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RESEARCH ARTICLE

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Forearm postural control during unloading: anticipatory changes in elbow stiffness

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Abstract In this study, the equilibrium-point hypothesis of muscle-torque generation is used to evaluate the changes in central control parameters in the process of postural-maintenance learning. Muscle torque is described by a linear spring equation with modifiable stiffness, viscosity, and equilibrium angle. The stiffness is considered to be the estimation of the central command for antagonist-muscle coactivation and the equilibrium angle to be the estimation of the reciprocal command for a shift of invariant characteristics of the joint. In the experiments, a load applied to the forearm was released. The subjects were instructed to maintain their forearm in the initial horizontal position. Five sessions of approximately twenty trials each were carried out by eight subjects. During two "control" series, the load release was triggered by the experimenter. During three "learning" series, the load supported by one forearm was released by the subject's other hand. The elbow-joint angle, the angular acceleration, and the external load on the postural forearm were recorded. These recordings as well as anthropometric forearm characteristics were used to calculate the elbow-joint torque (which we called "experimental"). Linear regression analysis was performed to evaluate the equilibrium angle, joint stiffness, and viscosity at each trial. The "theoretical" torque was calculated using a linear spring equation with the found parameters. The good agreement observed between experimental and theoretical joint-torque time courses, apart from the very early period following unloading, argues in favor of the idea that the movement was mainly performed under a constant central command presetting the joint stiffness and the equilibrium angle. An overall increase in the stiffness occurred simultaneously with a decrease in the equilibrium angle during the "learning" series in all the subjects. This suggests that subjects learn to compensate for the disturbing effects of unloading by increasing the joint stiffness. The mechanism possibly responsible for the presetting of the central control parameters is discussed.

Key words Posture maintenance · Bimanual unloading · Joint stiffness · Equilibrium angle · Invariant characteristics

Introduction

In a bimanual load-lifting task, when one arm was supporting a load and the other voluntarily lifting the load, anticipatory adjustments are observed in the postural arm, which minimize the postural disturbance due to the unloading (Paulignan et al. 1989; Massion 1992; Ioffe et al. 1996). Two types of mechanisms may serve to maintain the position of the postural forearm when a disturbance is caused by a voluntary movement: (1) a feedback postural correction and (2) an anticipatory postural adjustment. The last mechanism was found to be the more efficient means of stabilizing the forearm position, because it is able to reduce or abolish the earliest effects of the disturbance. The first question which arises was therefore as follows: what parameters are used by the nervous system to control the feed-forward adjustment of the postural forearm?

The acquisition of the anticipatory postural adjustment of the postural forearm was further investigated using a new experimental procedure, where the load was released from the postural forearm by an electronic switch triggered by a load-lifting movement made by the other forearm (Paulignan et al. 1989; Massion 1992; Ioffe et al. 1996). After 40–60 trials, a significant decrease in the postural forearm-elbow flexion after un-

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loading was noted. The present study addresses the changes in the controlled parameters occurring during the learning process.

This analysis was based on the equilibrium-point (EP) hypothesis, which has been successfully used to investigate several motor tasks (Feldman 1979; Bizzi and Abend 1983; Flash 1987; Latash and Gottlieb 1992; Flanagan et al. 1993). In the framework of the EP hypothesis, the tonic stretch-reflex thresholds of antagonistic muscles are taken to be the main, centrally regulated parameters (Feldman 1979). These parameters determine the dependence of joint torque on joint angle and angular velocity. In the context of a spring-like model, this dependence can, in turn, be characterized by three main parameters: the equilibrium angle, the joint stiffness, and the joint viscosity. It was attempted to evaluate these parameters by recording both the postural forearm kinematics and the external forces acting on the forearm after unloading.

The increase in stiffness during learning, which provides the simplest explanation for postural maintenance, was indeed found as a result of calculations based on the kinematic recordings. The increase in the stiffness was furthermore found to be closely correlated with changes in equilibrium angle. These two parameters are in principle independent, since they are determined by the independent stretch-reflex thresholds of flexor and extensor muscles. This close correlation was taken to result from an anticipatory shift of the extensor stretch-reflex threshold in the feed-forward control process responsible for maintaining the postural forearm position. Via this single parametric change, the equilibrium angle and joint stiffness are both preset together.

Materials and methods

Experimental procedure

The experimental procedure used here has been described in detail elsewhere (Ioffe et al. 1996). In these experiments, one forearm (the postural forearm) was held in a given position, whereas the other arm (the moving arm) lifted a load. Four right-handed and four left-handed subjects were tested. The subjects were seated in an armchair with a back support. The elbow was placed on the arm of the chair, and the semipronated forearm was approximately horizontal. The subjects were instructed to gaze straight ahead at a line on the wall 4 m in front of them, to keep their forearm horizontal during the whole session, and not to pay any attention to disturbances which might occur. A load (1 kg) was electromagnetically locked to a bracelet (0.3 kg) attached to the forearm near the wrist. The experiment started with a "control" series (of about 20 trials), in which the load was unpredictably released. Two "learning" series (about 20 trials in each, with a 15-min break in-between) were then run, in which the load was released by the subject lifting a weight (1 kg) from a force platform with the opposite arm. The load release from the postural forearm was triggered when the force measured by the force platform under the lifting arm reached half of the initial value. A second "control" series (of 10 trials) and a third "learning" series (of 20 trials) completed the experiment. The second control series was run in order to check whether the amplitude of the unloading-induced movement in the "control" series depended on the intervening series with voluntary unloading ("learning" series). The third learning series was run in order to determine whether the learning process was still occurring. The subjects were instructed to keep their forearm horizontal in both the "control" and "learning" series. Two learning sessions were run with each subject with each arm (dominant and nondominant) serving as the postural arm (see Ioffe et al. 1996).

