

## RECONSTRUCTION OF SHIFTING ELBOW JOINT COMPLIANT CHARACTERISTICS DURING FAST AND SLOW MOVEMENTS

M. L. LATASH\*† and G. L. GOTTLIEB‡

\*Department of Physical Medicine and Rehabilitation, Department of Physiology, Department of Neurosurgery, Rush-Presbyterian St. Luke's Medical Center, 1753 W. Congress Parkway, Chicago, IL 60612, U.S.A.

‡Department of Physiology, Rush-Presbyterian St. Luke's Medical Center, Chicago, IL 60612, U.S.A.

**Abstract**—The purpose of this study was to experimentally investigate the applicability of the equilibrium-point hypothesis to the dynamics of single-joint movements. Subjects were trained to perform relatively slow (movement time 600–1000 ms) or fast (movement time 200–300 ms) single-joint elbow flexion movements against a constant extending torque bias. They were instructed to reproduce the same time pattern of central motor command for a series of movements when the external torque could slowly and unpredictably increase, decrease, or remain constant. For fast movements, the total muscle torque was calculated as a sum of external and inertial components.

Analysis of the data allowed reconstruction of the elbow joint compliant characteristics at different times during execution of the learned motor command. "Virtual" trajectories of the movements, representing time-varying changes in a central control parameter, were reconstructed and compared with the "actual" trajectories. For slow movements, the actual trajectories lagged behind the virtual ones. There were no consistent changes in the joint stiffness during slow movements. Similar analysis of experiments without voluntary movements demonstrated a lack of changes in the central parameters, supporting the assumption that the subjects were able to keep the same central motor command in spite of externally imposed unexpected torque perturbations. For the fast movements, the virtual trajectories were N-shaped, and the joint stiffness demonstrated a considerable increase near the middle of the movement.

These findings contradict an hypothesis of monotonic joint compliant characteristic translation at a nearly constant rate during such movements.

The  $\lambda$ -model of the equilibrium-point (EP) hypothesis,<sup>12,13,17</sup> has substantially influenced motor control studies during the past 20 years. However, it remains controversial in a number of aspects. Questions have been raised concerning its ability to predict the electromyographic (EMG) patterns observed during single-joint movements,<sup>11</sup> its ability to interpret phenomena of variability in motor performance,<sup>8</sup> and its applicability to the analysis of movement dynamics.<sup>21,45</sup> The first two aspects have recently been addressed.<sup>1,2,36,37,39,40</sup> The present paper deals with an experimental demonstration of certain basic features of the EP hypothesis related to movement dynamics.

One of the central notions of the  $\lambda$ -model is that of a joint compliant characteristic (JCC).§ The JCC

describes the static interdependence of joint torque and joint angle under conditions of unchanging central control. Slope and intercept of a JCC can be centrally regulated by two parameters (one for the agonist,  $\lambda_{ag}$ , and one for the antagonist muscle,  $\lambda_{ant}$ ). Feldman<sup>15,16,18</sup> suggested that single-joint control can be described by these two variables or by an equivalent pair  $r$  and  $c$  defined as:

$$r = \frac{\lambda_{ag} + \lambda_{ant}}{2}$$

$$c = \frac{\lambda_{ag} - \lambda_{ant}}{2}$$

The new ( $r$ ,  $c$ ) pair are attractive since they suggest direct relations to traditional physiological notions of reciprocal activation and coactivation. That is, shift in  $r$  corresponds to unidirectional changes in  $\lambda_{ag}$  and  $\lambda_{ant}$  improving conditions for activation of one of the muscles and worsening them for the other (reciprocal activation). A shift in  $c$  corresponds to contra-directional shifts in  $\lambda_{ag}$  and  $\lambda_{ant}$  improving conditions for activation for both muscles (coactivation). These parameters can also be directly related to position ( $r$ ) and slope ( $c$ ) of the JCC:

$$\alpha = kr + f(c)T, \quad (1)$$

†To whom correspondence should be addressed.

§The originally introduced term "invariant characteristic" (IC<sup>14</sup>) is somewhat misleading. It was first introduced to describe force-length relationships of single muscles when central commands could only translate the IC along the length axis without changing its slope. However, the JCC is the algebraic sum of the ICs of the agonist and antagonist muscles, and it can not only move along the angle axis but also change its slope, therefore making the term "invariant" hardly applicable.

**Abbreviations:** JCC, joint compliant characteristic; EP, equilibrium-point; IC, invariant characteristic; EMG, electromyographic, electromyogram.

