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Simulation Studies on the Control of Posture and Movement in a Multi-Jointed Limb

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Abstract. Simulation studies were performed to evaluate the effectiveness of different control schemes in stabilizing a multi-jointed limb (human arm) in response to force perturbations. The mechanical properties of the arm were modeled as a linear visco-elastic system and the effectiveness of negative feedback of angular position and torque was evaluated. The effectiveness of a given amount of position feedback depended strongly on the initial position of the arm and on the perturbation, while torque feedback was much more consistently effective in damping the motion of the limb.

Introduction

There have been numerous modeling studies concerning the control of posture and movement and several review articles have dealt with this topic recently (Agarwal and Gottlieb 1982, 1984a, 1984b; Stein 1982). These models have attempted to represent the mechanical properties of the musculo-skeletal system to varying degrees of complexity, the simplest models taking the form of a linear, second order system. In addition, these models have attempted to incorporate the effect of afferent feedback. The simplest such model assumes that this feedback acts to maintain the visco-elastic properties (in particular the stiffness) of the system constant (Houk and Rymer 1981). According to that hypothesis the system (limb, muscles and afferent feedback) can be modeled adequately as a second order system. Other models have instead represented the effect of afferent feedback on the electromyographic activity of muscles as being proportional to changes in position and its derivatives delayed by the conduction time of the loop, i.e. as length feedback (cf. Agarwal and Gottlieb 1984b; Terzuolo et al. 1981). Force feedback and a combination of length and force feedback have also been considered (Stein 1982).

All of these models have been restricted to one degree-of-freedom systems, that is, they have dealt only with the case where motion is restricted to one limb segment. In general, however the control of posture and movement requires that the motion at several joints be controlled simultaneously (cf. Abbs and Gracco 1984; Nashner and McCollum 1985). For several reasons, it is not clear that the predictions of models restricted to one degree of freedom can be extrapolated in a straightforward manner to the general case.

First of all, the equations of motion for a limb with several degrees of freedom are coupled, implying that the feedback control of motion of one limb segment will affect the motion of other segments, proximally and distally. Secondly, these equations contain nonlinear terms which are not negligible under all conditions (Hollerbach and Flash 1982). Thus, even if one assumes that the stiffness and viscosity terms are linear, the overall behavior of the musculo-skeletal system will be nonlinear. Thirdly, the anatomical arrangement of different muscles must be taken into consideration (cf. Abraham and Loeb 1985; Nashner and McCollum 1985). Some muscles cross more than one joint while the action of others is restricted to one limb segment. One cannot assume that the effectiveness of mono- and multi-articular muscles will be the same under all conditions.

We have recently begun to address some of these problems experimentally by applying force perturbations to the human arm, the upper arm and the forearm being free to move. Under such experimental conditions, a force applied proximally or distally to the elbow results in simultaneous angular motion at the shoulder and elbow joints. The amount and direction

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of each of these angular motions depend on the point of application (arm or forearm) and direction of the external force and on the amount of extension at the elbow. In general, posteriorly directed forces on the upper arm result in backward extension at the shoulder and flexion at the elbow, while downwardly directed forces acting on the forearm lead to extension at the shoulder and elbow.

We have found that when such perturbations are applied to the arm, the response of elbow flexors depends on the angular motion at both the elbow and the shoulder (Lacquaniti and Soechting 1984, 1986a, 1986b). This holds true for biceps (which spans the elbow and shoulder joints) as well as for brachioradialis and brachialis (whose action is restricted to the elbow joint). Furthermore, the response of both mono- and bi-articular elbow flexors to force perturbations is not consistent with the expected behavior of a feedback of muscle length or its derivatives. Instead, the pattern of biceps responses is best correlated with the changes in net torque at the elbow, suggesting the presence of a torque feedback (Lacquaniti and Soechting 1984, 1986a). Furthermore, the evoked patterns of activity in mono- and bi-articular muscles can differ considerably under some conditions, for example, when a perturbation is applied to the upper arm. The activity in all three elbow flexors changes in parallel and they appear to act synergistically when the force is applied distally to the elbow.

These experimental observations prompted us to perform some simulations of simple models of the postural control system. They were aimed at the following questions: 1) What might be the advantage of a differential control of mono-articular and bi-articular muscles as suggested by experimental observations? 2) What is the efficacy of position or torque feedback in postural stabilization when more than one limb segment is free to move? and 3) Since the equations of motion are nonlinear, will conclusions reached when perturbations are applied under static conditions also hold true when they are applied while the limb is moving?

Mathematical Model

The equations which describe planar motion of the arm, according to Newtonian mechanics, are

$$T_s=(I_s+I_e+2A\cos\phi)\ddot{\theta}+(I_e+A\cos\phi)\ddot{\phi}-A\sin\phi(\dot{\phi}^2+2\dot{\phi}\dot{\theta})+B\sin\theta+C\sin(\theta+\phi), \quad (1)$$

$$T_e=I_e\ddot{\phi}+(I_e+A\cos\phi)\ddot{\theta}+A\sin\phi\dot{\theta}^2+C\sin(\theta+\phi), \quad (2)$$

where T_s and T_e are the net torques acting at the shoulder and elbow joints, respectively, and θ and ϕ represent the angles of flexion at the shoulder and elbow (see Fig. 1). As defined, a positive torque will tend to induce flexion at that joint. The net torque (T_s and T_e) is the resultant of moments due to externally applied forces and the passive (visco-elastic) and active forces of muscles acting at that joint. I_s and I_e are the moments of inertia of the upper arm and forearm and the coefficients A, B, and C are constants. The terms containing B and C represent the gravitational moments acting on the arm when the arm lies in the vertical plane. Typical values for these parameters, used in the simulations to be described below, are: $I_s=0.30$, $I_e=0.15$, and $A=0.20$ kg-m^2 and $B=10$, $C=5$ kg-m^2/s^2.

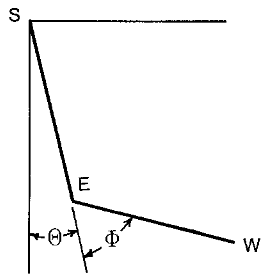

Fig. 1. Schematic of the human arm. S, E, and W denote shoulder, elbow and wrist connected by rigid links. θ corresponds to the angle of forward flexion at the shoulder and ϕ the angle of elbow flexion

Quasi-Static Model

It now remains to define more precisely the torques acting at the shoulder and elbow joints. One component is due to externally applied forces on the arm and will be defined as T_s' and T_e'.