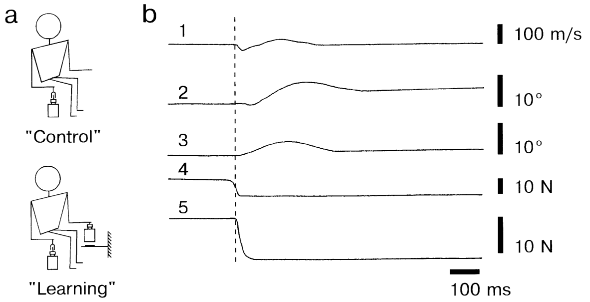


Fig. 1 **a** Experimental setup for the "control" and "learning" series. **b** Recording of a single trial in the learning series. The time course is shown for the following parameters: (*1*) angular acceleration of the postural forearm, (*2*) elbow-joint angle of the lifting arm, (*3*) elbow-joint angle of the postural forearm, (*4*) force-platform recording under the lifting arm, and (*5*) postural forearm load release. The *vertical dashed line* corresponds to the load-release onset

The positions of the two forearms were recorded with potentiometers; the vertical acceleration of the postural forearm was monitored by means a linear accelerometer placed at the level of the wrist; the force acting on the postural forearm was recorded with strain gauge on the bracelet. The analog signals were filtered using a second-order Butterworth filter with a cut-off frequency of 150 Hz. The joint angle and angular velocity were calculated by integrating the recorded acceleration. Good agreement was obtained between the calculated and recorded angles in all the trials, which indicates the accuracy of the kinematic measurements. The integration can be said to have served as a kind of smoothing procedure. No further smoothing was performed on the angles and angular velocities.

The sampling rate used for digitizing and storing the analog parameters was 1000 Hz. Example of the experimental recording is given in Fig. 1.

The model

It is well known that the neuro-muscular system is able to generate forces compensating for external disturbances. This ability is based on both the biophysical properties of the muscles and the way in which the stretch-reflex loop operates. In spite of the complexity of the neuro-muscular system, its ability to resist external disturbances can be compared with the behavior of a simple, nonlinear visco-elastic spring. It is generally recognized that the spring-like behavior of the neuro-muscular system plays an important role in the maintenance of posture. In the EP hypothesis (Feldman 1979), this spring-like behavior is mainly determined by the intrinsic muscle properties and the functional principles underlying the stretch-reflex loop, which is controlled by the central nervous system at supraspinal level. The central control specifies the tonic stretch-reflex thresholds applicable to the muscles around a joint. In each muscle, the stretch reflex determines the relationship between muscle forces and muscle length. According to the EP hypothesis, the movement control consists of shifting the curve describing this relationship along the muscle-length axis. This curve is called the muscle invariant characteristic (later on, we will deal with the equivalent relationship between muscle torque and joint angle). The sum of the invariant characteristics of the agonist and antagonist muscles constitutes the joint characteristic (JC) (Fig. 6). For the sake of simplicity, we take the invariant characteristics of antagonistic muscles to be symmetrical. When muscles' invariant characteristics (ICs) shift in the same direction, the point of intersection of JC with the angle axis changes. This means that a reciprocal command, r(t), is involved. When muscles' invariant characteristics shift in opposite directions, the slope of the JC (joint stiffness) changes. This means that a coactivation command, c(t), is involved (Feldman 1980). When a single invariant characteristic shifts, this results in changes of both the joint stiffness and the point of JC intersection. As an example, Fig. 6 illustrates a shift of antagonist (extensor) invariant characteristic to the left. It was assumed that these two central commands, r(t) and c(t), mainly control spring-like properties of the elbow joint during unloading.

The invariant characteristics of individual muscles have been found to be rather nonlinear (Feldman 1966; Shadmehr and Arbib 1992), but the coactivation of antagonists results in JC, which is practically linear (Feldman 1980). Hence, in a first approximation, the joint torque, T_{th}, can be described by the linear spring equation:

$$\mathrm{T}_{\mathrm{th}} = -k(\theta - \theta_0) - v\dot{\theta}, \qquad \text{(Eq. 1)}$$

where θ is the joint angle (its increase corresponds to flexion, see Fig. 6), $\dot{\theta}$ is the angular velocity, θ_0 is the intersection of the JC with the angle axis, k is the stiffness, and v is the viscosity. The torque T_{th} will be referred to below as "theoretical". The stiffness, k(t), and the intersection, θ_0(t), can be taken to reflect the central commands c(t) and r(t). The viscosity, v(t), can be taken to reflect the damping effect produced mainly by afferent feedback. It has been postulated that this parameter may be centrally controlled via gamma-dynamic MNs (Feldman 1979). The simplified, linear spring model (Eq. 1) has been widely used in motor-control studies (Mussa-Ivaldi et al. 1985; Flash 1987; Gomi and Kawato 1996).

The experimental measurements were used to calculate the joint torque according to the formula:

$$\mathrm{T}_{\mathrm{exp}} = \left(I + M_{br} L_f^2\right) \cdot \ddot{\Theta} + MGL_{cg} \cos(\theta) + M_b$$
$$+ M_{br} GL_f \cos(\theta) + FL_f \cos(\theta), \qquad \text{(Eq. 2)}$$

where θ is the angle between the horizontal axis and longitudinal axis of the forearm in the rotation plane, $\ddot{\Theta}$ is the angular acceleration (which is equal to the measured linear acceleration divided by the length of the forearm), I is the total moment of inertia of the forearm and the hand relative to the axis of elbow rotation, M_{br} is the mass of the bracelet from which the load was suspended, L_f is the length of the forearm, M is the total mass of the forearm and the hand, L_{cg} is the distance from the axis of elbow rotation to the center of gravity of the forearm, F is the unloading force acting on the postural forearm, and G is the gravity acceleration (G=9.8 m/s^2). The first term describes the inertia of the forearm, the hand, and the bracelet; the second the torque of the gravity forces acting on the forearm and the hand; the third the torque of the gravity forces acting on the bracelet; and the fourth the torque of the unloading forces (unloading is not effected instantaneously, see line 5 of the experimental recording (Fig. 1).

The length of the forearm, L_f, and that of the hand, L_h, were measured directly; L_{cg} was taken to be half of the length of the forearm plus the hand, and the total mass of the forearm and the hand was calculated from the body weight, W using the formula M=0.0265 W (Drillis et al. 1964); the approximate value of the moment of inertia relative to the axis of rotation in the elbow was calculated using the formula $I=M(L_f+L_h)^2/12+M\,L_{cg}^2/2$. The moment of inertia varied depending on the subject from 0.04 kg·m^2 to 0.12 kg·m^2. The elbow joint torque calculated from Eq. 2 will be referred to below as "experimental".