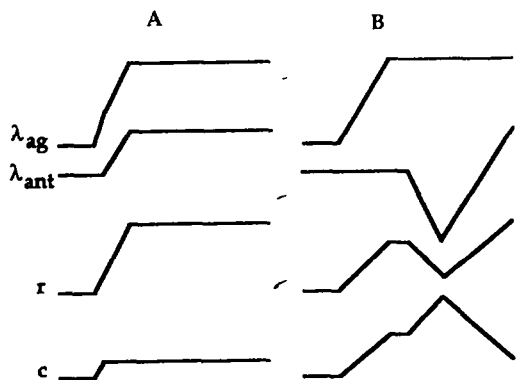


Fig. 1. According to Feldman and his colleagues, fast single-joint movements are controlled by a ramp shift in  $r$  with a simultaneous increase in  $c$  (A). Changes in  $\lambda_{ag}$  and  $\lambda_{ant}$  are calculated as  $\lambda_{ag} = r + c$ ;  $\lambda_{ant} = r - c$ . According to our assumptions, the control pattern for fast single-joint movements can be described by a ramp shift in  $\lambda_{ag}$  with a delayed shift in  $\lambda_{ant}$  (B). Changes in  $r$  and  $c$  are calculated as:

$$r = \lambda_{ag} + \lambda_{ant}/2; \quad c = \lambda_{ag} - \lambda_{ant}/2.$$

where  $k$  is a constant,  $f$  is a monotonically decreasing function,  $\alpha$  is joint angle and  $T$  is joint torque. This equation describes joint position for a constant or slowly changing external load and constant or slowly changing central parameters.

The  $(r, c)$  pair has an intuitively useful physical interpretation. The parameter  $r$  is identifiable with the equilibrium position of the joint in the absence of external torque. One can regard this as a central representation of the limb's planned trajectory over time, a "virtual" trajectory (cf. Refs 20, 52), which a massless, frictionless limb would follow if unopposed by external torque. The coefficient  $f(c)$  is the compliance of the joint describing the effects of external torque on joint position.

The actual trajectory followed by a limb deviates from the "virtual" trajectory. One cause of deviation could be the application of external torque. The application of external torque is the method commonly used to measure static JCCs.<sup>4,9,12,13,24,53</sup> Another reason is limb inertia which causes the actual limb trajectory to trail behind the virtual trajectory. During fast movements, the inertially induced deviation between the actual and virtual trajectories generates the forces (because of the compliance) that accelerate and decelerate the limb.

In an attempt to describe the emergence of the EMG patterns commonly observed during single-joint movements, Feldman and his colleagues<sup>1,2</sup> suggested the following scheme (Fig. 1A): movement of a single joint is controlled by a ramp change in reciprocal activation ( $r$ ) with a simultaneous increase in coactivation ( $c$ ). According to this scheme, the antagonist muscle demonstrates an EMG burst exclusively because of kinematic feedback as it lengthens. This approach allows qualitative predictions of the EMG phasic patterns similar to those observed experimentally. However, it contradicts some empirical and theoretical results. For example, if fast move-

ments are performed against a heavier inertial load, the model predicts a decrease in the antagonist burst because movement speed decreases. This decrease in EMG does not correspond to experimental observations.<sup>26,43,49</sup> Modeling based on certain optimization criteria also predicts non-monotonic shifts in a parameter analogous to  $r$  describing the central command.<sup>29,30</sup>

We have recently advanced alternative control rules for  $\lambda_{ag}$  and  $\lambda_{ant}$  (or  $r$  and  $c$ ) in the framework of the EP hypothesis<sup>36,40,41</sup> (Fig. 1B). The equivalence between  $r/c$  and  $\lambda_{ag}/\lambda_{ant}$  allows the model to be described in terms of either pair. The choice of which pair to work with is based upon which has a simpler behavior. In our model, simple patterns of controlling  $\lambda$  can lead to relatively complex changes in  $r$  and  $c$ . It differs from Feldman's approach by the introduction of independent control of the antagonist burst with a delayed shift in  $\lambda_{ant}$  resulting in significantly different patterns of  $r$  and  $c$ . In particular, for fast movements,  $r$  demonstrates a non-monotonic, N-shaped behavior, and  $c$  has a peak near the middle of the movement. The way to resolve the differences between these two approaches would be to record changes in the control variables  $r$  and  $c$  or  $\lambda_{ag}$  and  $\lambda_{ant}$ .

JCCs have previously been recorded only with instructions requiring that subjects do not change their motor commands voluntarily when an external perturbation is applied.<sup>4,9,12,13,24,53</sup> We will refer to these as measurements of "static" JCCs. The method of recording static JCCs was premised on the assumed ability of subjects to "fix" the voluntary motor command, an assumption which does not seem to admit to direct testing. Therefore, the premise of "dynamic" shifting JCCs to perform a voluntary movement looks more like an abstraction than an empirically testable hypothesis. It is also possible that dynamic processes which change central motor commands can also change the JCC slope, not just cause its translation. The ability to reconstruct the shifting JCCs of a time-varying motor command would be an important piece of evidence that the  $\lambda$ -model can provide both a theoretical and empirical framework for understanding voluntary motor control processes.

