition the actual movement had to be worked out, its details depending on the conditions assumed at the beginning and end of the movement.

The above model has been initially derived for single-joint movements (Hogan, 1984) but most natural movements are multi-dimensional, i.e. they involve simultaneous rotations about several joints. In extending the maximum smoothness principle to the multi-joint case, however, a crucial question is what coordinates should be used in order to define the above measure of smoothness. For example, the vector **r** may relate to the position coordinates of the hand in space, or to the angular coordinates of the different joints (e.g., shoulder and elbow). A basic postulate of this theory is that the objective of motor coordination should be expressed in the coordinate system in which movement planning is assumed to occur. Since, as discussed above, experimental observations have indicated that arm movements are planned in terms of hand trajectories, the vector **r** was chosen to be expressed in terms of the Cartesian coordinates of the hand. The minimization of this cost resulted in analytic expressions for the description of both point-to-point and curved trajectories. For point-to-point movements, starting and ending at rest, the expressions derived for the description of $x(t)$ and $y(t)$, the hand position coordinates were:

$$x(t) = x_o + (x_f - x_o)\,(6(t/t_f)^5 - 15(t/t_f)^4 + 10(t/t_f)^3 \quad (17.2)$$

$$y(t) = y_o + (y_f - y_o)\,(6(t/t_f)^5 - 15(t/t_f)^4 + 10(t/t_f)^3$$

where (x_o,y_o), (x_f,y_f) are, respectively, the initial and final hand positions, t is the time and t_f is the movement duration.

These predicted movements were shown to have the following characteristics:

1) The trajectories of the hand follow straight paths.

2) The velocity profile for moving along that path is smooth and unimodal.

3) The shape of the trajectory is invariant under translation, rotation, amplitude, and speed scaling.

Experimental studies of planar horizontal arm movements have shown that these predictions agree quite well with the experimental observations. Figure 17.1 shows theoretical predictions and experimental observations for two typical point-to-point movements.

Several studies indeed have reported that during point-to-point motions the path of the hand through extrapersonal space is essentially straight and the velocity profile is basically bell-shaped independently of end-point locations (Morasso, 1981; Flash and Hogan, 1985), thus satisfying the prediction that the trajectory is invariant under translation and rotation. It is both true for large and small movements and for movements at different speeds, thus, satisfying the predictions that the trajectories are invariant under amplitude and speed scaling.

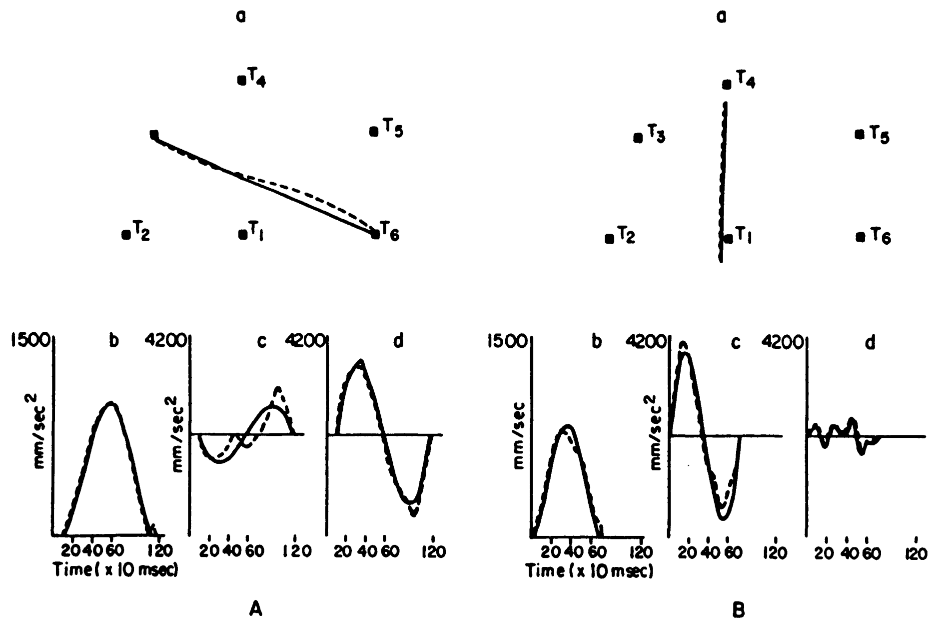

Figure 17.1: Overlapped predicted (solid lines) and measured (dashed lines) hand paths (a), speeds (b) and acceleration components along the y-axis (c) and along the x-axis (d) for two point-to-point movements. (From Flash and Hogan, 1985; reproduced with permission.)

To account for the kinematic features of curved movements, again the maximum smoothness model was applied assuming that curved motions are generated by specifying a small number of accuracy ("via") points along the trajectory. The hand is then required to pass through these points on its way between the initial and final positions. The time at which the hand passes through these points, or the velocity at that time, need not be *a priori* specified. These are predictions of the model. As before, limb motion was expressed in terms of hand coordinates. Taking the simplest case of one via point between the initial and final positions, the theory yielded explicit mathematical expressions for the description of curved motions (see in Flash and Hogan, 1985) as well as the following predictions:

1) The hand velocity profile exhibits two peaks with a valley between them.

2) The depth of this valley increases with the lateral deviation of the via point from the straight line joining the initial and final positions.

3) The hand path exhibits a single curvature peak.

4) The peak in curvature temporally coincides with the valley in tangential velocity.

5) The shape of the trajectory is invariant under translation, rotation amplitude and time scaling.

6) The durations of the motions from the initial position to the via point, and from the via point to the final position are almost always equal, except for cases in which the via point is located very close to either one of the movement end-points. This behavior will be referred to below as the ***isochrony principle*** (Viviani and Terzuolo, 1982).

Each of these predictions was corroborated by observation. Figure 17.2 compares between theoretical predictions and experimental observations for two typical curved movements. Peak in curvature, valleys in velocity profiles, and the time coincidence between them were reported both for curved and obstacle–avoidance movements (Abend et al., 1982) and for handwriting (Viviani and Terzuolo, 1980; Edelman and Flash, 1987). Likewise, for drawing movements it was observed that the same law of motion applies whether the movements are large or small, slow or fast (for a review see Lacquaniti, 1989). The additional prediction corroborated by experimental data is the isochrony principle, namely, the phenomenon that within a given trajectory, movement durations for large and small segments are roughly equal.