A further component of torque is attributable to the visco-elastic properties of muscle. Consider first a mono-articular muscle acting at the elbow joint. As a first approximation, its change in length Δl is proportional to the change in elbow angle

$$\Delta l \simeq a\Delta\phi, \quad (3)$$

where a is the moment arm of the muscle. If the muscle is assumed to have spring-like properties, the force f developed by the muscle is given by

$$f=ka\Delta\phi, \quad (4)$$

where k is a coefficient of proportionality (stiffness). The moment developed by that muscle is given by the product of the force times moment arm a

$$T_e=-ka^2\Delta\phi. \quad (5)$$

A similar derivation applies for muscles which cross the shoulder and elbow joints

$$\Delta l \simeq a\Delta\phi+b\Delta\theta \quad (6)$$

where a and b are the moment arms of that muscle about the elbow and shoulder joints. This muscle will contribute torque at both joints

$$T_e = -k(a^2 \Delta\phi + ab\Delta\theta), \quad (7)$$

$$T_s = -k(ab\Delta\phi + b^2 \Delta\theta) \quad (8)$$

which can be expressed more compactly in matrix form

$$\begin{Bmatrix} T_s \\ T_e \end{Bmatrix} = -k \begin{bmatrix} b^2 & ab \\ ab & a^2 \end{bmatrix} \begin{Bmatrix} \Delta\theta \\ \Delta\phi \end{Bmatrix}. \quad (9)$$

Note that this matrix is symmetric, i.e. that the two off-diagonal terms are identical and that the relative size of each of the terms depends on the moment arms of the muscle.

Since the muscles act in parallel, the overall effect of all the muscles acting at the shoulder and elbow can be modelled by adding terms such as those given by (5) for mono-articular muscles to those in (9) for bi-articular muscles. Furthermore, since muscle also has viscous properties, viscosity terms must also be included in the visco-elastic contribution $\underline{T}_v$ to joint torque

$$\underline{T}_v = -\begin{bmatrix} K_\theta & K_{\theta\phi} \\ K_{\theta\phi} & K_\phi \end{bmatrix} \begin{Bmatrix} \Delta\theta \\ \Delta\phi \end{Bmatrix} - C \begin{bmatrix} K_\theta & K_{\theta\phi} \\ K_{\theta\phi} & K_\phi \end{bmatrix} \begin{Bmatrix} \dot\theta \\ \dot\phi \end{Bmatrix}. \quad (10)$$

We have made the simplest possible assumptions, namely that the viscous terms are linear and that viscous and elastic terms are proportional to each other, related by the constant C.

Position and Torque Feedback

The form of position feedback $\underline{T}_F$ was chosen to be similar to the visco-elastic torque $\underline{T}_v$, with a time delay τ

$$\underline{T}_F = -\begin{bmatrix} F_\theta & F_{\theta\phi} \\ F_{\theta\phi} & F_\phi \end{bmatrix} \begin{Bmatrix} \Delta\theta(t-\tau) \\ \Delta\phi(t-\tau) \end{Bmatrix} - C_F \begin{bmatrix} F_\theta & F_{\theta\phi} \\ F_{\theta\phi} & F_\phi \end{bmatrix} \begin{Bmatrix} \dot\theta(t-\tau) \\ \dot\phi(t-\tau) \end{Bmatrix}. \quad (11)$$

Torque feedback was defined simply as

$$\underline{T}_F = -F_T \begin{Bmatrix} T_s(t-\tau) \\ T_e(t-\tau) \end{Bmatrix}. \quad (12)$$

The overall torque acting at the shoulder and elbow is then given by

$$\begin{Bmatrix} T_s \\ T_e \end{Bmatrix} = \underline{T}' + \underline{T}_v + \underline{T}_F + \text{const}, \quad (13)$$

where $\underline{T}'$ is the torque due to externally applied forces, $\underline{T}_v$ is the visco-elastic contribution to the torque (10) and $\underline{T}_F$ the feedback component (11 or 12). The changes in shoulder and elbow angle ($\Delta\theta$ and $\Delta\phi$) were calculated relative to the initial condition, i.e.

$$\Delta\theta = \theta - \theta_0$$

and the constant term in (13) was required to balance the gravitational terms in (1) and (2).

Equations (1), (2), and (13) were integrated numerically using standard procedures. Two types of perturbations were used in these simulations. One was due to a force applied to the upper arm ($T_s' = \pm 10$, $T_e' = 0$); the other resulted from an upwardly or downwardly directed force on the forearm ($T_s' = T_e' = \pm 10$). The perturbation lasted 50 ms.

Quasi-Static Simulations

Joint Stiffness

It is known that the stiffness of a muscle increases with the level of its activation (Cannon and Zahalak 1982). The effect that a change in muscle stiffness has on the visco-elastic coefficients (10) contributing to joint torque depends on whether or not that muscle crosses more than one joint. Thus, increased activation of muscles such as brachio-radialis and brachialis which do not cross the shoulder joint would serve to increase K_ϕ without affecting $K_{\theta\phi}$, while increased activation of a bi-articular muscle such as biceps would lead to an increase in both K_ϕ and $K_{\theta\phi}$. [Given the moment arms of biceps at the shoulder and elbow (Fick 1911), one would expect the biceps contribution to K_ϕ to be about twice as large as that to $K_{\theta\phi}$.] Thus, theoretically there is the possibility that each of the stiffness coefficients K_θ, K_ϕ, and $K_{\theta\phi}$ can be regulated independently.

We investigated the consequences of this hypothesis on the motion of the forearm following pulse perturbations by carrying out simulations in which the cross-coupling term of the stiffness $K_{\theta\phi}$ was varied while keeping the other stiffness terms (K_θ and K_ϕ) fixed. Some of the results of such simulations are presented in Fig. 2. We assumed that the feedback terms $\underline{T}_F$ were zero and the stiffness parameters K_θ and K_ϕ were each fixed to be 30 N-m/rad. For small perturbations, Mussa-Ivaldi et al. (1985) have reported values for each of these parameters ranging from 20 to 40 N-m/rad, while Lacquaniti et al. (1982) obtained the same range of values for K_ϕ while the arm was undergoing large amplitude oscillations. The viscous coefficient C was fixed at 0.05 s^{-1}, somewhat larger than the values determined experimentally by Lacquaniti et al. (1982).

In these simulations $K_{\theta\phi}$ was varied from 0 to 30 N-m/rad, the latter value being the same as K_θ and K_ϕ. Physiologically, increasing the cross-coupling stiffness and keeping the other parameters constant would result from increased stiffening of bi-articular muscles with a compensating decrease in the stiffness of mono-