## EXPERIMENTAL PROCEDURES

### Methodological problems

In static experiments it is assumed that the subject does not change the voluntary motor command, and therefore does not shift the position of the JCC when the external load changes. These external changes lead to changes in the joint position. Joint angle and torque are measured at new equilibrium states and plotted as points on a "torque-angle" plane. Interpolation of the points defines a static JCC.

The fact that JCCs have never been recorded during voluntary movements is due to a number of methodological problems.

(1) Let us, for the sake of simplicity, temporarily accept a simple linear shift of  $r$  as a control signal for single-joint movements:

$$r(t) = r_0 + \omega t, \quad (2)$$

where  $r_0$  is initial value of  $r$  at  $t = 0$ , and  $\omega$  is a constant.

It takes time  $\Delta t$  for the peripheral motor apparatus to come to a new steady-state after a change in the external load. If central motor commands (e.g.  $r$ ) change, as is assumed to happen during voluntary movements, the new state at which torque and angle are measured would correspond to a new value of  $r$ . That is, if a perturbation is applied when  $r(t) = r_1$ , the measurements will be made  $\Delta t$  later at a different value of  $r$  (cf. with eq. 2):

$$r_2 = r_1 + \omega \Delta t. \quad (3)$$

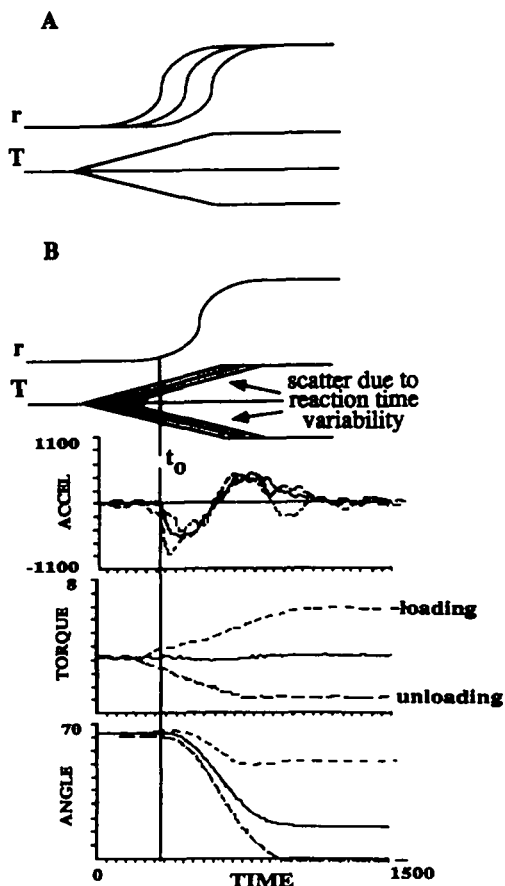


Fig. 2. Schematic illustration of the experiment. (A) In real time, the torque always started 100 ms after the tone signal while voluntary movements started with different reaction time delays. We assume that the subjects reproduced some time pattern of the central motor command ( $r$ ). (B) After the alignment according to the first visible deflection of the acceleration trace ( $t_0$ ),  $r(t)$  functions overlap while the torque traces become scattered. Angle, torque, and acceleration were measured at certain times  $t_i$  after  $t_0$ . Values of angle and total torque (a sum of the external torque and the inertial component) for same  $t_i$  in different trials were plotted on the torque-angle plane, and linear regression analysis was performed. Below: an example of three aligned slow movements, loaded, unloaded, and unperturbed. Angle, velocity, and acceleration scales are in  $^\circ$ ,  $^\circ/s$ , and  $^\circ/s^2$  correspondingly. Time scale is in ms.

Thus, initial and final values of torque and angle pertain to different static JCCs (corresponding to  $r_1$  and  $r_2$ ) and cannot be directly compared.

(2) The experimentally reconstructed JCC is a sum of two components. The first one is due to intrinsic compliant properties of the muscles in the absence of any changes in recruitment of  $\alpha$ -motoneurons. The second one is defined by autogenic reflex recruitment (or derecruitment) of  $\alpha$ -motoneurons due to an increase (decrease) in muscle length. The introduced parameters  $\lambda_{ag}$ ,  $\lambda_{ext}$ ,  $r$ , and  $c$  relate here to the second component.<sup>14,17</sup> Therefore, if a movement starts from a relaxed state, i.e. in the initial absence of  $\alpha$ -motoneuron activity, all these parameters are undefined. This corresponds to an undefined constant  $r_0$  in eq. 2 thus creating a problem if one wants to define time changes in  $r$  introduced by a voluntary motor command.