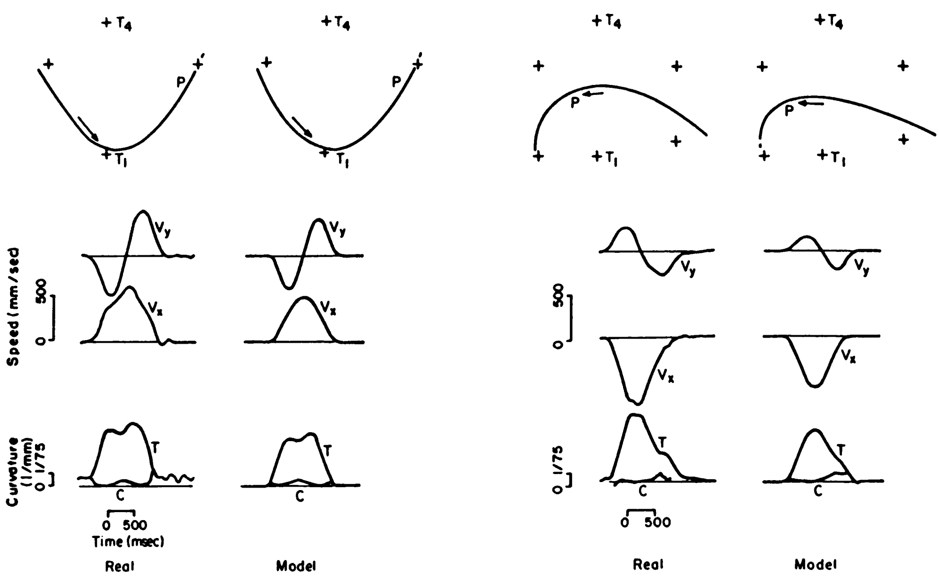

Figure 17.2: Two examples of measured (real, left columns) and predicted (model, right columns) curved trajectories. Displayed are the hand paths, *P*, and plots of hand speed, *T*, curvature, *C* and velocity components, V_x and V_y, versus time. (Reproduced with permission from Flash and Hogan, 1985.)

Since this theory was based on the hypothesis that arm movements are planned or coordinated based on hand motions in external space, the success of this theory in accounting for the observed behavior provided further support for this hypothesis. How does this view agree with other observations of arm movements? It has been reported that in straight pointing movements performed in the vertical plane the ratio between joint velocities approaches a constant value towards the end of the movement. This finding served as an argument in favour of the idea that arm movements are planned in terms of joint coordinates (Soechting and Lacquaniti, 1981). The motions, recorded in these studies, were directed away from the body and ended near the boundaries of the workspace. Based purely on mathematical grounds, Hollerbach and Atkeson (1987) have shown, however, that if the hand follows a straight path, the ratio of joint velocities is bounded to converge to a constant as the hand approaches the workspace boundaries. Thus, such movements cannot provide evidence for joint–based planning.

Not all point-to-point movements are ideally straight. Several researchers presented experimental observations showing that although some pointing movements, performed in the vertical plane, follow straight paths, others are characteristically quite curved (Atkeson and Hollerbach, 1985; Flanagan and Ostry, 1990). To account for the curvature of some of these movements, Hollerbach and Atkeson (1987) have proposed a joint-based strategy which they called ***staggered joint interpolation***. The suggestion was that the velocity profiles of all joints have the same kinematic form. The times at which the joints begin moving, however, might be delayed or staggered with respect to one another. These velocity profiles are also appropriately scaled with respect to amplitude and duration. Choosing appropriate parameters, this strategy can produce essentially straight lines in certain parts of the workspace. This strategy, however, does not allow joint reversals during the performance of any movement. Hence, Hollerbach and Atkeson (1987) have argued that in regions where the performance of straight paths requires joint reversals, the movements are bound to be curved.

The trajectories observed in many studies of point-to-point movements do display, however, joint reversals and are also very close to being straight (Hogan, 1988; see also Figure 4 in Flash and Hogan, 1985). The predictions of the staggered-joint interpolation strategy, therefore, are incompatible with experimental observations, at least in the case of horizontal planar movements. Why pointing motions are more curved is not yet clear. However, as will be shown in the next section, it has been possible to account for the deviations of horizontal planar point-to-point movements from straight paths by considering how desired motion plans are possibly executed by the neuromuscular system. Whether this conclusion can be extended to movements in the vertical plane remains to be seen.

The maximum-smoothness objective, as expressed by the above theory, is independent of limb kinematics and the neuromuscular dynamics. This theory is, therefore, completely consistent with the notion that there exists an abstract representation of movement that is independent of the mechanical effectors used in the performance of the motor task (Bernstein, 1967). This theory is also consistent with the notion that movement generation is heirarchically organized, whereby at higher levels only the more general features of movement, i.e. those that remain invariant under changes in the temporal and spatial scales of the movement, are represented (Keele, 1981). Specific motion parameters, such as end-point or via-point positions and movement durations, defined on the basis of the current task demands, are then used to obtain a more detailed specification of any particular movement (Flash and Hogan, 1985).

Although hand jerk was shown to decrease with practice (Schneider and Zernicke, 1989), it should be stressed that nowhere does this theory hypothesize or suggest that hand jerk is actually sensed, or that minimum-jerk trajectories are computationally derived by the nervous system. Thus, one possible physiological interpretation for the success of this theory in accounting for the observed behavior is that the central nervous system employs a trajectory planning strategy that is captured by this model. Another possible explanation is that the smoothness of motion is an outcome of the intrinsic properties of the neural and musculoskeletal hardware [Flash and Hogan, 1985; Chapter 19 (Seif-Naraghi and Winters)]. The possible rationale for maximizing smoothness might be the wish to maximize the predictability of the trajectory, which is consistent with minimizing its higher time-derivatives (Hogan, 1984; Flash and Hogan, 1985), or the wish to minimize the amount of information that needs to be presented and proccessed in the planning and execution of motor tasks.

Similar optimization principles may also apply in the generation of more complicated movements. In handwriting or drawing, for example, the system need not internally represent all possible letters or figural forms, but may use, instead, a limited set of basic primitives or strokes which can then be concatenated to form more complicated figural shapes (Morasso and Mussa-Ivaldi, 1982; Lacquaniti, 1989). These strokes, themselves, might be internally represented, based on a limited set of position and shape parameters, and generated according to motion planning rules, similar to the ones described above (Edelman and Flash, 1987). These internal constraints may again give rise to the observed coupling between motion speed and curvature.

In naturally executed drawing movements, angular velocity was found to decrease with increasing curvature and to be proportional to the two-thirds power of the latter (Lacquaniti et al., 1983). The gain factor of this relationship was demonstrated to be piecewise constant and to be determined by the linear extent of each individual segment (Viviani and Cenzato, 1985). These observations were interpreted to suggest that in spite of the apparent continuity of drawing movements, they are, in fact, intrinsicly discontinuous and are constructed of individual segments or strokes (Morasso and Mussa-Ivaldi, 1982; Viviani and Cenzato, 1985). It has been suggested that hand velocity during any movement need not be explicitly coded but is automatically derived from the coupling between speed and curvature expressed by the two-third power law (Lacquaniti, 1989). It is not yet known how this relationship between geometrical form and velocity comes about in the natural execution of movement, but it is possible that optimization theories of the type presented above may offer a possible explanation. (See also Nelson, 1983; Stein et al., 1985; Wann et al., 1988.)