Stiffness and viscosity

Although θ_0 and k in Eq. 1 are generally time dependent, it can be assumed that, in the absence of central regulation, they are practically constants. In the case of the abrupt unloading triggered by the subject's other hand, it can also be assumed that the central regulation is likely to be triggered prior to the unloading-induced movement of the postural forearm and to accompany it only during early stages. The movement can therefore be largely described by the simple linear model corresponding to Eq. 1 with constant θ_0, k, and v. Linear regression analysis was performed to approximate the dependence of the joint torque on the joint angle and the angular velocity in each "control" and "learning" trial. The entire set of torque values calculated on the basis of Eq. 2 from each kinematic time-curve sample was taken as the dependent variable. The entire set of joint angles and angular velocities calculated at each sampling point by integrating the acceleration recordings were taken as the independent variables. Regression coefficients were used to evaluate the intersection θ_0, stiffness k, and viscosity v according to Eq. 1 in each trial.

The linear regression analysis yielded the intercept value, $k\theta_0$, and regression coefficients $-k$, and $-v$. The JC intersection, θ_0, can be determined as the intercept value divided by k. In order to eliminate any differences in the initial elbow angle, θ_0, between trials, the JC intersection θ_0 was calculated relative to the initial position.

Statistical analysis

To evaluate the changes in the stiffness k, viscosity v, and JC intersection θ_0 during the experimental series, the dependencies of their values upon the number of the trial were fitted to straight lines using the least-square method. The slope of the regression line was taken as an index of the changes in the corresponding parameter during the series. The mean values of the parameters were evaluated in each series. Two series were taken to be "statistically different" when their 95% confidence limits did not intercept.

The correlation between k and θ_0 in each series was examined. In order to evaluate the validity of a correlation coefficient between k and θ_0, the number of degrees of freedom in each series was estimated for each of these parameters. For this purpose, the independence of the values of k in adjacent trials of each series was first checked. The value k calculated in each trial was taken as the dependent variable and the value k calculated in the adjacent trial as the independent variable. If the correlation between these two variables was non-significant (P>0.05 using Student's criteria), we concluded that the values in the adjacent trials were independent and the number of degrees of freedom in the series in question was said to be equal to the number of trials in this series minus 2. The same procedure was used in the case of θ_0.

Results

General characteristics of torque, joint stiffness, and JC intersection

Linear regression analysis was carried out on the results of all the trials in each experimental session in order to evaluate the changes in stiffness, viscosity, and JC intersection occurring during the learning process. In all trials, the regression coefficients were statistically significant and the square of the coefficient of multiple linear regression ranged between 0.72 and 0.98. The values of k, θ_0, and v obtained were substituted on the right hand side of Eq. 1 and the theoretical torque time course was calculated. Good agreement was obtained between the theoretical and experimental torque time courses throughout the movement, except for the short period at the beginning (10–20 ms) in all trials (Fig. 2a).

To estimate the JC intersection, the stiffness value obtained was substituted into the JC intersection formula based on Eq. 1:

$$\theta_0(t) = \left(\mathrm{T}_{\mathrm{exp}} + k\theta - v\theta\right) / k$$

The time course of JC intersection θ_0(t) is given in Fig. 2b. It can be seen from this figure that, during the interval starting 10 ms after the onset of unloading up to the

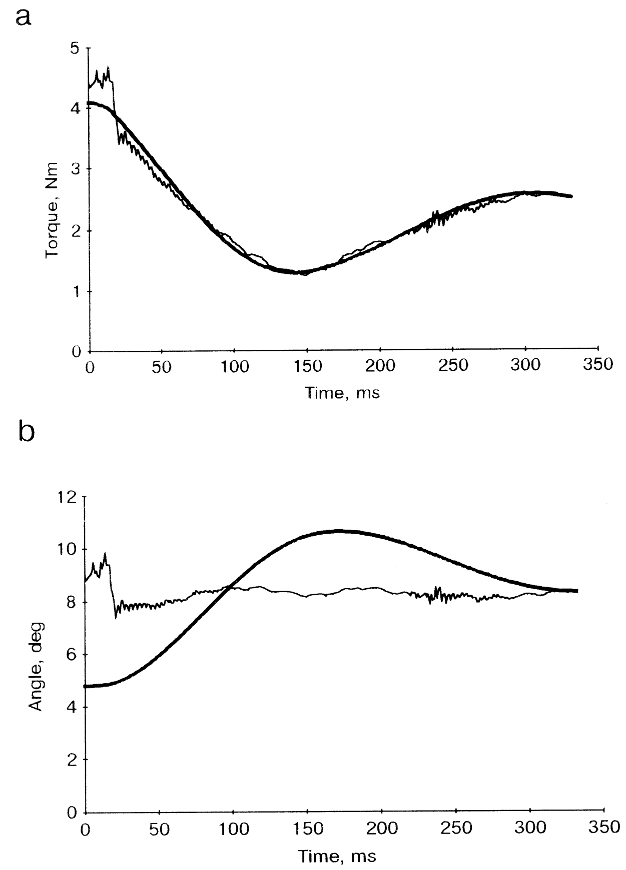


Fig. 2 **a** Comparison of the theoretical (*smooth curve*) and experimental (*noisy curve*) torque time courses as well as **b** the elbow angle (*smooth curve*) and JC intersection (*noisy curve*) time courses. Data from a single trial are shown. They are representative of both "control" and "learning" trials. Since, in the final forearm position, there was an external force equal to the weight of the forearm, the JC intersection $\Theta_\varnothing$ is not equal to the final angle θ_f (see Fig. 6). To illustrate the fact that the joint angle tends towards the equilibrium angle, the constant value *T/k* (*T* is the joint torque in the final position of the forearm, and *k* is the stiffness) was added to θ_0. The decrease of JC intersection during the initial period of movement should be considered as a meaningless consequence of the calculations

end of the unloading-induced movement, the JC intersection was practically constant. It never changed significantly in either the "control" or "learning" series. The fact that initial parts of the curves differed substantially suggests, however, that the linear model does not fit this part of the movement.

The difference between the theoretical and experimental joint torques during the movement was calculated as follows:

$$\Delta = \frac{1}{T_{max}} \int_0^{\tau} \frac{1}{\tau} \left(T_{exp}(\mathrm{t}) - T_{th}(\mathrm{t}) \right)^2 \mathrm{d}$$

where T_{max} is the maximum of the experimental joint torque, τ is the total duration of the unloading induced movement, T_{th}(t) and T_{exp}(t) are the theoretical and experimental joint torques calculated from Eqs. 1 and 2, respectively. The values of Δ varied between trials and between subjects from 2% to 4%.