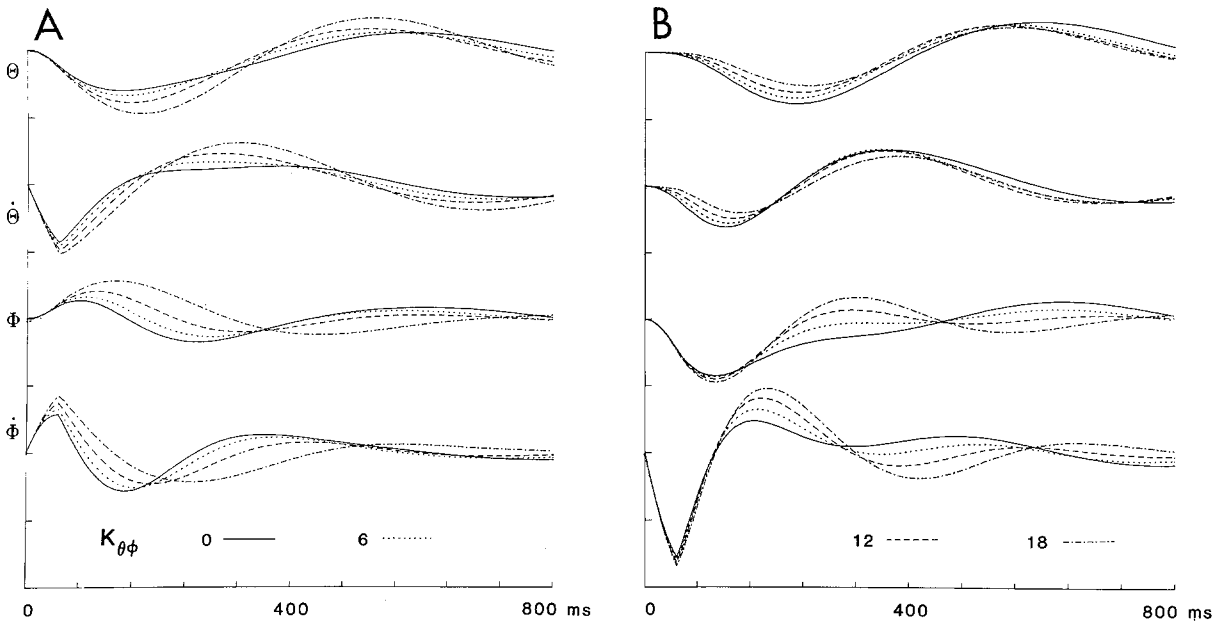

Fig. 2A, B. Limb motion resulting from a 50 ms pulse of force applied to the upper arm (**A**) and to the forearm (**B**). The traces from top to bottom depict changes in shoulder angle (θ) and angular velocity ($\dot{\theta}$) and elbow angle (ϕ) and angular velocity ($\dot{\phi}$). The initial angle of elbow flexion was 90°. In these simulations cross-coupling stiffness $K_{\theta\phi}$ was varied from 0 to 18 N-m/rad, K_θ and K_ϕ were 30 N-m/rad in both cases. Scale: 8° per division for angles and 80°/s per division for angular velocities

articular shoulder and elbow muscles. The maximum value attainable by $K_{\theta\phi}$ is probably about 50% of K_ϕ, based on (7). Experimental values of $K_{\theta\phi}$ determined by Mussa-Ivaldi et al. (1985) were $37 \pm 13\%$ of K_ϕ.

Figure 2A shows the effect of varying the cross-coupling stiffness when the force is applied to the upper arm; the corresponding responses to forces applied to the forearm are shown in Fig. 2B. The angle of elbow flexion ϕ is 90° in both instances. In Fig. 2A, the perturbations result in angular motions at the shoulder and elbow which are oppositely directed: extension at the shoulder and flexion at the elbow. Thus the two terms contributing to the visco-elastic torque $\underline{T}_v$ at the shoulder and at the elbow initially have opposite signs. Therefore it should not be surprising that the cross-coupling stiffness $K_{\theta\phi}$ decreases the effective stiffness at the shoulder and elbow and consequently, the amplitude of the angular oscillations at both joints increases as $K_{\theta\phi}$ is increased.

When the external force acts on the forearm (Fig. 2B), there is initially extension at the shoulder and elbow joints and increasing $K_{\theta\phi}$ does serve to decrease the amplitude of the initial deflection at the shoulder. At the same time, however, there is a small increase in the angular deflection at the elbow and subsequent elbow motion becomes more oscillatory as $K_{\theta\phi}$ is increased.

To quantify the effect of changing this parameter on arm motion resulting from the perturbation, we defined several error criteria, namely the sum of the absolute value of the deviations in the angles or their velocities

$$E_1 = \Sigma|\Delta\theta| + |\Delta\phi| \tag{14}$$

and also the time weighted sum of these values

$$E_2 = \Sigma t(|\dot{\theta}| + |\dot{\phi}|)\,. \tag{15}$$

(The second criterion puts a greater penalty on oscillations which are poorly damped.) The summation was carried out over an 800 ms interval following pulse onset.

Figure 3 shows the variation of these error criteria with $K_{\theta\phi}$, the light lines denoting the sum of angular displacements (14) and the heavier lines the time-weighted sum of velocities (15). All values were normalized with respect to the error score for $K_{\theta\phi} = 0$. The plot shows the mean and standard deviations for results obtained at four different elbow angles, ϕ ranging from 30° extension to 135° flexion. Note that both criteria yield qualitatively similar results. Increasing $K_{\theta\phi}$ leads to progressively larger excursions of the arm when the force is applied to the upper arm, while moderate values of $K_{\theta\phi}$ (6 to 18 N-m/rad) tend to decrease the amplitude of the oscillations of the arm when the force is applied to the forearm.

Position Feedback

As with the cross-coupling stiffness $K_{\theta\phi}$, the effectiveness of position feedback with a given set of parameters

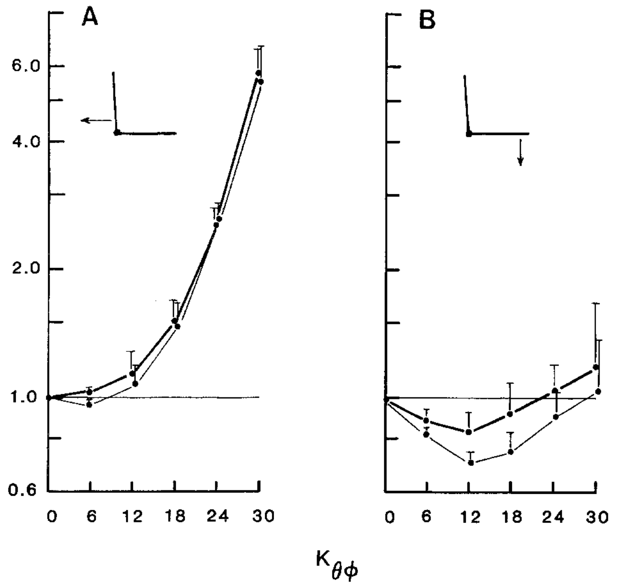

Fig. 3A, B. Effect of varying cross-coupling stiffness on response to force perturbations on upper arm (**A**) and on forearm (**B**). Light traces show variation of normalized angular error, the heavy traces the time-weighted error in angular velocity. The data points represent average values obtained at 4 angles of elbow flexion: 30°, 60°, 90°, and 135°

depends strongly on where the perturbation is applied and on the angle of elbow flexion. Figures 4 and 5 show the results of simulations in which different combinations of feedback parameters were used. For these simulations, we fixed $K_\theta = K_\phi = 30$ N-m/rad and $K_{\theta\phi} = 15$ N-m/rad. The viscous coefficients C and C_F (11) were fixed at 0.05 s^{-1} and 0.10 s^{-1} and a time delay $\tau = 40$ ms was assumed for the feedback terms. We again explored responses to forces applied to the upper arm (Fig. 4) and to the forearm (Fig. 5) at angles of elbow flexion ϕ ranging from 30° to 135°.