17.3 Trajectory Execution

In the previous section we have focused on the topic of motion planning. To execute a desired motion plan, however, appropriate joint torques and muscle activation patterns must be generateed. How are these trajectory plans realized by the system? One possible way that this can be achieved (Hollerbach, 1982) is by transforming hand trajectory plans into joint rotations. The required joint torques can then be derived by solving the second-order nonlinear dynamic equations of motion (the so called "inverse dynamics" problem). For multi-jointed arms, there exist inertial dynamic interactions between the moving skeletal segments and several muscles pull across more than one joint [e.g., Chapter 18 (Gielen et al.); Chapter 8 (Zajac and Winters)]. As indicated by a study of point-to-point movements (Hollerbach and Flash, 1982), all interaction torques, including Coriolis and centripetal forces, are significant when the entire course of the movement is considered even at slow movement speeds. Moreover, the latter forces completely dominate arm dynamics at movement midpoint, when all the other torque terms which depend on joint accelerations go through zero as the hand switches between acceleration and decceleration. Also, joint torque profiles, required for the generation of one particular point-to-point movement, cannot be used in the generation of a kinematically similar movement between a different pair of end-points. Since the motor system seems to be capable of executing quite complicated multi-joint movements, this implies that it must have devised some means for computing or appropriately compensating for the interaction forces. It has been suggested, however, that the time-scaling property of human movement may simplify dynamic computations. Since for arm trajectories which simply scale with speed, the rate-dependent torque terms also simply scale with speed, this may indicate that the *CNS* has developed a trajectory formation strategy which reduces some of the complexities involved in motor execution (Hollerbach and Flash, 1982).

If indeed the system explicitly computes or, alternatively, derives the necessary joint torques from look-up tables (e.g. Atkeson, 1989), these torques must still be distributed among a considerable number of muscles. Moreover, having internal models of arm dynamics is not sufficient, since it does not guarantee robustness of the behavior in the face of unpredictable external disturbances or errors in internal models. Such robustness can be guaranteed, however, by the utilization of the viscoelastic properties of muscles [see Chapter 9 (Hogan)].

Is the derivation or computation of joint torques the only possible scheme for executing limb movements? As the theory presented below will suggest, there exists an alternative possible scheme that may allow the system to circumvent the need to solve the complicated inverse dynamics problem. Instead, the brain may only transform the desired hand trajectory plans into hand equilibrium trajectories. The forces needed to track the equilibrium trajectory may then be automatically generated as a consequence of the mechanical properties of muscles [Hogan, 1985; Flash, 1987; Chapter 12 (Feldman et al.), Chapter 9 (Hogan)].

The force exerted by a muscle on the limb increases as the muscle is stretched. The magnitude of this force depends on both the muscle stiffness and rest length, which are specified by the level of the neural activation of the muscle (for a review see Houk and Rymer, 1982). Consequently, several investigators have proposed that postural control is achieved by the motor system through the choice of a particular pair of torque–angle curves for the agonist–antagonist muscle pairs acting on the limb (Bizzi et al., 1976; Feldman, 1986; Chapter 12). This choice will determine the equilibrium position for the limb and the stiffness about the joint. According to the ***final position*** hypothesis for movement generation, motion towards a specified final position can be achieved without explicit planning of the trajectory of the limb, but merely on the basis of a pulse-like shift of the equilibrium point to the final position (Bizzi et al., 1976; Feldman, 1986). Recent observations of single–joint elbow movements in monkeys have indicated, however, that the *CNS* generates a control signal which defines a series of equilibrium positions and not merely the final position (Bizzi et al., 1984).

17.3.1 The Control of Arm Posture

The mechanical properties of muscles may also play an important role in the control of multi-joint posture and movement [Hogan, 1985; Berkenblit et al., 1986; Chapter 9 (Hogan)]. In particular, the actions of individual arm muscles ultimately combine to produce the overall mechanical behavior of the hand during posture. The net spring-like behavior of the hand was recently characterized by measuring the elastic field at a number of locations within the horizontal plane (Mussa–Ivaldi et al., 1985). The hand was displaced from equilibrium and the resulting restoring forces were measured at the displaced positions at steady state and before the onset of voluntary reactions. The field of forces, measured at the hand during posture, indicated that this field is mechanically conservative and can be completely described, in the vicinity of each hand position, by the stiffness matrix which relates force to displacement vectors. The hand stiffness matrices, obtained from these measurements, were graphically represented as ellipses, characterized by three parameters (see also Chapter 9): size (the area of the ellipse), shape (the ratio between the lengths of the major and minor axis) and orientation (the direction of the ellipse major axis with respect to a laboratory fixed coordinate system).

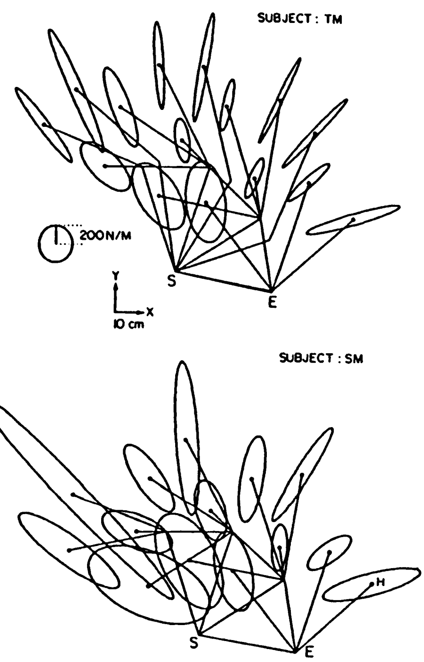

Figure 17.3: Hand stiffness ellipses obtained from two subjects during the postural task. Each ellipse was derived by regression on about 60 force and displacement vectors. The upper arm and forearm are represented by the two line segments (*S–E*) and (*E–H*), respectively, and the ellipses are placed on the hand (*H*). The calibration for the stiffness is provided by the circle to the left, which represents an isotropic hand stiffness of 200 N/m. (Reproduced with permission from Flash, 1987.)

The experimental findings indicated the existence of a strong and systematic dependence of the shape and orientation of the stiffness ellipse on the location of the hand in the horizontal plane. In particular, the results shown in Figure 17.3 indicate that the major axis of the hand stiffness ellipse at any location was observed to be nearly coaligned with the direction of the radial axis of a polar coordinate system located at the shoulder, where this radial axis is defined by the line connecting the hand with the shoulder. As far as shape is concerned, the ellipses became more elongated (i.e. hand stiffness was less isotropic) as the hand approached the distal boundary of the workspace, the major axis being in the proximal-distal direction. These patterns of stiffness shape and orientation were observed to be the same in all the subjects participating in the study and to remain invariant over time. In contrast, the values obtained for the size parameter varied substantially among subjects and in the same subject among experimental sessions. Even when a disturbance force in a well-specified direction was imposed on the hand, Mussa-Ivaldi et al. (1985) have found that only minor changes could be seen in the orientation and shape of the stiffness field.