"Control" unloading

During the "control" series, the load release was triggered by the experimenter. It was previously established (Ioffe et al. 1996) that the amplitude of the unloading-induced movement did not differ significantly between the first and second "control" series. In view of this fact, the first "control" series was combined in our analysis with the second into a single "long control" series.

The mean values and standard deviations of the stiffness, viscosity, and JC intersection obtained in the "long control" series in various subjects are presented in the Tables 1–3, respectively. The first line corresponds to the dominant arm of each subject and the second line to the nondominant arm. Each subject worked within his own individual range of control parameters. The slopes of the straight-line approximations of the parameter values versus the number of trial were used to evaluate the changes in the parameters occurring within the series. No systematic changes actually occurred within the series: both increasing and decreasing patterns of change in the parameters (both positive and negative signs of the slopes) were observed. There were no significant variations in the stiffness, viscosity, or JC intersection values during the "long control" series. On the basis of these results, the mean of stiffness and viscosity values obtained in the "control" series were used as control values for these parameters in the "learning" series.

"Learning" unloading

During the "learning" series, a load lifting by one hand triggered the release of the load supported by the other forearm. Changes in both the stiffness and the JC intersection were observed during the learning process.

Changes in stiffness and viscosity

The mean stiffness values obtained in the "learning" series were larger than in the "control" series (Table 1). Furthermore, the straight-line approximations of the stiffness versus the number of trial in the "learning" series fell above the approximations obtained in the "control" series in the case of almost all subjects (Fig. 3). To analyze the overall process of learning, three "learning" series were combined into "long learning" series in a sequential order, as was done with the "control" series. Some changes in the stiffness certainly occurred from one "learning" series to another. However, the learning continued throughout the series and, by combining them into "long learning" series, we assumed that it could be possible to examine both the changes within series and between series.

The straight-line approximations of the stiffness versus the number of trial, with the 95% confidence limits obtained in the "long control" and "long learning" series, are given in Fig. 4 for the dominant arm of subject SA. It

Table 1 Forearm moments of inertia, mean values (M_s), standard deviations (σ), and slopes (with the probability level P) of the straight-line approximations of elbow-joint stiffness obtained in the "long control" and "long learning" series. The data on the *top line* for each subject correspond to the dominant arm and those on the *second line* to the non-dominant one

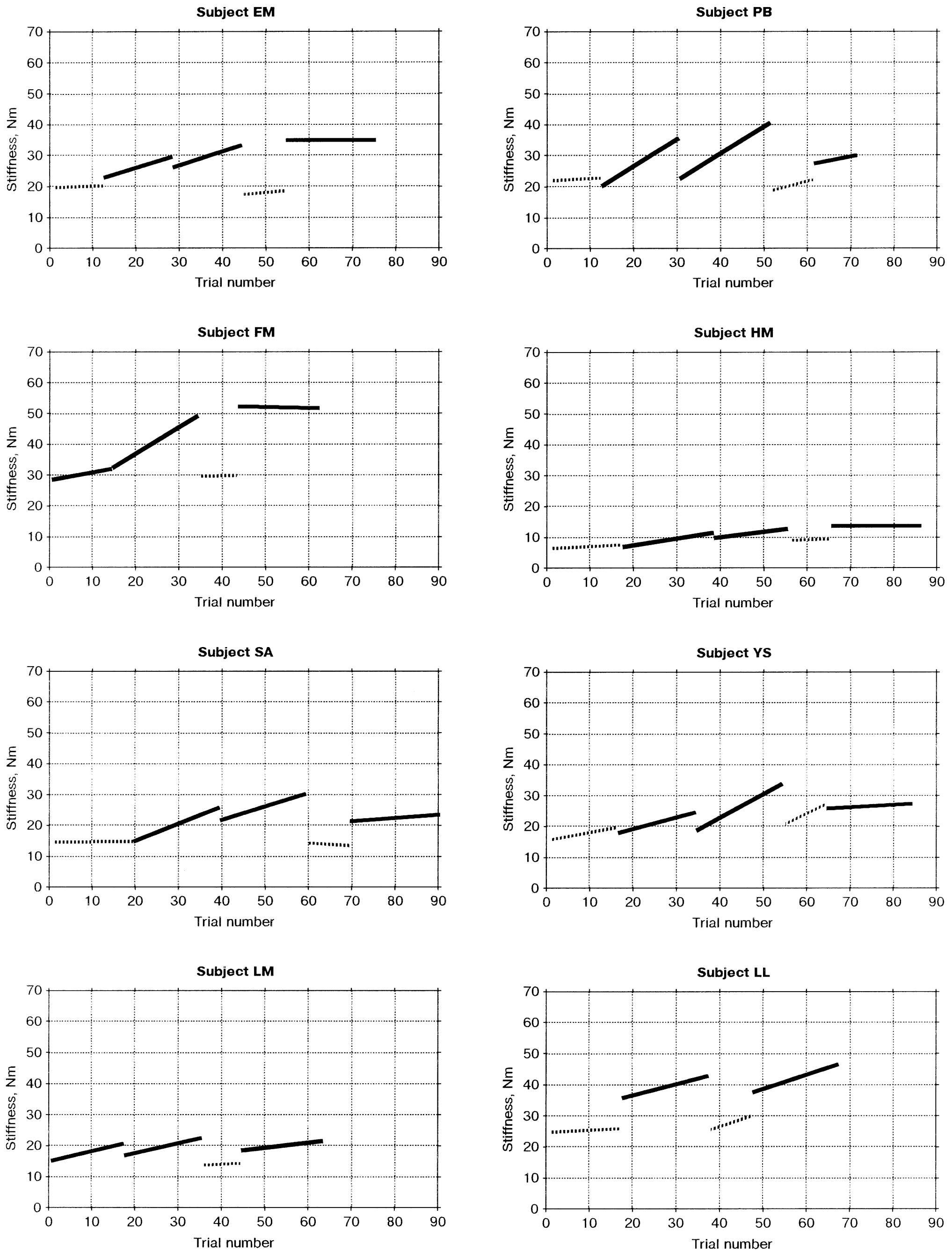
Subject	Moment of intertia [kg·m^2]	"Long learning" series		"Long control" series	
		M_S±σ [Nm]	Slope (*P*)	M_S±σ [Nm]	Slope (*P*)
EM	0.08	30.6±5.5	0.25 (0.00)	19.2±2.9	–0.11 (0.29)
		31.1±6.5	0.25 (0.00)	12.8±1.8	0.09 (0.02)
FM	0.12	41.9±10.6	0.57 (0.00)	29.9±6.9	0.06 (0.95)
		41.1±9.9	0.32 (0.00)	33.3±6.2	–0.77 (0.00)
SA	0.05	22.8±5.0	0.08 (0.02)	14.6±1.2	–0.04 (0.17)
		24.0±4.1	0.07 (0.03)	15.6±1.6	0.03 (0.37)
LM	0.04	19.1±4.0	0.08 (0.02)	14.2±0.3	0.06 (0.22)
		18.7±3.8	0.18 (0.00)	16.5±3.8	0.23 (0.00)
PB	0.10	29.5±5.7	0.16 (0.00)	21.6±4.4	–0.08 (0.60)
		31.7±7.2	0.24 (0.00)	–	–
HM	0.04	11.3±2.8	0.12 (0.00)	9.3±0.7	0.13 (0.00)
		13.1±7.2	0.20 (0.00)	10.5±1.6	0.05 (0.12)
YS	0.07	24.7±4.6	0.16 (0.00)	20.3±5.0	0.43 (0.00)
		29.7±7.1	0.23 (0.00)	21.5±2.0	0.10 (0.05)
LL	0.10	40.6±8.6	0.21 (0.08)	26.5±2.1	0.17 (0.00)
		34.7±6.5	0.21 (0.00)	28.6±3.1	0.09 (0.19)