(3) Fast perturbations, applied during a movement, often give rise to phasic reactions (mono-, oligosynaptic, and/or triggered).<sup>3,22,23,28,44</sup> These reactions lead to transient angle and torque changes so that a stable steady-state is achieved only after at least 200–300 ms. However, after this time the central parameter  $r$  will have changed (see point 1) creating difficulties in interpretation of the measurements. Slow perturbations, even if they evoked no phasic reflex responses, would end after a considerable change in  $r$ .

(4) Fast movements must overcome considerable inertial and possibly viscous torque<sup>26</sup> from the limb itself. An external device (e.g. strain-gauge) does not measure these components and supplies information on only a part of the total torque developed by the muscles (cf. eq. A1 in Appendix).

In order to cope with the mentioned problems, a procedure was designed which included recording of angle and torque changes during movements performed on the background of a slowly changing torque.

#### Design of the study

The general idea of the study is related to the "do-not-intervene-voluntarily" paradigm used in all the experiments which recorded static JCCs in human subjects.<sup>4,9,12,13,24,53</sup> In static experiments, the experimenters assumed and relied upon the subject's ability to "fix" the voluntary motor command. This assumption has always been a weak point in interpreting the JCC recordings. Attempts to prove that the subjects were in fact fixing a central control signal<sup>21</sup> have not been strong enough to satisfy the skeptics.<sup>24</sup>

In our experiments, the main goal of the instruction and training (see below) was to teach the subject to perform a standardized and consistent time profile of a voluntary motor command by practicing a simple voluntary elbow flexion movement. After training, the subjects were given an instruction, very similar to the one used in the "do-not-intervene-voluntarily" paradigm of static experiments, requesting reproduction of the same time profile of the learned voluntary command while ignoring changes in the externally applied load.

The subjects practiced movements from a fixed initial position to a fixed final position with "the same speed" from movement to movement. A computer-generated tone provided the signal to begin the movement. Consistent movement trajectories, in the absence of external torque changes, were taken as evidence of a similar consistency in the motor command. After sufficient practice, subjects could generate consistently repeatable kinematic profiles, and we assume, therefore, a standard voluntary motor command. A hypothetical, monotonic function  $r(t)$  as such a profile is shown in Fig. 2A. Three movement commands are illustrated, differing only in their reaction time from the signal to start moving. The externally applied torque ( $T$ ) begins to change with a constant latency after the signal and may assist or oppose the movement, or remain unchanged.

The subjects reproduced the learned voluntary flexion motor command against an extending torque bias generated

by a torque-motor. All the movements were assumed to start from the same initial value of  $r(r_0)$ , determined by the non-zero initial muscle torque. There is usually a slight coactivation of antagonist muscles while holding a joint position against an external torque bringing about some initial value of  $c(c_0)$ . Generally speaking,  $r_0$  and  $c_0$  are defined only as a pair (cf. Fig. 12 in Discussion) and one parameter cannot be uniquely related to external torque. Although we do not know the value of  $c_0$ , we assume that it is the same throughout the course of one experimental series but did not test this assumption (as it was done in all the previous "static" experiments with reconstruction of JCCs). Reproducibility of the experimentally reconstructed c-related coefficient  $k_2$  (see Results) is consistent with and assumed to indirectly corroborate this assumption.

During a movement, the torque could unexpectedly change in either direction (loading and unloading) or it could stay constant. Changes in external torque occurred over 300 ms for fast movements and over 800 ms for slow movements. Torque changed fast enough to induce considerable change over the course of a movement, but slow enough to be significantly longer than (and let us ignore) an unknown delay in the hypothetical reflex loop forming the basis of the  $\lambda$ -model (see details in Appendix). Previous experiments with perturbation of a stationary limb<sup>39</sup> showed that monosynaptic reflexes and/or triggered reactions would not be evoked if perturbations were applied gradually over 300 ms or more. There was a 100-ms delay after the tone signal until the external torque started to change. This ensured that the torque ramp started before the voluntary movement, since the latency of the first visible deflection in the agonist EMG (the premotor reaction time) varied from 140 to 200 ms in most of the trials. Natural variability in reaction time led to different delays between the beginning of the torque change and each movement's initiation (Fig. 2A). During slow movements, the inertial torques were considerably lower than during fast movements (peak inertial torques for a 1000 ms movement are about 6% of those of a 250 ms movement). We performed a simplified analysis for most of the slow movement experiments ignoring the inertial torque component. We also performed additional analysis to estimate the degree of error resulting from this simplification.

The individual records from a set of movements were aligned so that time "zero" corresponded to the beginning of the acceleration changes due to the voluntary motor command. This point ( $t_0$ , Fig. 2B) is easily detected by visual inspection of individual records on a computer monitor. The lower part of Fig. 2B illustrates three movements performed against increasing, decreasing, and unchanged external torques. Deflection of the acceleration trace must start after the central parameter changes. This delay is due to transmission of neural signals to the muscles, the rate of muscle contraction, and inertial properties of the limb. We assume that this delay is constant if the initial conditions (joint angle and torque before the movement) are the same in successive trials and the subjects are reproducing the same command. Therefore in all the trials  $t_0$  corresponds to the same value of  $r(r_0)$ . After alignment, torque traces will be scattered (Fig. 2B) because of reaction time variability. Therefore, after  $t_0$  total torque values will differ between trials, even though the central motor commands are the same, because of differences in external torque.