In a subsequent study, the underlying causes for the observed spatial pattern of variation of the hand stiffness ellipse were investigated (Flash and Mussa-Ivaldi, 1990). Three possible factors that could have contributed to the observed characteristics of the stiffness field were considered. First, for a given vector of joint torques the magnitude and direction of the net force experienced at the hand depends on the configuration of the arm (see Chapters 9 and 11). Consequently, even if the values of all joint stiffnesses were to remain constant throughout the workspace, the geometrical parameters of the hand elastic field would be expected to change with hand position. Second, the contribution of each muscle to the resultant joint stiffness depends on the muscle moment arm. Since the lengths of muscle moment arms change with joint angles, the stiffness contributions of muscles are also expected to change with arm configuration. Third, muscle stiffness depends on muscle length and activation through the length-tension relationships. Hence, the spatial features of hand stiffness at different positions of the workspace are also affected by neural activation as well as by the muscle spring-like properties.

Examining the effects of these factors on the characteristics of the hand stiffness field and on the patterns of variations of the joint stiffness matrix with hand position, it was found that arm configuration alone can not be the mere cause for the experimental observations. Using anatomical data derived from the study by Wood et al. (1989) and considering the effects that muscle cross-sections and changes in muscle moment arms have on the joint stiffness matrix, we found that these anatomical factors are also not sufficient to account for the observed pattern of variation of joint stiffnesses in the workspace. However, based on the mathematical analysis of the relation between hand and joint stiffness matrices, it was found that in order for the stiffness ellipse to have the observed characteristics, the shoulder stiffness must covary in the workspace with the stiffness component provided by the two-joint muscles (Flash, 1987; Flash and Mussa-Ivaldi, 1990).

This condition was indeed found to be satisfied by the measured joint stiffness components. Figure 17.4 shows stiffness surfaces describing the variations of the net shoulder, net elbow and two-joint stiffnesses with elbow and shoulder angles. Thus, as these results indicate, the two-joint and the net shoulder stiffnesses do covary with arm configuration while the net elbow stiffness surface displays a different pattern of variation. We then examined whether the coupling between shoulder and two-joint stiffnesses may result from the coactivation of the muscles contributing to these stiffnesses. *EMG* signals were recorded from shoulder, elbow, and two-joint muscles. However, our results indicated that, while some muscle coactivation may indeed exist, it can be found for only some of the muscles and in only part of the workspace.

Nonetheless, these results have indicated that functional muscle synergies can be identified. In this context, the concept of a synergy implies that in spite of the excessive number of arm muscles, there is nearly a fixed relationship between the stiffnesses contributed by different muscle groups. This coupling finds its manifestation in the net mechanical response of the human arm to external disturbances. At least in principle (Hogan, 1985), the redundant number of arm muscles offers the *CNS* the possibility of selectively tuning the hand stiffness field according to task requirements. The indicated limited capability of the system to significantly modify the characteristics of the stiffness field may, therefore, indicate the operation of coordinative constraints which might also be present during movement generation.

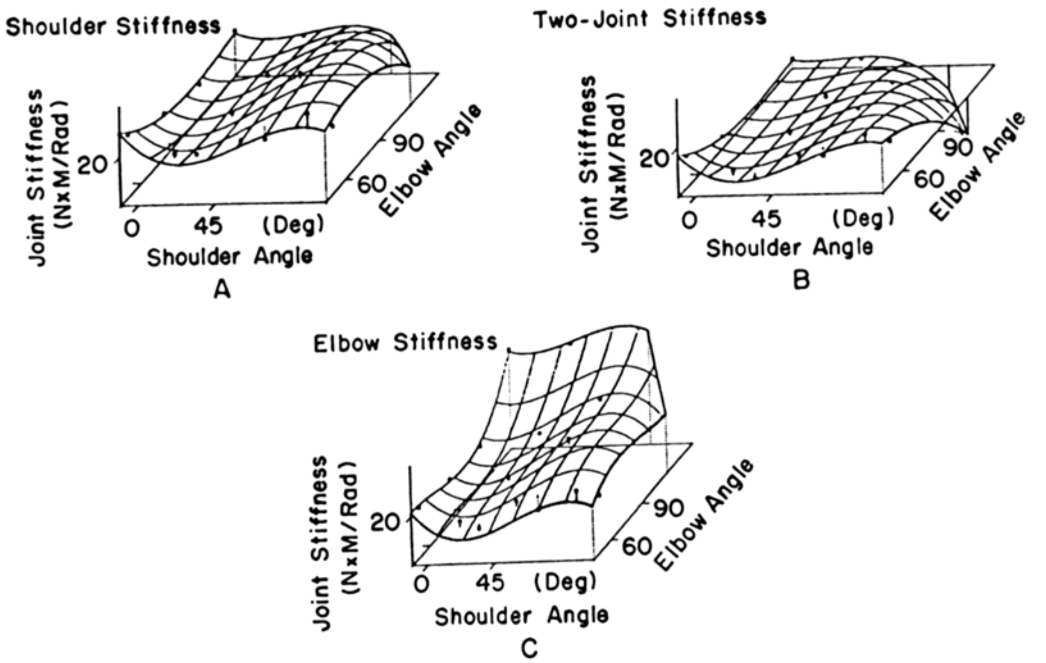

Figure 17.4: Variations of the measured joint stiffnesses with shoulder and elbow angles. ***a)*** Net shoulder stiffness. ***b)*** Two-joint stiffness. ***c)*** Net elbow stiffness. (Reproduced with permission from Flash and Mussa-Ivaldi, 1990.)

17.3.2 The "Equilibrium Trajectory" Control Theory

The above section has concentrated on the importance of the mechanical properties of muscles in the control of multi-joint arm posture. Do these properties play any role in the execution of multi-joint movement? As postulated by the ***equilibrium trajectory*** theory discussed below, the motor system may use muscle "spring-like" properties to obviate the need for dynamic computations. Furthermore, as indicated by a recent simulation study, the control of arm trajectories, at least in the context of kinematically unconstrained movements, might not be fundamentally different from the control of posture (Flash, 1987).

According to the equilibrium trajectory hypothesis, limb movements are achieved by gradually shifting the hand equilibrium position between the movement end-points (Hogan, 1985; Flash, 1987). The magnitude and direction of the forces acting on the arm, at any point in time, are determined by the magnitude and direction of the displacement vector of the hand from equilibrium and by the hand elastic and viscosity fields about the equilibrium positions.

The equilibrium position and trajectory and the characteristics of the stiffness and viscosity fields are determined by the neural activations of arm muscles. Given the "spring-like" properties of muscles, an equilibrium position and trajectory for the limb can always be defined. Are they, however, explicitly controlled or coded for by the brain? As the model presented below suggests, the system might use the equilibrium trajectory control scheme as a vehicle in the realization of desired motion plans. To test the validity of this hypothesis, an explicit model of arm trajectory control was developed (Flash, 1987). The model was based on the notion that the execution of reaching movements involves explicit planning of straight hand equilibrium trajectories which are invariant under translation, rotation, amplitude, and time scaling. A simple mathematical description of the musculoskeletal system was constructed and the suggested control scheme was implemented in computer simulations. The stiffness values used in these simulations were derived from the experimentally measured static stiffness values (Mussa-Ivaldi et al., 1985), under the assumption that the orientation and shape of the stiffness field, when the arm moves through any workspace location, are similar to those of the static field at that location. The simulations were used to derive hand equilibrium trajectories from measured movements. These equilibrium trajectories were found to follow straighter paths than the actual movements. Forward computations were also performed. An equilibrium trajectory, derived from one representative movement, was used (after suitable amplitude and time scaling, translation, and rotation) to simulate actual movements of different amplitudes, directions, and speeds.