Table 2 Mean values (M_v), standard deviations (σ), and slopes (with the probability level P) of the straight-line approximations of elbow-joint viscosity obtained in the "long control" and "long learning" series. The data on the *top line* for each subject correspond to the dominant arm and those on the *second line* to the non-dominant one

Subject	"Long learning" series		"Long control" series	
	M_V±σ [Nms]	Slope (*P*)	M_V±σ [Nms]	Slope (*P*)
EM	1.1±0.3	–0.010 (0.00)	0.4±0.3	–0.004 (0.72)
	1.2±0.3	0.005 (0.08)	0.1±0.1	0.004 (0.09)
FM	1.7±0.8	–0.030 (0.00)	1.2±0.5	–0.040 (0.57)
	2.8±0.4	–0.001 (0.83)	1.9±0.4	–0.020 (0.26)
SA	0.6±0.2	–0.007 (0.00)	0.4±0.1	–0.006 (0.05)
	0.5±0.3	–0.008 (0.00)	0.6±0.2	–0.002 (0.62)
LM	0.4±0.2	0.000 (0.90)	0.1±0.1	–0.005 (0.04)
	0.6±0.2	0.002 (0.28)	0.5±0.2	0.013 (0.19)
PB	1.1±0.4	–0.009 (0.03)	1.6±0.2	–0.002 (0.74)
	1.0±0.3	0.002 (0.56)	–	–
HM	0.4±0.2	–0.006 (0.00)	0.3±0.2	–0.006 (0.09)
	0.4±0.2	0.003 (0.12)	0.6±0.1	–0.010 (0.00)
YS	0.6±0.2	0.001 (0.43)	0.2±0.2	0.010 (0.03)
	1.0±0.4	–0.001 (0.63)	0.5±0.2	0.000 (0.99)
LL	1.3±0.8	0.015 (0.18)	0.3±0.2	0.005 (0.45)
	1.6±0.6	0.015 (0.00)	0.9±0.3	–0.020 (0.00)

Table 3 Mean values (M_{in}), standard deviations (σ), and slopes (with the probability level P) of the straight-line approximations of JC intersection in the "long control" and "long learning" series. The data on the *top line* correspond to the dominant arm and on the *second line* to the non-dominant one of each subject

Subject	"Long learning" series		"Long control" series	
	M_{in}±σ [deg]	Slope (*P*)	M_{in}±σ [deg]	Slope (*P*)
EM	9.3±2.2	–0.10 (0.00)	14.1±1.8	0.13 (0.03)
	8.6±2.7	–0.11 (0.00)	15.9±1.6	–0.04 (0.24)
FM	8.2±2.6	–0.14 (0.00)	10.9±1.8	0.05 (0.83)
	8.3±1.9	–0.07 (0.00)	9.7±1.8	0.20 (0.01)
SA	7.2±2.1	–0.06 (0.00)	8.0±3.1	0.20 (0.00)
	10.5±3.0	–0.10 (0.00)	16.9±2.0	–0.02 (0.56)
LM	11.6±2.9	–0.17 (0.00)	13.5±2.8	–0.17 (0.00)
	7.4±2.8	–0.13 (0.00)	13.5±0.7	–0.18 (0.05)
PB	10.8±2.6	–0.09 (0.00)	15.0±2.6	0.06 (0.48)
	7.9±2.3	–0.08 (0.00)	–	–
HM	19.4±7.0	–0.31 (0.00)	29.7±6.1	–0.41 (0.00)
	11.2±5.3	–0.21 (0.00)	19.7±3.5	–0.05 (0.49)
YS	9.3±2.0	–0.09 (0.00)	10.6±1.2	–0.10 (0.00)
	9.7±3.1	–0.10 (0.00)	13.4±1.2	–0.03 (0.36)
LL	8.8±1.8	–0.08 (0.00)	13.4±0.9	–0.06 (0.00)
	12.4±2.5	–0.09 (0.00)	16.4±1.4	–0.04 (0.20)



Subject EM

Subject PB

Subject FM

Subject HM

Subject SA

Subject YS

Subject LM

Subject LL

Fig. 3 Straight-line approximations of the stiffness values versus number of trial for all eight subjects (*EM–LL*). The dominant arm was chosen as the postural one. The series within the experimental session were taken in sequential order: *dashed lines* were used for the “control” series and *solid lines* for the “learning” one

can be seen from Fig. 4 that the difference between “long learning” and “long control” was statistically significant. This was so in the case of all subjects except HM and LM, who operated in a low stiffness range (Table 1).