If one measures torque and angle values at different times ( $t_i$ ) after  $t_0$ , these values, in different trials, correspond to the same  $r_i$  or to the same position of the JCC. If all the assumptions are correct, and the subject was successfully reproducing the same time profile of motor command in successive trials, plotting the values of torque and angle measured at a particular  $t_i$  would give a set of points pertaining to the same JCC but measured at different levels of external torque. This exactly corresponds to sets

of datapoints used for plotting JCCs in classical static experiments.

A JCC for a time  $t_i > t_0$  can be obtained by linear regression analysis of a set of datapoints from one set of trials. Each regression line (JCC) can be characterized by two parameters: slope and intercept.

$$T = k_1 - k_2 \alpha$$

$$\alpha = \frac{k_1}{k_2} - \frac{1}{k_2} T, \quad (4)$$

where  $k_1$  and  $k_2$  are the coefficients of the regression line at each value of  $t_i$ . These coefficients can vary with  $t_i$ . Note that the regression line (eq. 4) is identical in form to the JCC (eq. 1) so that we can equate their coefficients. Thus,

$$k r = \frac{k_1}{k_2} \text{ and } f(c) = -\frac{1}{k}. \quad (5)$$

Linear regression analysis for the sets of datapoints measured at different times after  $t_0$  will show how both  $r$  and  $c$  parameters change over the time-course of the movement.

The actual value of  $T$  produced by the muscles used in eq. 4 is not the external torque (measured with a strain-gauge) but a total value representing the sum of the inertial, and external components. We did not incorporate a viscous torque component into the analysis because of the lack of reliable assessments of possible changes in the coefficient of viscosity during movements. Possible effects of this assumption are discussed later.

Averaging the unperturbed trials yields an "actual" trajectory of the learned movement. This trajectory can be compared with changes in  $r$  (expressed in angle units) derived from the regression analysis. Then, one can compare changes in both the central control parameter, the virtual trajectory, and the actual trajectory plotted on the same scale.

As a check of the method, we also applied it to the analysis of static JCCs from experiments with the traditional "do-not-intervene-voluntarily" instruction. In that series, it was not necessary to realign the trials, since there were presumably no changes in the central motor command and movement was due solely to the changing external torque. Therefore, values of torque and angle in individual trials were measured at different times after  $t_0 = 100$  ms (the beginning of the perturbations). The prediction for this experiment is that  $r$  and  $c$  will not change as a function of  $t_i$ .

#### Methods

**Subjects.** Eight neurologically healthy male volunteers aged 18–54 participated in the experiments after giving an informed consent according to the procedure approved by the Human Investigation Committee of the Rush Medical Center. Two of the subjects had considerable experience in similar experiments and understood the rationale of the study; the other six were naive in both aspects. Four subjects took part in both slow and fast movement series.

**Apparatus.** The subjects sat comfortably in a chair and positioned the right elbow on a horizontal, low friction, light weight manipulandum (moment of inertia is 0.0861 Nm s<sup>2</sup>/rad) with the arm abducted at 90°. The axis of rotation of the lower arm corresponded to the center of the elbow joint.

A video monitor, positioned about 1.5 m in front of the subject, continuously displayed a position of the limb, a starting reference position and a target window. The target window was a bar, aligned with the direction of the movement, which defined both the movement distance and target width. A digital computer controlled the experiment, and digitized and recorded joint angle, acceleration, and torque. Elbow angle was measured by a variable capacitance transducer mounted on the shaft of the manipulandum. Tangential acceleration was measured by an accelerometer mounted on the distal end of the manipulandum, and velocity was derived from integration of the acceleration signal after low

pass filtering at 25 Hz. Torque was measured by a strain-gauge transducer and filtered at 25 Hz.

A torque motor provided both the bias and the time-varying external torque. For slow movement studies, each series consisted of 20 trials, during 10 of which a ramp change in the torque took place over 800 ms. In the fast movement experiments, each series consisted of 24 trials, during 12 of which a ramp change in the torque took place over 300 ms. The perturbed trials were selected by the computer pseudo-randomly. A new level of external torque was maintained for 1 s and returned to the bias value. The fast movements were performed against the 3-Nm bias; the final values of torque in perturbed trials were approximately 0, 1, 4, and 6 Nm (each value was repeated three times during each series). Most of the slow movements were also performed against the 3-Nm bias; the final torque values were 0, 1, 4, 6, and 10 Nm. In three subjects, additional series were recorded with the bias of 1 Nm. In these series, the final values of torques in perturbed trials were 0, 0.5, 1.5, 2, and 3 Nm.