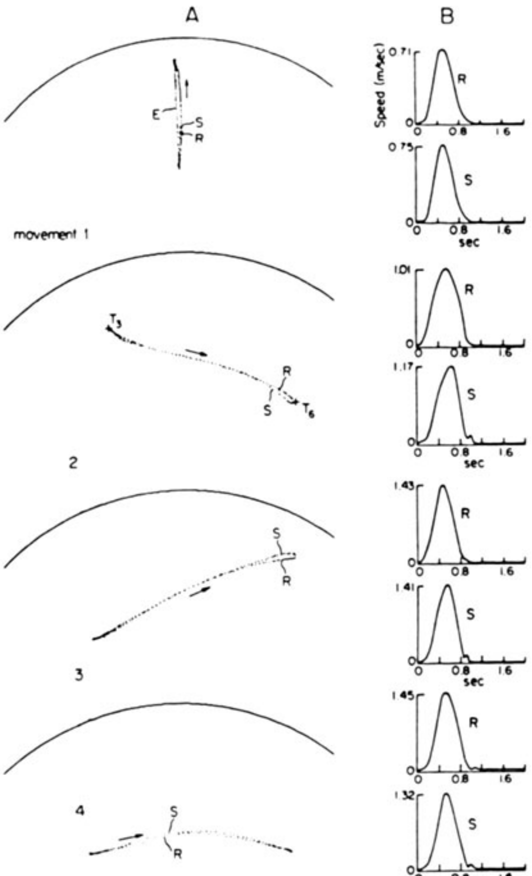

Figure 17.5: Comparison of simulated (*S*) and observed (*R*) point-to-point movements in the horizontal plane. Column A shows hand paths. Column B shows profiles of hand speed along the path. A virtual trajectory (marked *E*) was derived from observations of movement 1 (top panel) and used with appropriate scaling and rotation to simulate movements 2, 3 and 4. (Reproduced with permission from Flash, 1987.)

As seen in Figure 17.5, the predicted trajectories captured the observed features of the measured movements down to fine details of kinematics. In particular, the curvatures of the measured movements were successfully accounted for, as well as the presence of small hooks or movement overshoots as the hand approaches the final target and the kinematic differences observed between movements generated between the same pair of targets but in opposite directions.

On the basis of the success of this model in accounting for the fine details of movement curvature, we may argue that the characteristic deviations from ideally straight paths observed in actual data may reflect the combined effects of arm inertia, centrifugal and interaction torques, and the local characteristics of the arm stiffness and viscosity fields. Were joint torques explicitly computed by the brain and then distributed among the muscles, there would have been no apparent reason why the desired straight hand paths could not be generated. The success of this model in capturing the observed behavior therefore suggests that at least in the case of point-to-point movements, the inverse dynamics problem is not explicitly solved by the brain. The system, therefore, has seemed to adopt a simpler control strategy even at the price of movement accuracy. Moreover, since the stiffness fields used in these simulations were assumed to have similar characteristics to the static ones, this may indicate that similar coordinative constraints operate during both posture and movement.

17.3.3 An Alternative Model

The view presented in this chapter is that the transformation of behavioral goals into actual movements involves a step-by-step process. The first step is only concerned with movement kinematics and deals with the generation of motion plans. The second step involves the execution of these plans by taking advantage of the physiological properties of the neuromuscular system. Recently, an alternative view to the one presented here was suggested (Uno et al., 1989, Kawato et al., 1990). Again, it was postulated that motor commands are directly calculated from the goal of the movement, represented by some performance index. However, in contrast to the maximum-smoothness objective which was expressed in terms of world coordinates, Uno et al.

(1989) have postulated that the underlying criterion for the selection of specific motions from the infinite number of possible ones can be defined as follows:

$$C_T = \frac{1}{2}\int_0^{t_f} \sum_{i=1}^{n} \left(\frac{dz_i}{dt}\right)^2 dt \qquad (17.3)$$

where z_i is the joint torque for actuator i. Hence the proposed performance index is the sum of square of the rate of change of joint torques, integrated over the entire movement. This movement objective, unlike the one proposed by Flash and Hogan (1985), is critically dependent on the dynamics of the musculoskeletal system.

The results obtained from the minimization of C_T were found to be in good agreement both with the observed behavior and with the predictions of the minimum-jerk model. For certain movements, however (e.g., movements starting when the hand is stretched away from the midline), the trajectories predicted by this model were more curved than the ones predicted by the minimum-jerk model and in better agreement with the data. This was also found to be the case for certain observations made with respect to curved movements.

Independently from the above study, computationally efficient trajectory planners based on the multi-grid approach were developed and were applied to this problem of finding the unique trajectories which minimize C_T for a two-joint arm (Ben-Zvi, 1987; Flash, 1988). In this latter study, however, different predictions were obtained from the ones obtained by Uno et al. (1989). These differences do not seem to result from the differences between the methods used to arrive at the optimal solution, but to reflect differences in the values of the inertial parameters used to model the upper limb. Since, as stressed above, C_T strictly depends on arm dynamics, the results obtained from the minimization of this cost are highly sensitive to the values used for these parameters.

As was explained above, however, the curvature seen in measured point-to-point movements can be accounted for by considering the strategy used by the system to execute the desired motion plans (see Figure 17.5). Hence, the actual movements produced on the basis of the equilibrium trajectory control scheme are more curved than the ones that are assumed to be planned based on the minimization of hand jerk. This is indicated in Figure 17.6, where the trajectories predicted by the minimum-jerk and the equilibrium trajectory models are displayed side by side. However, when using the same inertial parameters as the ones used in the equilibrium trajectory model to predict the trajectories that would result from the minimization of C_T, the resulting movements failed to match the measured ones. These findings indicate that multi-joint movement generation may indeed involve a step-by-step trajectory control process and that arm dynamics may not be internally represented as postulated by the minimum-torque change model (Uno et al., 1989; Kawato et al., 1990).