The solid traces in Figs. 4 and 5 show changes in shoulder and elbow angles and angular velocities in the absence of feedback, while the dashed and dotted lines illustrate the effect of different combinations of feedback parameters. For example the dotted lines correspond to feedback restricted to the shoulder ($\{F_\theta, F_{\theta\phi}, F_\phi\} = \{6, 0, 0\}$). This particular combination of feedback parameters had almost no effect when the arm was extended ($\phi = 30°$) for forces applied to the upper arm (Fig. 4B) or to the forearm (Fig. 5B). When the arm was flexed ($\phi = 135°$), such a feedback of shoulder angle increased the apparent stiffness primarily at the shoulder (Fig. 5A) or at the shoulder and elbow (Fig. 4A), as can be seen by the decrease in the period of the damped oscillations in the angles. A combination of feedback of shoulder and elbow angle $F_P = \{6, 0, 6\}$ actually tended to destabilize the arm when it was extended (Figs. 4B and 5B) as can be seen by the prolonged duration of the oscillations. On the contrary, the addition of feedback at the elbow had little effect when the arm was flexed (Figs. 4A and 5A). Also, the effectiveness of the cross-coupling feedback term $F_{\theta\phi}$ depended on the initial elbow angle and on the perturbation. Finally, in none of the examples shown was position feedback effective in markedly reducing the amplitude of the initial excursion in

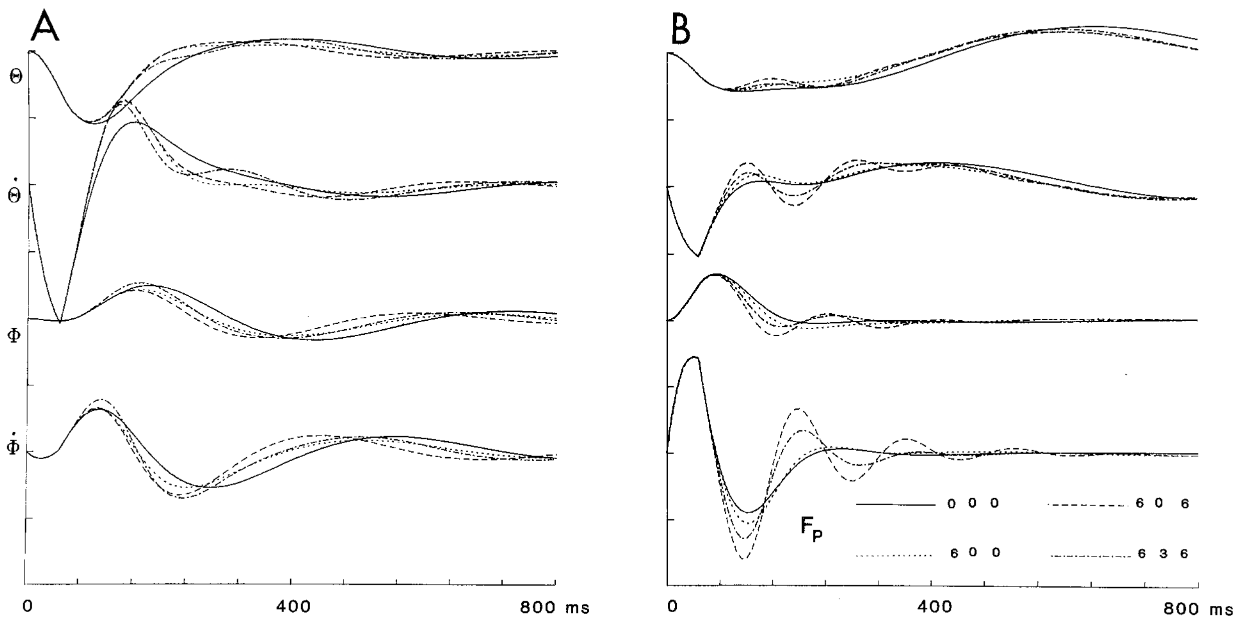

Fig. 4A, B. Effect of different combinations of position feedback on the response to a force perturbation to the upper arm. In **A**, the forearm was flexed ($\phi = 135°$) and extended (30°) in **B**. The values of the feedback coefficients $\{F_\theta, F_{\theta\phi}, F_\phi\}$ are indicated in the figure

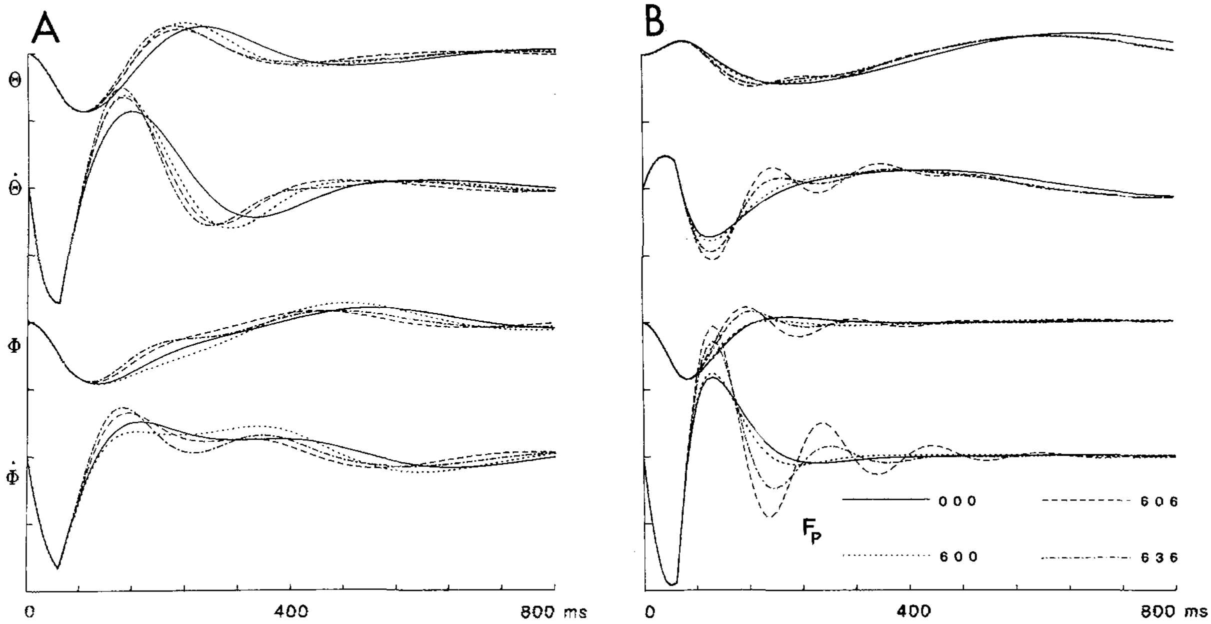

Fig. 5A, B. Effect of different combinations of position feedback on the response to force perturbations to the forearm. In **A**, the forearm was flexed ($\phi = 135°$) and extended (30°) in **B**