Inertial torques were calculated by multiplying the acceleration by an estimated value for the moment of inertia of the manipulandum and the limb.<sup>48</sup> A total moment of 0.188 Nm s<sup>2</sup>/rad was used for all the subjects. Note that total muscle torque during fast movements could be significantly higher than the largest externally applied torque due to the inertial component.

**Instruction and training.** The subjects were instructed to perform smooth elbow flexion movements of 36° or 54° from an initial position of 120° (180° corresponds to the fully extended arm). They were told not to pay attention to accuracy, and to consider the target as a point. Before each movement they had to occupy the initial position, wait for the tone, smoothly move to the final position, and stay there until the tone ended. No corrections were permitted even if the movement terminated outside the target. The subjects were instructed "to practice a movement with the same speed until it becomes automatic" and given about 5 min for the practice. The chosen speed was adjusted by the experimenter (with remarks like "a little bit faster", "a little slower") so that it consistently corresponded to movement time in the range of either 200–300 ms (fast) or 600–1000 ms (slow).

After this first stage of training was complete, a bias torque (3 Nm) was introduced, and the subjects were asked to practice movements with "the same speed" against the constant bias. All the other instructions remained the same.

Next, a series of trials was performed "rehearsing" the experiment. Subjects were asked to perform the "same time course of effort" (not a "constant effort") and not to change it even if external torque changed during the movement ("do the same, no matter what the motor does"). During the perturbed trials of this rehearsal, the subjects were reminded not to correct their movements if they missed the target. During this series, they became used to the idea that the task was not to hit the target but rather not to react or try to compensate, even if the target was going to be missed. This was difficult for all the naive subjects. However, with practice, all of them managed to master it and to perform at a high level of reproducibility (see the Results below).

**Procedure and data analysis.** The first experimental series reproduced the rehearsal, but the subjects performed it without any verbal assistance from the experimenter. The subjects themselves assessed their performance. If they were subjectively satisfied, this series was not repeated. If they thought that they could perform better (more reproducibly), they repeated the series once. This happened in approximately half of the series.

Three of the subjects also performed a second set of movements against a smaller bias (1 Nm). One or two series were recorded in this condition depending upon their own subjective assessment of their performance.

Seven subjects took part in static experiments similar to those used for recording JCCs during slow movements. They were asked to occupy an initial position against a torque bias (3 Nm against the flexor muscles) and not to change their motor command in cases of torque changes: "let your arm do what it wants". Three levels of ramp loading and two of unloading over 800 ms were applied pseudo-randomly, each level repeated three times. Final values of torque were approximately 0, 1, 4, 6, and 10 Nm.

In three of the subjects, the static JCCs were recorded for three different initial positions: 60°, 90°, and 120°. Since the data for these three positions looked very similar, as expected from earlier studies,<sup>10,11,21</sup> static JCCs in the other four subjects were recorded only for the 90° initial position.

After the experiments on each subject were completed, the set of movements was reviewed on a computer monitor, and appropriate times were chosen at which joint angle, acceleration, and external torque were measured in individual trials. In most of the experiments with slow movements, the measurements were made at  $t_i = 100, 200, 400, 600, 800$ , and 1000 ms after  $t_0$ . In most of the experiments with fast movements, the measurements were made at  $t_i = 50, 100, 125, 150, 175, 200, 300$ , and 500 ms after  $t_0$ . For each  $t_i$ , for fast movements, total torque in individual trials was calculated as a sum of instantaneous external and inertial components.

The sets of datapoints for each value of  $t_i$  in each set of trials were plotted on separate graphs (angle vs torque) and linear regression analysis was performed. The regression lines were extrapolated, and their slopes and the intercepts were calculated. The values of slope and intercept were later plotted versus  $t_i$ . The time variation of the intercept in angle units (equivalent to virtual trajectory, see Introduction) was compared with the average unperturbed trajectory ("actual" trajectory). Joint angles of the unperturbed trajectory were calculated for the same values of  $t_i$  and were averaged over the individual records to estimate this actual trajectory.

## RESULTS

### *Compliant characteristics during slow movements*

The analysis yielded high coefficients of linear correlation for most of the datapoint sets. In all the subjects, statistically significant correlations ( $P < 0.05$ ) were observed for the data sets for the times over 200 ms after  $t_0$ . In four of the subjects, statistically significant coefficients of correlation were also found for the datapoint sets measured 100 and 200 ms after  $t_0$ .