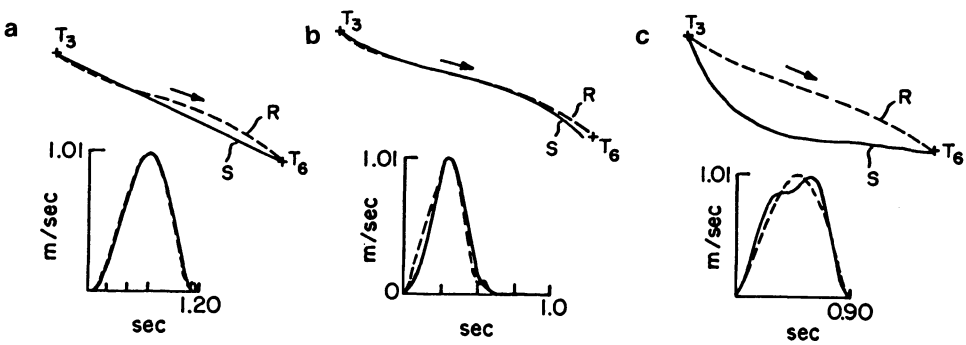

Figure 17.6: Comparison of measured (dashed line) and predicted (solid line) movements. *a)* The minimum-jerk model. *b)* The equilibrium-trajectory model. *c)* The minimum–torque rate of change model. (Reproduced with permission from Flash, © 1988 *IEEE.*)

17.4 Arm Trajectory Modification

So far we have discussed the topics of motion planning and execution, focussing mainly on the generation of point-to-point and curved movements. During many daily activities, however, we do not simply generate motions towards static visual objects, but must also actively interact with the environment or respond efficiently and quickly to dynamic changes in the locations of external objects. Reaching towards visual targets in space involves a series of events and sensorimotor transformations leading from the neural encoding of target location, derived from vision or memory, to the performance of aimed movements. As was discussed in the section on trajectory planning, the temporal scales of any specific movement, i.e. motion amplitude and duration, are used to transform the general motion plans into a detailed trajectory for the hand through space. When, however, the target towards which we intend to move our limb suddenly changes its location, our motor response must be planned and executed while the arm is no longer at rest. Even if the target is displaced during the reaction time, it can be assumed that the first planning process has already begun. How, therefore, does the nervous system modify an ongoing motion or update an ongoing planning process?

The characteristics of aimed movements when the target changes location either during the reaction or movement time have been described by several investigators (e.g. Georgopoulos et al., 1981; Gielen et al., 1984). Basically, these studies indicated that the change in target location elicits a graded movement towards the first target, followed by a change in movement direction and a subsequent motion towards the second target. Occasionally, for a short interstimulus interval (*ISI*; the time elapsing between target presentation and its displacement), the hand moved directly to the second target or in between the two targets. The duration of the initial motor response to the first target was found to be a linear function of the *ISI* and no delays were found beyond the normal reaction time, i.e., there was no appreciable psychological refractory period. The orderly modifications of movements produced in response to double target displacements suggested that the aimed motor commands are emitted in a continuous fashion as a real time process that can be interrupted at any time (Georgopoulos et al., 1981).

It is not yet clear, however, what strategy is used by the brain in the modification of ongoing motion plans.

To investigate this issue, human horizontal planar movements were recorded using the double-step target displacement paradigm. The experiments were performed in a darkened room, eliminating any visual feedback from the moving limb (Henis and Flash, 1989; Flash and Henis, in preparation). The target was displaced once or twice along the x or y axes or obliquely, using various directions and amplitudes of target displacements and ISI's ranging between 50 and 700 ms. In general, our findings were consistent with previously reported results.

One plausible strategy for trajectory modification may involve aborting the rest of the initially planned trajectory and replacing it by a new movement between the location of the hand (at the modification time) and the final target position. For the two movement parts to be smoothly joined together, since motion planning preceeds its execution, this strategy would require of the brain to predict, or derive, information about the kinematic state of the hand at the switching time.

In this section, we summarize evidence that the system may use an alternative and simpler modification scheme than the one described above. Instead of aborting the rest of the initial trajectory plan, it is suggested here that this plan continues unmodified until its intended completion and is vectorially summed with a second, time-shifted point-to-point hand trajectory plan for moving between the initial and new target locations. Thus, both trajectory units start and end at rest and each trajectory is separately planned regardless of the other one. Since the initial trajectory is neither aborted nor modified when the second part is injected, this guarantees that the second target location will always be reached independently of the modification time. However, the exact details of the combined motion plan, and consequently of the actual movement executed by the system, do strongly depend on the time shift between the initiation of the two superimposed trajectory plans and on their durations.

In this context, it should be mentioned that the idea that more complicated movements may emerge from the superposition of basic trajectory primitives was postulated in the context of speech (Munhall and Lofquist, 1987), locomotion (Flashner et al., 1988), and both single (Adamovitch and Feldman, 1984) and multi–joint arm movements (Morasso and Mussa–Ivaldi, 1982). The validity of this hypothesis was also tested for movements recorded in double–step target displacement trials (Massey et al., 1986). However, the underlying assumption made in that study was that the superimposed trajectories should have the same durations as control point-to-point movements separately performed by the same subject when moving between the two target pairs. Since in that study, the simulated movements that were predicted by this scheme failed to match the measured ones, it was concluded that arm trajectory modification cannot possibly involve the superposition strategy.

In our work (Henis and Flash, 1989), no *a priori* assumption was made with respect to the durations of the superimposed trajectory plans. Instead, we wished to test whether the modified movements may emerge from the vectorial summation of "control-like" point-to-point trajectories, i.e., movements that have the same kinematic form as simple reaching motions, whatever their durations might be. To assess the success of this scheme in accounting for the data, the following analysis was separately applied to the x and y components of each individual measured modified movement. The simulated x and y components were then combined to predict the entire measured trajectory:

a) Time scaled velocity profiles corresponding to a point-to-point minimum jerk trajectory between the initial and first targets were superimposed on the initial part of the movement.

b) The time of the first detectable deviation of the measured speed profile from that of the superimposed control movement (t_s) was extracted.

c) From this time on, the following fifth-order polynomial was added to the first polynomial.

$$x(t) = (x_2 - x_1)\,(a_3 t_r^3 + a_4 t_r^4 + a_5 t_r^5) \qquad (17.4)$$

where $t_r = (t - t_s)/(t_f - t_s)$, t_f is the total duration of the modified movement, derived from data, a_3, a_4 and a_5 are coefficients to be calculated, and $(x_2 - x_1)$ is the x component of the displacement vector between the first and second target locations. The expression for $y(t)$ was analogous to *Eq. 17.4*. This family of trajectories has zero initial positions as well as zero initial (but not final) velocities and accelerations.

d) The values of the three unspecified coefficients of this polynomial were determined using a least-square fitting method based on the position error between the simulated and measured movements.

For the modified motions, the analysis showed that point-to-point minimum–jerk trajectories between the first and second targets provided the best fit for the second trajectory units. Statistical tests further showed that the coefficients of the added trajectory units are not significantly different from the measured ones. Thus, the modified movements were found to result from the vectorial summation of the initial unmodified trajectories with point-to-point trajectories between the first and second target locations which have the same kinematic form as simple point-to-point movements. Following the first detectible deviation, the motions resulting from the superposition scheme were found to be in good agreement with the measured ones.

The recorded hand paths and velocity profiles for all target configurations and all *ISI*s were successfully accounted for. Figure 17.7 shows two examples of measured modified movements, the corresponding trajectories predicted by the superposition scheme, and the superimposed trajectory units. The exact kinematic details of any modified movement were found to depend on the specific durations of the superimposed trajectories and on the time delays between their initiation. The alternative strategy for trajectory modification which involves aborting the rest of the initial trajectory and replacing it by a new trajectory plan was also mathematically modelled. However, the movements predicted by this scheme failed to match the measured ones. Hence, this scheme was significantly less successful than the superposition model in accounting for the observed behavior.