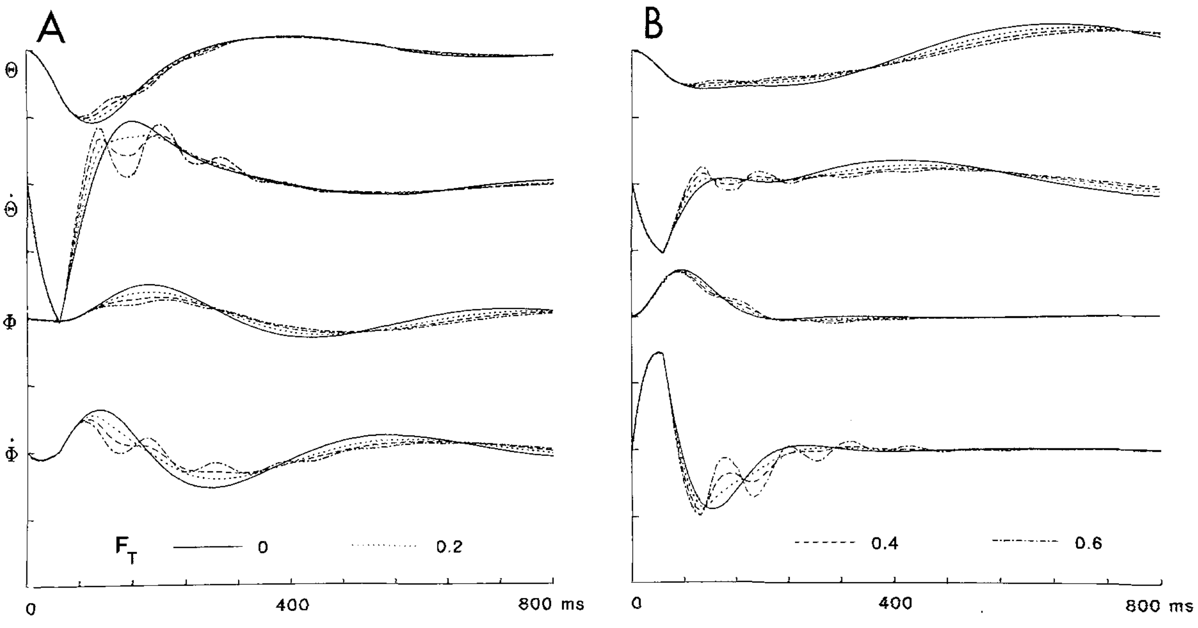

Fig. 6A, B. Effect of different values of torque feedback on response to pulse perturbations to the upper arm, with the forearm flexed ($\phi = 135°$) in **A** and extended (30°) in **B**

shoulder and elbow angles. In some instances, it was effective in damping out the oscillations in arm position more rapidly, while in other instances it clearly was not (Figs. 4B and 5B).

The effectiveness of different combinations of position feedback parameters in damping out the response to force perturbations was quantified by calculating the time-weighted error in angular velocities according to (15). The results are presented in Fig. 8A. It is obvious that, on average, none of the combinations investigated was particularly effective; only position feedback restricted to the shoulder ($F_\theta = 6$) led to a slight reduction in the average error score. For all combinations the standard deviations were large, ranging from 0.12 to 0.37. Thus, a particular combination of feedback parameters could be effective in some instances and detrimental in others, as already pointed out above.

This variability in the effectiveness of a particular set of feedback parameters in arresting the motion following the perturbation stems from the fact that the extent of dynamic interaction between forearm and arm motion varies. When motion is restricted to only one limb segment, position feedback (with the same parameters) is much more effective. For example, position feedback at the elbow ($F_\phi = 6$) gave a time weighted velocity error of 0.82 relative to the one in the absence of feedback while feedback at the shoulder ($F_\theta = 6$) gave an error score of 0.87 when the other joint was fixed.

Torque Feedback

Torque feedback had a much more consistent effect in decreasing the amplitude of the movement and in dampening the oscillations following the perturbation. Figures 6 and 7 show the results of some simulations in which a variable amount of torque feedback [F_T ranging from 0 to 0.6, (12)] was assumed. As for the case of position feedback, we assumed a time delay of 40 ms for torque feedback. Figure 6 shows the responses to a force applied to the upper arm, with the forearm flexed (Fig. 6A) and extended (Fig. 6B) and can be compared with the results presented in Fig. 4 for position feedback. (The same stiffness and viscosity parameters were used in both cases.) The results presented in Fig. 7 are for the same experimental conditions as those in Fig. 5 (force on the forearm, forearm flexed in Fig. 7A and extended in Fig. 7B).

Torque feedback begins to be unstable at a feedback gain of 0.6 as can be seen from the high frequency oscillations in the angular velocities which persist for 400 ms in Figs. 6 and 7. This is also apparent in Fig. 8B, which shows the dependence of the time-weighted velocity error on the torque feedback gain. This error decreases monotonically up to a gain of 0.5.

Time Delay

The value of the time delay τ can also have an appreciable influence on the effectiveness of position or torque feedback. In the results of simulations presented so far τ was fixed at a value of 40 ms. Figure 9 shows how the time-weighted velocity error varies as a function of the time delay, ranging from 4 to 100 ms. The figure presents average values obtained using five different angles of elbow flexion ranging from 30° to 150° and for forces applied to the upper arm or the forearm. For any given combination of position feedback parameters (left panel), the error increases monotonically with τ, as one might expect. However, the effectiveness of torque feedback actually increases as the time delay increases up to about 80 ms and on average the error given a time delay of 76 ms is about 15% less than it is for a time delay of 4 ms.