An example of the datapoint sets and regression lines for one of the subjects is represented in Fig. 3. The external extending torque was considered negative in sign. Note that the times ( $t$ ) are given relative to movement onset ( $t_0$ ), not relative to the beginning of torque perturbations. For movements with long reaction times, external torque could reach its final value in as little as 200–300 ms after  $t_0$ . The lower graph in Fig. 3 shows all the regression lines plotted at a common scale. The regression equations may be represented as:

$$T = k_1 - k_2\alpha, \quad (6)$$

where  $T$  is torque,  $\alpha$  is angle,  $k_1$  is intercept, and  $k_2$  is slope.

Since there is a separate equation calculated at each value of time ( $t_i$ ), we can represent the coefficients  $k_1$  and  $k_2$  as time functions. Plotting these

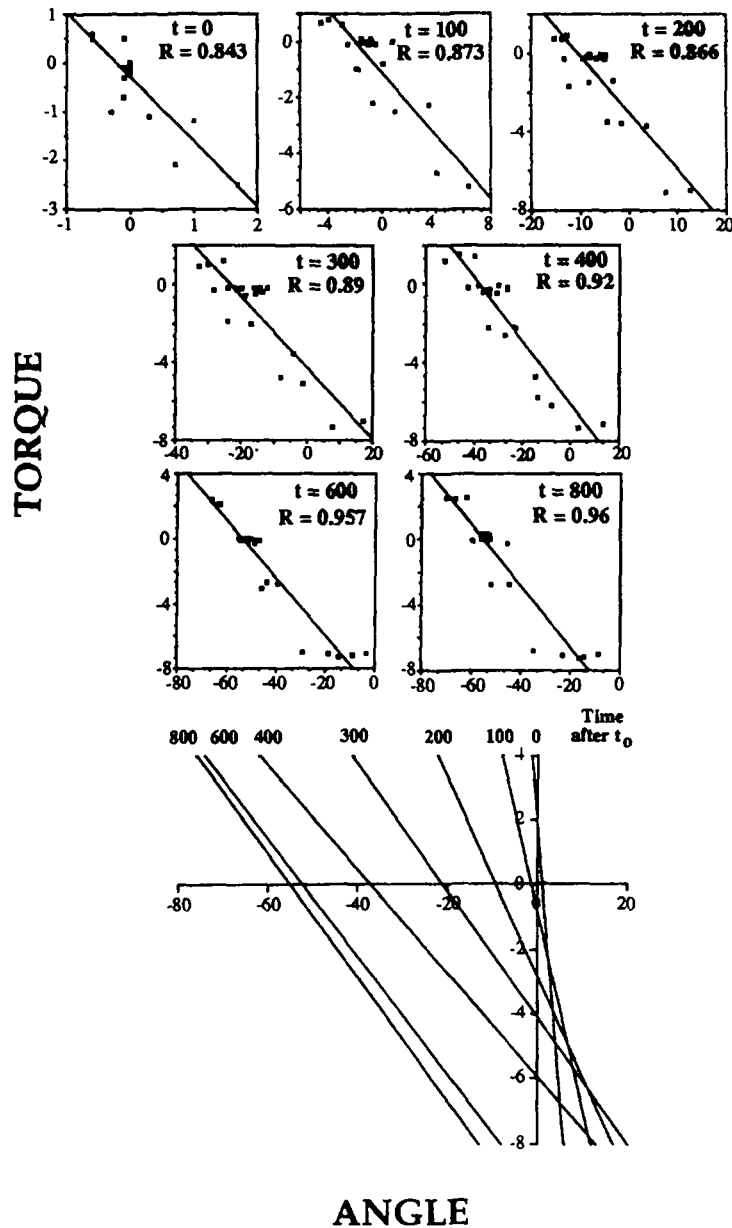


Fig. 3. Datapoints and regression lines for a series of slow movements performed by one of the subjects. Joint torque and angle were measured at different times after  $t_0$ . These values for all the trials of a series were plotted on a torque-angle plane. Note high coefficients of linear correlation. Zeroes of the scales correspond to the initial values of torque ( $-3$  Nm) and angle ( $120^\circ$ ). Different angle scales were used for different  $t$  in order to visualize the scatter of the data. Below: all the regression lines are plotted at a common scale. Torque scale is in Nm, angle scale is in degrees. Time after  $t_0$  is given in ms.

functions (Fig. 4A) shows monotonic changes in both  $k_1$  and  $k_2$ .

#### *Compliant characteristics during fast movements*

For fast movements, inertial torques represented a sizable part of the total torque. Peak values of acceleration were of the order of  $10^{40}/s^2$ . Multiplying acceleration by the moment of inertia (see Methods) gives a peak inertial torque of about 30 Nm as compared with the 3-Nm bias and 6-Nm maximal external torque level. Therefore, it is impossible to

ignore inertial torque, as was done for slow movements.

Examples of the sets of datapoints and regression lines for one of the subjects are shown in Fig. 5. More than 90% of all the sets for all the subjects demonstrated coefficients of linear correlation over 0.75. Lower coefficients of correlation were usually observed at the first two points of measurement at the beginning of the movement.