The mean viscosity values were greater in the case of voluntary unloading than in that of unloading imposed by the experimenter in the majority of the series ($P<0.1$ by signs criteria) (Table 2).

An increase in stiffness was observed during the “learning” series. The slopes of the straight-line approximations of the stiffness values versus the number of trial were significantly ($P<0.05$) positive in 15 of the 16 “long learning” series (Table 1). The broad outline of the learning process was as follows (Fig. 3): learning in the second series sometimes began at the same level or at an even lower level of stiffness than at the beginning of the first series; as a rule, learning in the first and second series was faster than in the third one, during which the stiffness hardly changed or even decreased. However, an overall increase in the stiffness took place during the “long learning” series in all subjects, whether the postural forearm was the dominant or non-dominant arm. This finding suggests that the subject learned to decrease the effects of the disturbance due to the unloading by increasing the elbow-joint stiffness.

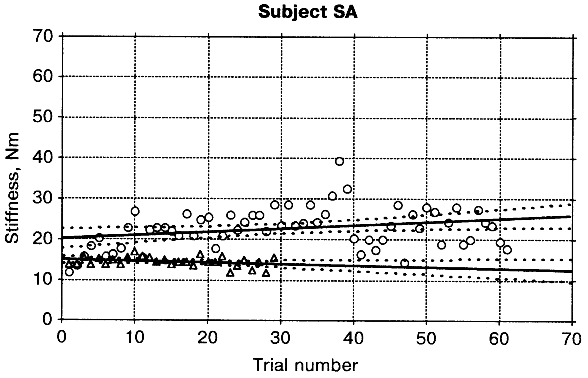


Fig. 4 The stiffness value versus number of trial and the straight-line approximations for the "long control" (*triangles*) and the "long learning" (*circles*) series with subject SA (dominant arm). The absence of interception of the 95% confidence limits was taken to indicate the existence of a statistically significant difference between the "control" and "learning" series

In contrast with the stiffness changes, no particularly noteworthy changes in the viscosity values were observed, either within or between the "learning" series during the learning process: the slopes of the straight-line approximations of the viscosity versus the number of trial were small and were either positive or negative (Table 2).

Changes in JC intersection

The difference between the JC intersection and the initial angle was found to decrease during the learning process (Table 3). Since stiffness increased during the learning process, the following question arose: does a correlation exist between stiffness and JC-intersection changes? To investigate this correlation, the independence of the values of both the stiffness and JC intersections calculated in the adjacent trials was first checked in order to assess the significance of the regression coefficients. The stiffness or JC intersection value obtained in each trial was taken as the dependent variable and this value obtained in the adjacent trial as the independent variable. In 80 experimental series (two "control" and three "learning" series with the right and left forearms for each of the eight subjects), the slope was non-significant ($P>0.05$ based on Student's criteria) in 70 series and significant ($P<0.05$) in ten series. Assuming the stiffness and JC intersection values in each series to be independent, we calculated the correlation between them. The correlation was found to be significant ($P<0.05$, Student's t-test) in 75 of the 80 series. The square of the correlation coefficient varied from 0.57 to 0.96, depending on the trial and on the subject. No statistically significant differences were observed either between "control" and "learning" series or between the earlier and later stages of the learning sequence. As an example, the straight-line approximations of the stiffness versus JC intersection with 95% confidence limits are given in the Fig. 5 for subject EM (dominant arm) in both "long control" and "long learning" series. It can be seen that the stiffness and JC intersection were significantly correlated and cannot be taken as independent variables. This means that actually only one centrally controlled parameter is responsible for the presetting of the stiffness and the JC intersection.

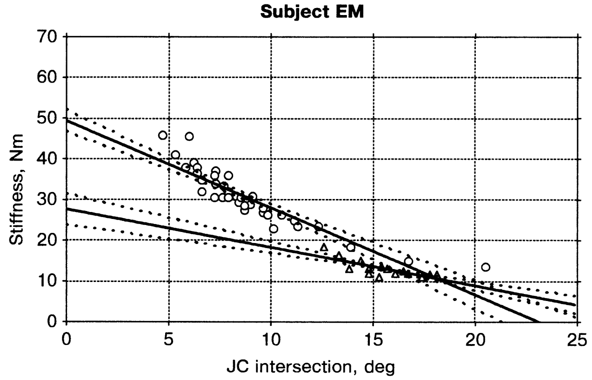


Fig. 5 Straight-line approximations of stiffness versus JC intersection with confidence limits for the "long control" (*triangles*) and "long learning" (*circles*) series with subject EM (dominant arm)

Discussion

The present results confirm that the linear spring model is a useful tool for analyzing unloading induced movements. Here, they throw some light on the mechanism possibly underlying the anticipatory control of movements of this kind.

Basic assumptions

Forearm postural control during abrupt unloading was analyzed in the framework of the spring-like model, which qualitatively accounts for those properties of the neuro-muscular system that prevent external disturbances from affecting the maintenance of posture. The spring-like properties of the elbow joint are determined by the combined functional effects of antagonistic muscles. Although the properties of individual muscles are known to be nonlinear (Feldman 1966; Shadmehr and Arbib 1992), when the elbow-joint angle changes within the range of angles where the invariant characteristics of antagonistic muscles overlap, their combined effects result in a linear torque-angle dependence (Feldman 1980). The linear spring-like model may still be inaccurate for the following reasons, however. First, in the initial position, the load can be maintained by the agonist only without antagonist coactivation (Paulignan et al. 1989). During the movement, the joint angle then crosses the antagonist invariant-characteristic threshold. In the vicinity of this threshold, the JC is obviously nonlinear. Second, although under the static conditions the joint angle varies within the range of angles where the invariant characteristics of antagonistic muscles overlap, so that the static torque-angle relationship can be taken to be linear, the dependency of the torque on the angular velocity may result in a shift of the angular activation threshold, so that it is again crossed by the angle during the movement (Feldman 1986). The fact that a silent period was consistently observed in the EMG activity in response to unloading (Angel et al. 1965; Paulignan et al. 1989) is in line with this suggestion. In the vicinity of the activation thresholds, it is not possible to decompose the muscle torque into its elastic and viscous components. Third, neither the reflex delay nor the time constants of the torque generation were taken into account in the present model. Fourth, the activation thresholds of agonist and antagonist muscles can vary during the movement. Since the shift of antagonist invariant characteristics increased the coactivation, it may have resulted in overestimating the stiffness values.