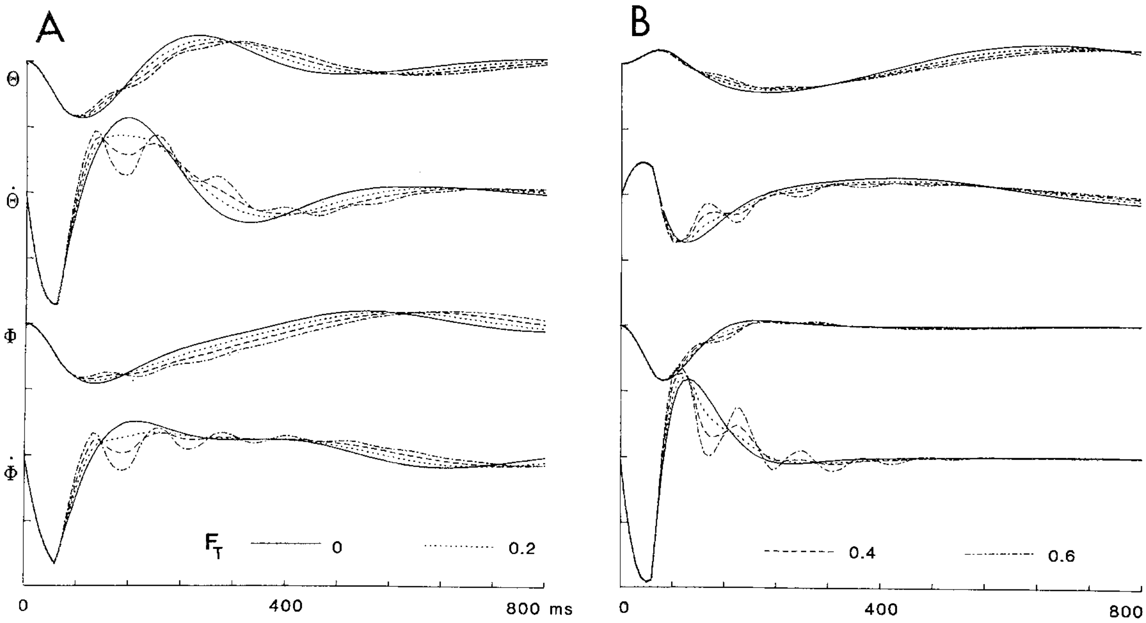

Fig. 7A, B. Effect of different values of torque feedback on response to pulse perturbations to the forearm, flexed (135°) in **A** and extended (30°) in **B**

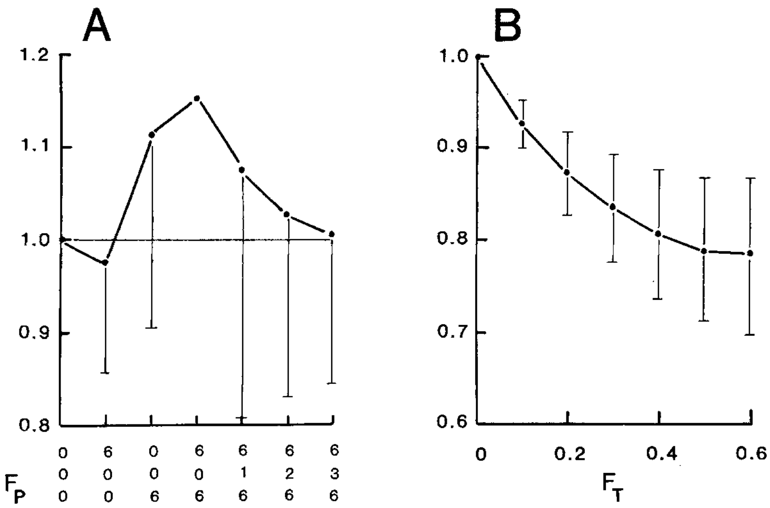

Fig. 8A, B. Dependence of time-weighted velocity error on position *(left panel)* and torque feedback *(right panel)* parameters. Each of the data points shows average values of the normalized error for eight different experimental conditions: four different values of elbow flexion (30°, 50°, 90°, and 135°) and for forces applied to the forearm or to the upper arm. The standard deviation for the position feedback combination {6,0,6} which is omitted for clarity is 0.37

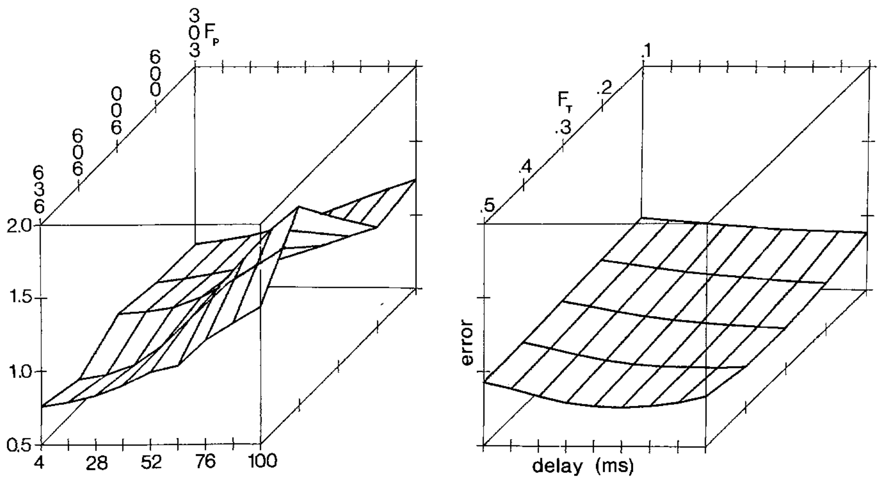

Fig. 9. Dependence of time-weighted velocity error on the feedback delay (τ) for position *(left panel)* and torque feedback *(right panel)*. Feedback delay varied from 4 to 100 ms in 12 ms increments and the values of the feedback coefficients are indicated in the figure. The figure depicts average values of the normalized error for ten different experimental conditions (five values of elbow flexion ranging from 30° to 150° and forces applied to the forearm or the upper arm)

Feedback Control of Movement

Under the quasi-static conditions we have examined so far, the nonlinear velocity terms in the equations for torque (1 and 2) are negligible and the dominant contribution to shoulder and elbow torque is provided by the acceleration terms. However, the velocity terms can be as large as or larger than the acceleration terms during intentional arm movements (Hollerbach and Flash 1982). Thus the question remains whether the conclusions reached when a stationary arm is perturbed are also valid when an external force is applied while the limb is in motion.

Figures 10 and 11 present the results of simulations of a pointing movement during which force perturbations were applied at the arm. The solid lines in Fig. 10 show the trajectory of the wrist of the unperturbed movement which was obtained experimentally (Soechting and Lacquaniti 1981) by asking the subject to point to a target. The movement began with the upper arm vertical and the forearm horizontal and involved flexion of the upper arm and extension of the forearm. The duration of the movement was 650 ms (a relatively fast movement). Shoulder and elbow angles were measured experimentally or derived trigonometrically (Soechting and Lacquaniti 1981) and from these data, shoulder and elbow torques required to produce the movement were calculated.