Our results were therefore consistent with the assumptions of the superposition model that the second target presentation activates a separate planning process while the first process continues

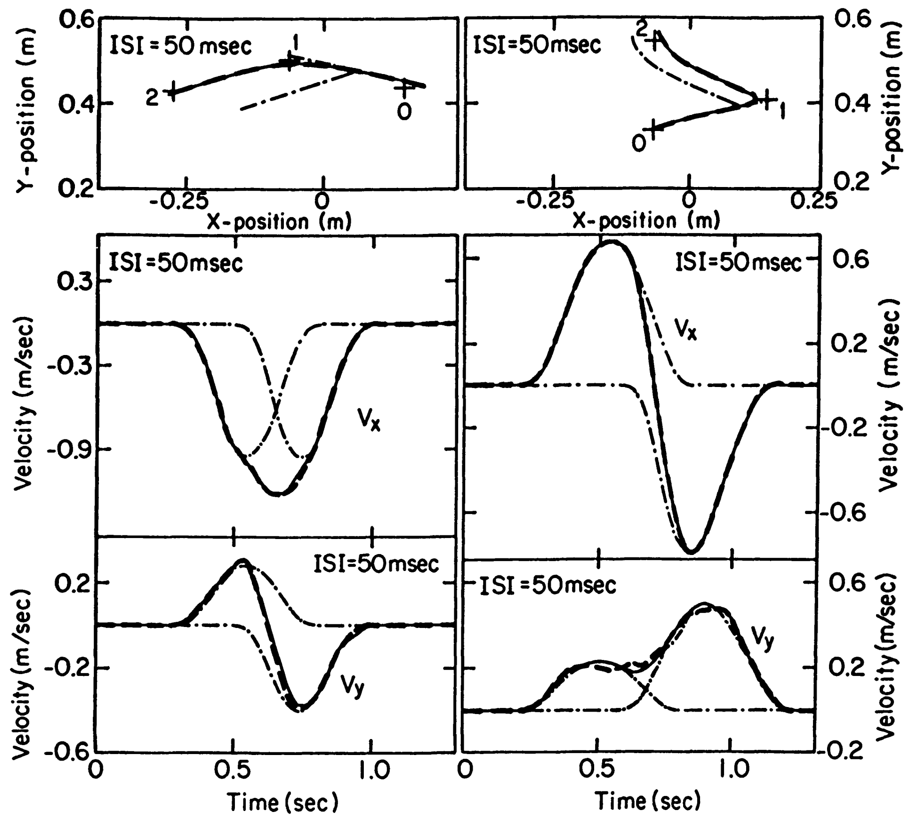

Figure 17.7: Comparison of measured modified movements (ISI = 50 ms) and movements resulting from the superposition scheme. The initial hand positions are marked by 0. The first and second target locations are marked by 1 and 2, respectively. Hand paths are shown in the top panels. The x and y components of velocity, V_x and V_y, respectively, are shown in the two bottom panels. Measured trajectories are marked by solid lines, superimposed initial and added trajectory units by alternating dots and dashes and their vectorial sums by dashed lines. In the top panels the added trajectories are shown to begin at the locations corresponding to the modification times.

unmodified. Using information about the first and second target locations, derived from vision, this process generates a trajectory plan that obeys the same relationship between movement amplitude, duration and speed as a single reaching movement starting and ending at rest. When this trajectory plan is ready, it is continuously added to the first plan to yield the combined motion. For long *ISI*s, the initial response is ready before the second process is activated, giving rise to movements initially directed towards the first target. For short *ISI*s, however, it was often observed that the hand either directly moves towards the second target, or along some intermediate direction [the "averaging" phenomenon (Van Sonderen et al., 1989)]. It remains therefore to be seen whether in this case, too, the modified trajectories result from the superposition of the initial trajectory plan with a second trajectory, or whether, for short *ISI*s, the initial trajectory is already directed towards some intermediate target located in between the first and second target locations. The simplicity of the proposed superposition scheme may explain the observed lack of a psychological refractory period. Furthermore, our findings may indicate the presence of parallel planning of trajectory primitives.

17.5 Conclusions

The studies reviewed in this chapter have indicated the existence of hierarchical control levels for arm trajectory generation. Higher levels are concerned with the planning of trajectories that maximize the smoothness of hand motion in extracorporeal space. These desired motions are then executed by taking advantage of the mechanical properties of muscles. An important consequence of the proposed hierarchical scheme is to make computational control of multi-joint arm movements much simpler. Since a hand location on the equilibrium trajectory can be directly associated with a co-contraction pattern of muscles, the joint torque profiles, required for the realization of the intended movements, are automatically generated whenever the actual hand position deviates from the instantaneous equilibrium position, thus eliminating the need for inverse dynamics computations.

The above scheme assumes two separate levels of trajectory planning and execution. One possible alternative scheme, which assumes that the cost that is minimized in movement execution is the rate of change of joint torques, does not adhere to this step-by-step transformation from the behavioral goal of movement to the neural activations to muscles. When comparing the predictions of these two alternative schemes, our results indicated that, in contrast to the findings presented by Uno et al. (1989), only the predictions of the step-by-step scheme were compatible with experimental observations. Hence, the studies reviewed here show that the observed kinematic data are completely consistent with the hypothesis that: ***a)*** simple movements are first planned in terms of desired hand motions in external space; ***b)*** are expressed in terms of equilibrium trajectories; and ***c)*** are executed via the mechanics of the neuromuscular system, which acts to keep the actual path of the limb reasonably close to the equilibrium trajectory.

In dealing with the modification of ongoing movements, the success of the superposition model in accounting for the observed behavior suggests that the system may have adopted a simple movement modification strategy that eliminates the need to rely upon efference copies of past motor commands or on kinesthetic information in order to derive or predict the expected hand position at the switching time. Instead, independently and possibly in parallel the system plans a second point-to-point trajectory, using information derived from vision about the first and second target locations. The two trajectory plans are then continuously summed together to give the combined plan for the modified movement. This combined plan can then be transformed into a combined hand equilibrium trajectory and executed in the same way as a separate point-to-point movement by relying upon the mechanical propertes of muscles. Since the superimposed primitives were shown to be hand trajectory plans, this provides an additional support for the hierarchical organization of the trajectory control processes and suggests that such an organization might be especially beneficial when coping with unpredictable disturbances or with dynamic motor tasks.

Given that the superimposed movements were shown to have the same kinematic form, as though derived from a common template, this indicates that more complicated motor acts and motion sequences might be constructed from the superposition of more elementary trajectory primitives.

17.6 Recommended Future Directions

The issues discussed in the previous sections have dealt with several aspects of arm trajectory control. Of course, there are many other aspects of multi-joint arm movement generation that were not addressed here and many questions remain. Here, we will discuss only several recommendations for future research directions. Some of these recommendations address issues that arise mainly in the context of three-dimensional arm movements and movements in the vertical plane, while others address more general problems.