Although nonlinearities are obviously present during forearm unloading, the linear approximation used here turned out to be surprisingly predictive of the actual torque changes recorded. The calculated stiffness, viscosity, and JC intersection can, therefore, be taken to constitute coefficients of the equivalent linear system, which responds to the unloading by producing the same torque changes as the real system. Strictly speaking, one should denote these coefficients “conventional” stiffness, viscosity, and JC intersection. Although these parameters mirror the “global” behavior of the system, i.e., they were calculated using all the sampling points of the recorded movement, the reconstruction of the joint torque on the basis of these parameters is also in good agreement with the experimental torque “locally”, i.e., at each sampling point (Fig. 2). We therefore used these coefficients for our qualitative evaluation of the central commands during the unloading task, since the neglected nonlinear effects can be said to play a significant role only at the very beginning of the movement.

Actually, all the reasons mentioned above, which make the linear spring-like model inaccurate, are most significant at the very beginning of the movement. The initial part of the movement corresponds to the initial part of JC, which is nonlinear because only the individual nonlinear torque-angle relationship of the agonist contributes to the total JC (Shadmehr and Arbib 1992; Flanagan et al. 1993). The fact that the reflex delay was not taken into account here may also only be of some consequence during the beginning of the movement, because the external torque changes more rapidly during the short period just after unloading. During the subsequent part of the movement, due to the forearm inertia, the changes in the torque with time were much slower than the reflex delay, so that including the reflex delay would possibly not have greatly affected the results of the present analysis (cf. Latash and Gottlieb 1992). And, finally, one can reasonably assume that the shift of invariant characteristics occurred only after a small delay after unloading, if it occurred at all.

It should be mentioned that the nonlinearity of the joint torque during the beginning of the movement may also have been due to the dropping of the load and to the effects of passive contractile components of the muscles, as described by Hill’s law. These effects are most significant at the beginning of movement when the rate of torque change is the highest. A detailed numerical analysis of the contributions of various effects to the joint torque is beyond the scope of the present paper, however.

Central control parameters preset in the unloading task

It would be natural to assume that, when a task consists of stabilizing the joint position after unloading, the subject will resort to a strategy of co-contracting agonist-antagonist muscles (Akazawa et al. 1983; Milner and Cloutier 1993). The nervous system can use various preparatory strategies for limb-stiffness control: afferent feedback regulation (Paulignan et al. 1989), regulation of individual muscle stiffness (Houk 1979), regulation of the degree of co-contraction (Feldman 1980; Bizzi et al. 1982; Levin and Dimov 1997). It has been established (Paulignan et al. 1989; Milner and Cloutier 1993) that, because of the reflex delay, feedback compensation alone cannot provide an efficient basis for controlling postural maintenance. Leaving aside the regulation of stiffness in the individual muscles, in the present study we analyzed whether efficient joint-stiffness control can be achieved by an anticipatory command strategy setting the degree of muscle co-contraction. Various motor structures, such as the motor cortex (Humphrey and Reed 1983) and cerebellum (Smith 1996), are thought to be involved in agonist-antagonist co-contraction. Keeping within the framework of equilibrium-point theory, one might say that the tonic reflex thresholds of antagonists θ_{ag} and θ_{ant} (Fig. 6) are in fact the final effects of the supraspinal control.

The results of our analysis suggests a possible mechanism whereby the central control may increase the stiffness. As established above, the movement of the postural forearm after unloading is performed at constant stiffness and JC-intersection values. It can, therefore, be assumed that these parameters were preset before the beginning of the movement. It has been commonly observed that, during the initial postural maintenance of a loaded forearm, only the agonists are active. As no disturbances to the position of the forearm occur before the unloading: (1) the agonist invariant characteristics are not shifted in the process of control-parameter presetting; (2) the presetting of movement control parameters involves a preliminary shift of the antagonist invariant characteristics. After presetting JC, the movement is produced passively as the result of the properties of the stretch-reflex loop and the mechanical properties of muscles.

The possible mechanism for the presetting of antagonist’s invariant characteristics is illustrated in Fig. 6. The individual muscle characteristics are shown by the thin dotted lines, the summary JC by the thick lines. JC^1 corresponds to the “control series,” JC^2 to the “learning” one. Let the threshold of antagonist invariant characteris-

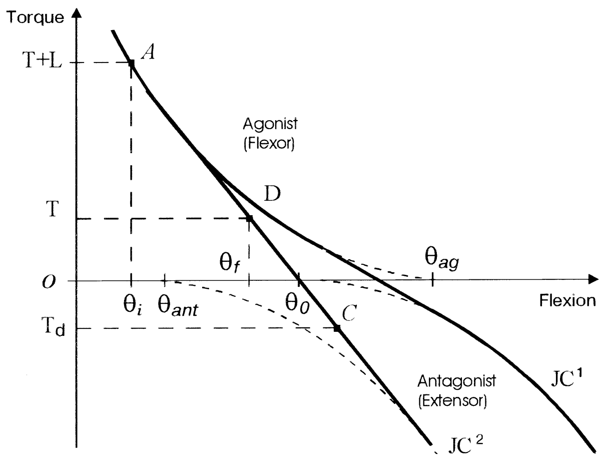


Fig. 6 Invariant characteristics of agonist and antagonist muscles (*thin dotted line*) and their sums, representing the joint-characteristics curves, JC (*thick line*). For simplicity, the agonist's and antagonist's characteristics are assumed to be symmetrical. *JC*^{1} corresponds to the "control" series, *JC*^{2} to the "learning" series. *JC*^{2} is shifted more to the left to reduce the activation threshold. This enhances the muscle coactivation and joint stiffness and reduces the JC intersection. θ_{ag} and θ_{ant} are the tonic stretch-reflex thresholds of the agonist and antagonist, respectively; θ_0 is the equilibrium position of the joint in the absence of the external forces (JC intersection). Point *A* corresponds to the initial position of the forearm, θ_i; *T*+*L* is the joint torque, which counterbalances the weight of the forearm and the bracelet (*T*) and load (*L*). Point *C* corresponds to the maximum deceleration torque, T_d; point *D* corresponds to the final position of the forearm, θ_f . The shift of this activation threshold towards extension results in a decrease in the amplitude of the postural forearm movement

tics be θ_{ant}. The threshold θ_{ant} is likely to be in a more flexed-angle position than the initial angle θ_i, because otherwise the shift would induce an extension movement before the unloading.