In these simulations we assumed that the feedback (position or torque) was related to the deviation from the reference values of angular position (θ_{ref}, ϕ_{ref}) or torque ($T_{s\mathrm{ref}}$, $T_{e\mathrm{ref}}$) during an unperturbed movement. Thus, for position feedback

$$T_F = -\begin{bmatrix} F_\theta & F_{\theta\phi} \\ F_{\theta\phi} & F_\theta \end{bmatrix} \begin{Bmatrix} \theta(t-\tau)-\theta_{\mathrm{ref}}(t-\tau) \\ \phi(t-\tau)-\phi_{\mathrm{ref}}(t-\tau) \end{Bmatrix} - C_F \begin{bmatrix} F_\theta & F_{\theta\phi} \\ F_{\theta\phi} & F_\phi \end{bmatrix} \begin{Bmatrix} \dot\theta(t-\tau)-\dot\theta_{\mathrm{ref}}(t-\tau) \\ \dot\phi(t-\tau)-\dot\phi_{\mathrm{ref}}(t-\tau) \end{Bmatrix} \quad (16)$$

and for torque feedback

$$T_F = -F_T \begin{Bmatrix} T_s(t-\tau)-T_{s\mathrm{ref}}(t-\tau) \\ T_e(t-\tau)-T_{e\mathrm{ref}}(t-\tau) \end{Bmatrix}. \quad (17)$$

We also assumed that the "equilibrium point" of the muscle changed during the movement (Bizzi et al. 1984) and was always equal to the reference angles so that the visco-elastic contribution to joint torque is

$$\underline{T}_v = -\begin{bmatrix} K_\theta & K_{\theta\phi} \\ K_{\theta\phi} & K_\phi \end{bmatrix} \begin{Bmatrix} \theta - \theta_{\text{ref}} \\ \phi - \phi_{\text{ref}} \end{Bmatrix} - C \begin{bmatrix} K_\theta & K_{\theta\phi} \\ K_{\theta\phi} & K_\phi \end{bmatrix} \begin{Bmatrix} \dot\theta - \dot\theta_{\text{ref}} \\ \dot\phi - \dot\phi_{\text{ref}} \end{Bmatrix} \quad (18)$$

and the overall torque acting at the shoulder and elbow is given by

$$\begin{Bmatrix} T_s \\ T_e \end{Bmatrix} = \underline{T}' + \underline{T}_{\text{ref}} + \underline{T}_v + \underline{T}_F . \quad (19)$$

In this formulation, during an unperturbed movement (that is $\underline{T}' = 0$) the visco-elastic torque $\underline{T}_v$ and the feedback $\underline{T}_F$ are both zero since the trajectory follows the reference angles. Note that the exact definition of the variation of the "equilibrium point" for the visco-elastic torque $\underline{T}_v$ is not crucial. The angles ϕ_{ref} and θ_{ref} in (18) could have been defined differently, as long as the sum $\underline{T}_{\text{ref}} + \underline{T}_v$ in (19) is equal to the joint torque required to generate the unperturbed movement.

For the simulations we used a force perturbation lasting 50 ms, applied either at the upper arm or at the forearm and at three different times during the movement (just before its onset, and 150 ms and 350 ms after the movement had begun). The results shown in Fig. 10 are for a force acting posteriorly on the upper arm applied 150 ms after movement onset. The same time delay as before ($\tau = 40$ ms) was assumed for the feedback terms.

Figure 11 shows the dependence of the normalized error on the values of the cross-coupling stiffness $K_{\theta\phi}$ and the position (F_P) and torque (F_T) feedback parameters. We calculated the error according to two criteria: 1) the sum of the distances of the wrist from its reference position during the movement (light traces) and 2) the sum of the absolute values of the deviations of joint angular velocities from their reference values (heavy traces). Each point represents the mean error for perturbations occurring at three different times and in opposite directions. In Fig. 11A, the force perturbation was applied to the upper arm and to the forearm in Fig. 11B. The standard deviations were small, generally less than 10% of the mean.

The results presented in Fig. 11 show the same general trends as those found when the perturbation was applied under quasi-static conditions. Thus, for example, increasing the cross-coupling term $K_{\theta\phi}$ led to a larger error in position and velocity when the force was applied to the upper arm but to a decrease in error for intermediate values of $K_{\theta\phi}$ when the force acted on the forearm (compare with Fig. 3). In this latter case, the two error criteria gave different results; position error decreased monotonically while velocity error decreased and then increased again.

As under quasi-static conditions, a given combination of position feedback parameters was not uniformly effective. For example, when the force was applied to the upper arm (Fig. 11A) the presence of the cross-coupling term $F_{\theta\phi}$ in the feedback led to a decrement in performance as measured by the position error (compare the results for $F_P = \{6, 3, 6\}$ with those for $\{6, 0, 6\}$) while it led to a marked improvement in position error when the force was applied to the

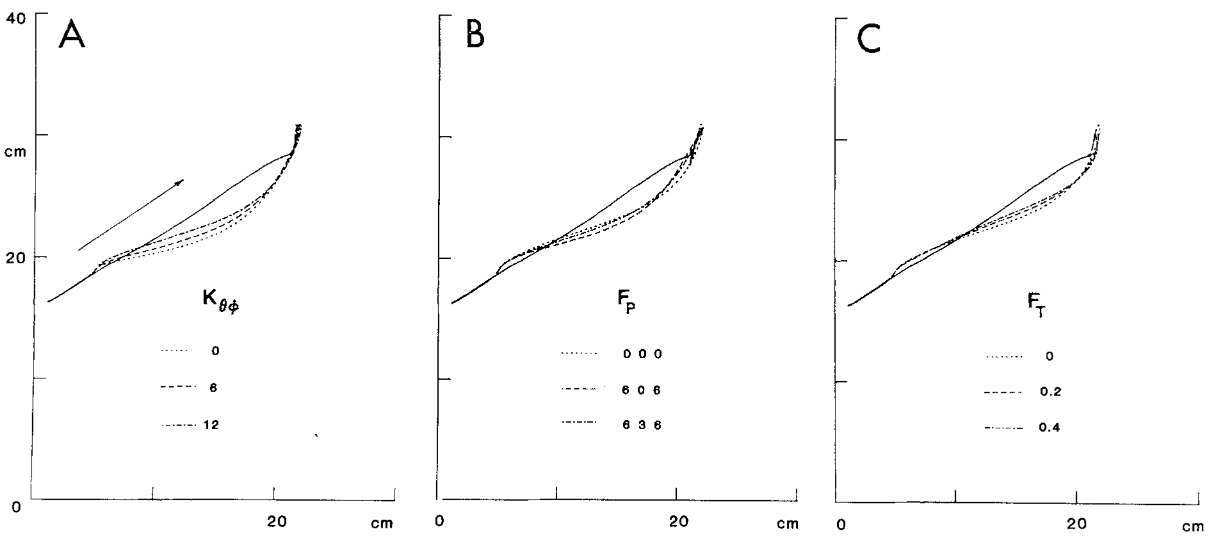

Fig. 10A–C. Effect of perturbations to the upper arm during a pointing movement. Effects of different values of cross-coupling stiffness (**A**), position feedback (**B**) and torque feedback (**C**) are illustrated