Of the three ill-posed motor problems that were discussed in the introduction to this chapter, we, as well as other investigators, have focussed mainly on the question of how the system resolves the task-level redundancy. There is a strong evidence to support the hypothesis that, indeed, arm movements are internally represented in terms of task-level coordinates. It is not yet clear, however, whether and how the system transforms these task-level motion plans into joint coordinates. Here we have focussed mainly on two-joint arm movements in the horizontal plane. An additional issue that does not arise in this context is the issue of kinematic redundancy. Based on the kinematic analysis of three-dimensional drawing movements, Soechting and Terzuolo (1986) have suggested that the brain is endowed with an explicit representation of movements in joint space and an algorithm for embedding a world 'space trajectory into joint rotations. It was also suggested that the internal representation of actual movement in joint space is not an exact reproduction of the intended hand movement, but is one that simplifies the transformation from hand to joint coordinates. Another consideration, for resolving redundancies, may involve, for example, the maximization of smoothness. Based on theoretical grounds, Jordan and Rosenbaum (1989) have suggested that a smoothness constraint in articulatory space, which implies that targets nearby in time are achieved using similar limb configurations, might be used to resolve kinematic redundancies. Thus, a greater research effort should be directed at investigating whether and how hand trajectory plans are transformed into joint movements. Nonetheless, for practical reasons, most of the studies addressing this and similar questions have focused on well-defined motions that are easy to study from within a laboratory setting (e.g., pointing movements, drawing ellipses, etc.). There is therefore a great need to examine what principles underlie the generation of more natural and perhaps less confined movements.

Another recommended direction for future studies has to do with the characterization of arm impedance, i.e. hand and joint stiffnesses and viscosities during movement, especially when gravity must be taken into account. As was suggested above, the observed curvature of some pointing movements in the vertical plane may result from the way by which the nervous system executes desired motion plans. As long as arm impedance cannot be measured and characterized during movement, the validity of this hypothesis, as well as the validity of the equilibrium trajectory hypothesis in the context of planar horizontal reaching movements, cannot be experimentally tested. Thus, it is strongly recommended that research efforts should be directed, as indeed they currently seem to be (e.g., Xu et al., 1989) at developing technical means that will enable us to measure arm stiffness and viscosity during movement.

It is also not yet clear how the system solves the ill-posed problem of muscle activation, i.e., selecting what muscles to activate, in what order, and to what level of activation. In many studies attempts were made to determine the rules, according to which the motor system specifies the pattern of activation of individual muscles. The minimization of various performance costs, such as the sum of muscle forces, stresses, etc. were hypothesized [e.g., see Patriarco et al., 1981 or review in Chapter 8 (Zajac and Winters)]. However, the force distributions predicted in these studies were found to depend more strongly on the muscle attachment geometry than on the types of cost functions being minimized. Furthermore, these methods failed to predict the coactivation of muscle synergists and antagonists, usually seen in experimental data [however, see Chapter 19 (Winters and Seif-Naraghi)]. In a recent paper assessing the question of the existence of particular muscle synergies during load perturbations or intentional arm movements, it was concluded that the concept of a muscle synergy is not appropriate to characterize, in any economical fashion, the activities of muscles involved in upper limb movements or the response of the muscles to applied load perturbations (Soechting and Lacquaniti, 1989). Instead, it was suggested that each muscle is related in a unique and different manner to the kinematic and dynamic variables of the motor task. Thus, it was argued that the simplification of the problem of controlling a large number of degrees of freedom does take place in the sense suggested by Bernstein (1967), but that this occurs at the level of limb kinematics and does not manifest itself in terms of fixed patterns of activation among different muscles. As indicated, however, by the findings reported by Hasan and Karst (1989, Chapter 16), it does seem that during planar horizontal two-joint point-to-point movements, the order of muscle activation, i.e. which muscles are first activated, is reproducible over trials and among subjects and depends on the initial limb configuration. Another promising line of investigation is reported in Chapter 18 (Gielen et al.). Hence, although some progress has been made with respect to this issue, further efforts should be directed at deciphering the rules that dictate what muscles to activate during multi-joint arm posture and movement.

Nothing was said in this chapter about the relevance of the studies reviewed here to neurophysiology or to the analysis of motor disorders. However, although very often neurophysiological findings can be interpreted in many different ways and do not always lead to unequivocal answers to theoretical questions, they may provide insight into the ways by which the brain solves some of the computational problems discussed above. For example, the hypothesis that arm movements are internally represented in terms of hand coordinates was supported by recent neurophysiological findings (for a review see Georgopoulos, 1986). These series of studies indicated that the motor cortex is a key area in the control of spatial aspects of hand trajectories. The direction of the population vector, which reflects the activity of a large population of neurons, was found to provide unique information concerning the direction of movement of the hand in *2-D* or *3-D* space. A signal related to the instantaneous hand velocity was also described. Although it has been argued that these findings might also be interpreted in other ways (Mussa–Ivaldi, 1988), the similarities that were shown to exist between the patterns of activities of cortical cell populations when moving the hand in the same direction but from different starting positions (Kettner et al., 1988) did support the idea of task–level representation of multi–joint arm movements. Further studies are therefore required either to establish, or to refute, this conclusion as well as additional studies designed to investigate whether and how motion plans are transformed into joint and muscle coordinates.

Another recommended direction for future studies is in the area of motor disorders. Thus, for example, the kinematic analysis of motion in basal ganglia or cerebellar disorders may offer a new opportunity to shed new light on the still mysterious role of these brain areas in motor planning and execution. Recently, for example, we have investigated the kinematic properties of planar horizontal point-to-point and curved movements in Parkinsonian patients (Flash et al., 1988). Pertinent to our discussion here are the findings related to the production of curved movements which showed that unlike healthy subjects, patients often stopped at points of maximum curvature before changing movement direction. Moreover, the isochrony principle (Viviani and Terzuolo, 1982) did not hold in patient movements: movement duration increased proportionally to the length of the movement segment. Thus, since it has been indicated that the performance of complex, i.e. sequential or simultaneous movements is especially impaired in Parkinson's disease (Benecke et al., 1986), the study of such motor tasks may provide new insight into the functional roles of these structures in neuromotor planning.

Finally, more research studies should focus on the areas of motor learning and adaptation. Such studies may offer us new opportunities to resolve the questions of what it is that the system learns during skill acquisition and when adapting to new loads or external disturbances, what performance costs does the system wish to minimize or optimize during skill acquisition, etc. Atkeson (1989) as well as Kawato et al. (1990) have claimed that the equilibrium trajectory scheme does not allow efficient learning from practice, but no evidence was provided to support this claim. In contrast, as indicated by a recent study based on the use of recurrent neural networks, motor learning based on the use of the equilibrium control scheme is at least feasible (Jordan, 1990). Thus, much more effort should be directed at investigating how it is that the motor system allows us to learn new skills or to improve motor performance on the basis of practice. Finally, efforts should be directed at developing theories that will account for the phenomenon of motor equivalence (e.g., in Berkenblit et al., 1986), which implies that even if external conditions do not vary, the system may generate a set of different solutions for one and the same motor task.

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