Point A corresponds to the time before unloading, when the initial position of the loaded forearm is θ_i. After unloading, the movement is performed through the nonlinear part of the JC. Then the antagonist comes into play, and the next part of the movement is performed through the approximately linear part of the JC. The point C corresponds to the maximum deceleration torque, T_d. The final phase of the movement consists of returning to point D, which corresponds to the final position of the forearm θ_f. In the "learning" series, the characteristics of the antagonist is shifted more that in "control" (cf. JC^1 and JC^2 in Fig. 6). The stiffness therefore becomes greater in the "learning" series.

In this way, the increase in joint stiffness, which takes place during the learning of forearm-position maintenance, can be explained by a preliminary shift of the antagonist invariant characteristics to a sub-threshold position. It is worth noting that this shift is not accompanied by either kinematics or EMG changes and that it can only be observed via the model. The underlying learning mechanism presumably involves a shift of the antagonist invariant characteristics to a position that gradually becomes closer to the initial forearm position.

Comparison of the results of the model with the data in the literature

Joint stiffness and viscosity were calculated in the present study using the linear-spring model. The values obtained with this method are in line with those published in the literature.

The compliance of single-joint systems has been investigated under both stationary conditions (Mussa-Ivaldi et al. 1985; MacKay et al. 1986; Flash and Mussa-Ivaldi 1990) and time-varying conditions (Flash 1987; Lacquaniti et al. 1982, 1993; Lacquaniti and Maioli 1989; Latash and Gottlieb 1991, 1992; Bennett et al. 1992; Gomi and Kawato 1995). Elbow stiffness increases slowly during the quasi-isometric transition from the state of non-resistance to applied perturbations to the state of actively resisting them (Lacquaniti et al. 1993). By contrast, elbow stiffness increases very rapidly during fast flexion movements (Latash and Gottlieb 1992) and is greatly modulated during sinusoidal movements (Bennett et al. 1992; Latash 1992). These examples show that the stiffness pattern is very task dependent. Upon comparison of the range of elbow-joint-stiffness and viscosity values obtained in our experimental series with data from studies using various motor tasks, movement conditions, and measurement techniques, the present values were found to be within a range comparable to those available in the literature.

The results of our analysis show that the unloading-induced movement of the postural forearm is performed

Table 4 Data on elbow-joint stiffness and viscosity cited in the literature. The values in *parentheses* correspond to static conditions. The forearm moments of inertia values used in the studies cited correspond to the 0.04–0.12 kg·m^2 range used in the present paper

Authors	Stiffness range [Nm]	Viscosity range [Nms]
Lacquaniti et al. 1982	20–40	
Mussa-Ivaldi et al. 1985	(13–41)	
Gottlieb et al. 1986		0.6
MacKay et al. 1986	(2–20)	(0.08–0.3)
Flash 1987	(27–47), 62–89	1.8–7.2
Lacquaniti and Maioli 1989	30–100	
Flash and Mussa-Ivaldi 1990	10–40	
Latash and Gottlieb 1992	8–26	
Bennett et al. 1992	(16–18), 2–15	0–0.7
Lacquaniti et al. 1993	(30–50), 18–46	(0.8–1.2), 0.7–1.5
Gomi and Kawato 1995	(10), 10–20	

under constant stiffness and viscosity values (Biryukova et al. 1995). The stiffness is in a range between 10 and 60 Nm, and the viscosity is in a range between 0.1 and 3.6 Nms, depending on the trials and subjects. Data in the literature on the stiffness and viscosity of the elbow joint are given in the Table 4 to facilitate comparisons with the present results. The ranges of stiffness and viscosity obtained here are completely in line with the data by MacKay et al. (1986), Bennett et al. (1992), Latash and Gottlieb (1992), Lacquaniti et al. (1993), and by Gomi and Kawato (1996), although these authors all used quite different methods to estimate visco-elastic parameters, such as the application of small pseudo-random disturbances during a free movement (Lacquaniti et al. 1982; Bennett et al. 1992; Gomi and Kawato 1996), calculations based on frequency-response characteristics at different maintained angles (MacKay et al. 1986), and regression analysis of temporal sections in successive trials reproducing the same motor-command time profile (Latash and Gottlieb 1992). On the other hand, the present joint-stiffness and viscosity values were significantly smaller than those calculated by Flash (1987) to fit the equilibrium trajectory and that measured during a movement with significant dynamic perturbations (Lacquaniti and Maioli 1989; Lacquaniti et al. 1993).

The ratio of mean viscosity to mean stiffness varied, depending on the subject, from 20 to 70 s and was thus in keeping with the experimental value for this ratio (50 s) obtained for the elbow joint by Cannon and Zahalak (1982). Cannon and Zahalak dealt with muscle torques ranging between 3 and 30 Nm, which corresponds to the torque values calculated above. In Lacquaniti et al. (1982), this ratio was found to range from 5 to 125 s (which encompasses our range) during the transition from the “resist” to the “do not resist” task.

We can therefore state the existence of qualitative agreement with the published data based on different experimental procedures. Concerning our values, it should be pointed out once more that:

1. Linear regression analysis was performed on sequences of torque values in each trial to estimate the stiffness and viscosity values.
2. The estimated values are the coefficients of a linear dynamic system, which responds to unloading by producing torque changes that match the torque changes occurring in the real system.
3. The degree of antagonists invariant characteristics overlap was taken to correspond to the joint stiffness, which can therefore be viewed as the degree of the agonist-antagonist co-contraction.

Conclusion

1. Torque generation during the unloading task can be qualitatively accounted for by the linear-spring model.
2. The unloading-induced movement is performed “passively” as the result of an anticipatory control, which provides a change of the stretch-reflex threshold in the antagonist alone. This change in a single parameter presets both the equilibrium position of the joint and the joint stiffness.
3. The gradual decrease in the disturbance of the initial forearm position observed in the course of learning is achieved by increasing the preset shift of antagonist invariant characteristics, which leads to an increase in the joint stiffness.

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