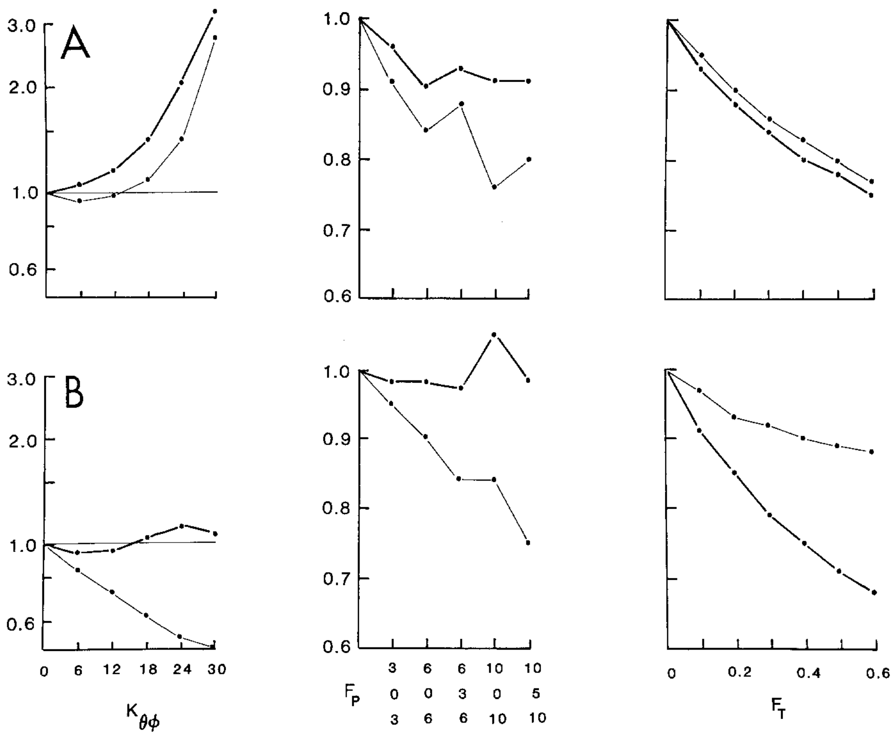

Fig. 11A, B. Effect of different parameter values of cross-coupling stiffness ($K_{\theta\phi}$), position feedback (F_P) and torque feedback (F_T) on normalized error resulting from a force perturbation applied to the upper arm (**A**) or to the forearm (**B**) during a pointing movement. The normalized error was computed in two ways: deviation of wrist from its reference trajectory *(light traces)* and sum of the deviations of angular velocities *(heavy traces)*

forearm. In both instances, the feedback led to little or no decrease in the velocity error. In contrast, torque feedback led to a marked decrease in velocity error in both cases, the decrease in position error being less pronounced when the force was applied to the forearm (Fig. 11B).

Discussion

We have used simple models of the postural control system to gain some insight into the efficacy of different feedback schemes in stabilizing the position of the limb under quasi-static conditions and during point-to-point movements. In particular, except for the dynamic terms [(1) and (2)], the models we investigated were linear and we made no attempt to reproduce exactly experimentally observed responses to force perturbations by varying parameters.

Nevertheless, the results of these simulations are in reasonable agreement with experimental data. Thus for example, the changes in angular position at the shoulder and elbow resulting from a force applied to the upper arm (Figs. 4B and 6B) closely approximate experimental data obtained under similar initial conditions (Figs. 5B and 6 of Lacquaniti and Soechting 1986b). In agreement with experimental observations, the deviation from the initial position of the shoulder angle is prolonged, showing a plateau, while elbow angle ϕ returns much more quickly to its original position. More generally, the period of the damped oscillations and the relative excursions in shoulder and elbow angles were close to those observed experimentally (Lacquaniti and Soechting 1986a, b). Perhaps this should not be surprising since the behavior of the system was dominated by the visco-elastic torque $\underline{T}_v$, whose parameters were based on experimentally derived values (Lacquaniti et al. 1982; Mussa-Ivaldi et al. 1985). It does indicate however that these values are also reasonable estimates for the characteristics of the system under the experimental conditions which the model presented here was designed to simulate.

As regards the behavior of the feedback models (position and torque) we investigated, some general comments need to be made. First, since the effects of the feedback terms were not large, it is not possible to deduce which of these models might be more appropriate to model physiological behavior by comparing the results of simulations with experimental data. Secondly, we made no systematic attempt to optimize each of these models such as by incorporating additional (nonlinear) terms.

The parameter values used in the simulations appear reasonable. Values of the moments of inertia of the arm (1 and 2) and for the visco-elastic coefficients (10) were based on available experimental data. While the value of the time delay which was used in most of the simulations ($\tau = 40$ ms) was greater than segmental conduction delays, this value agrees with estimates of feedback delays of the electromyographic response to perturbations restricted to the forearm (Dufresne et al. 1978). Similarly, the ratio of velocity to position feedback ($C_F = 0.1$) appears reasonable. The electromyographic response of muscles to perturbations when motion is restricted to one joint is related primarily to its angular velocity (Dufresne et al. 1978; Kearney and Hunter 1983). However, when the relationship between EMG activity and force output is considered, the low-pass filter characteristics of the latter relation will yield an overall feedback primarily related to angular position (Poppele and Terzuolo 1968; Rosenthal et al. 1970).

In the following, we shall discuss the results of these simulations from the point of view of several hypotheses which have been put forward concerning the role of muscle activity originating from afferents in stabilizing limb position. Thus, it has been suggested that afferent feedback acts to maintain muscle stiffness constant; in the absence of feedback the apparent muscle stiffness given a muscle stretch is smaller than its stiffness in shortening (Houk and Rymer 1981) and the increase in muscle activity following a stretch could compensate for this nonlinearity. The results presented in Figs. 2 and 3 show that such a scheme will not always be advantageous. In particular, for some perturbations (e.g. a force on the upper arm), it would in fact be preferable to maximize the stiffness of monoarticular muscles while minimizing the stiffness of biarticular muscles. Under other conditions, instead, a cross-coupling stiffness $K_{\theta\phi}$ about 40% of K_θ and K_ϕ appears optimal. Note that a differential modulation in each of the stiffness parameters was not observed by Mussa-Ivaldi et al. (1985). Furthermore, such a strategy would be useful only if the perturbation were predictable.

Position feedback can help stabilize the limb. However, it is obvious from the results presented in Figs. 4, 5, and 8 that an optimal choice of parameters depends on the elbow angle and the relative amount of external torque T' acting at the shoulder and elbow. Thus the feedback parameters would need to be highly task-dependent on variables which are known prior to the perturbations (such as the elbow angle) but also on variables (such as T') which cannot always be predicted. Since torque feedback already takes into account the dynamic interaction between limb segments, its efficacy depends to a much lesser extent on the initial conditions.

One final comment may be appropriate. Even torque feedback led to a reduction of not much more than 20% in the velocity error following the perturbation (Figs. 8B and 11) and a much smaller reduction in the maximum amplitude of the angular excursion at the shoulder and elbow (Figs. 6 and 7). While it is likely that other (for example nonlinear) feedback models could lead to better performance, this result is in agreement with conclusions reached by others who have suggested that the contribution of feedback mechanisms to postural stabilization may be modest (Stein 1982).

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