From eqs 4 and 5,  $k_1(t)$  and  $k_2(t)$  represent time-varying control signals. Reconstructing JCCs for

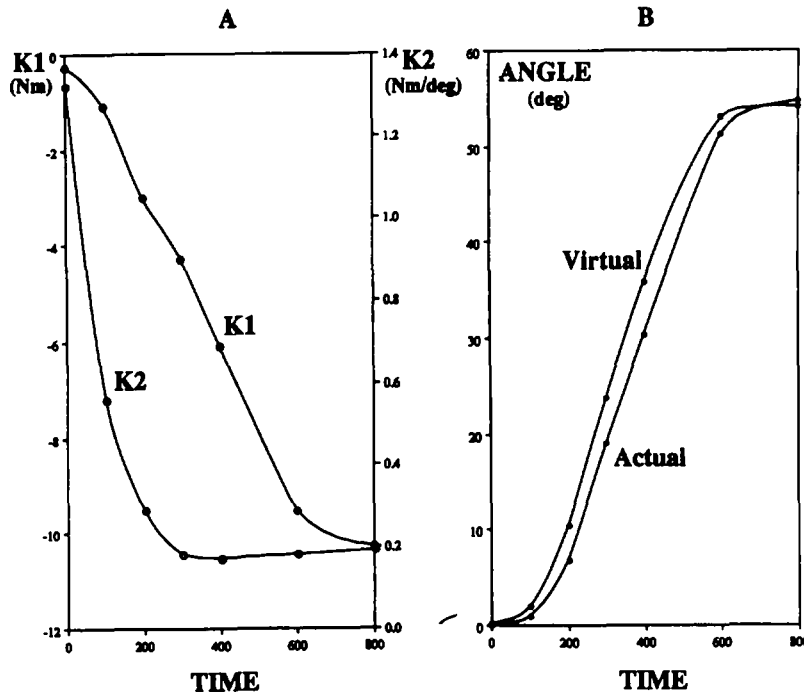


Fig. 4. (A) Shifts of regression equation coefficients  $k_1$  and  $k_2$  ( $T = k_1 - k_2\alpha$ ) calculated at different times after the onset of movement. Time scale is in ms,  $k_1$  scale is in Nm,  $k_2$  scale is in Nm/°. (B) Virtual and actual trajectories for the same set of data. The virtual trajectory is an interpolation of time changes of the ratio  $k_1/k_2$ . The actual trajectory is an interpolation of averaged angle values from the unperturbed trials. Time scale is in ms, angle scale is in degrees.

different  $t_i$  yields the time-course of changes in  $k_1$  and  $k_2$  shown in the lower left graph in Fig. 5.

#### Virtual and actual trajectories

In eq. 6,  $k_1$  is measured in the units of torque but during isotonic movements it is more natural to measure the central command in units of angle. The ratio  $k_1/k_2$  shows the JCC intercept in angle units. This ratio is equivalent to the hypothetical central command  $r$ , eq. 5, and its time changes can be regarded as a virtual trajectory for the movement. For slow movements, the reconstructed virtual trajectory and the actual trajectory for one subject are shown in Fig. 4B. At any instant, the virtual trajectory reflects current position (intercept) of the JCC, i.e. a joint position at which the limb would come to rest in the absence of changes in central commands and external load. The positions defined by the virtual and actual trajectories coincide only when the limb is in equilibrium or when external torque is equal and opposite to inertial torque.

The lower right graph in Fig. 5 shows an example of virtual and actual trajectories for fast movements. The virtual trajectory of fast movements is not monotonic but shows a more complex, N-shaped pattern. This pattern was observed in all the subjects. The virtual trajectory first leads the actual one, then reverses its direction and lags behind. At the end of the movement, the trajectories converge.

Time changes of  $k_2$  normalized with respect to the maximal value observed in each subject and

averaged across the subjects are shown in Fig. 6. The same figure also shows the average across the subjects of the actual trajectory. The coefficient  $k_2$  has units of stiffness (eq. 6) and shows a considerable increase near the middle of the movement (about 150 ms after  $t_0$ ).

We can define the angular lag between virtual and actual trajectories as a difference between their values measured at the same times. The lag between the virtual and actual trajectories averaged across all subjects for both slow and fast movement series is shown in Fig. 7. Note two major differences: a 10-fold increase in the lag values, and the reversal of its sign during fast movements. The lag for slow movements, averaged across the subjects, at an expanded scale is shown in Fig. 8. The Table below presents  $t$  and  $P$  values for a two-tailed Student's  $t$ -test comparing the lag with zero. Even for the small lags developed during slow movements, statistical significance is reached for three of four intermediate measures. No difference is expected at the end points.

#### Stiffness changes

Let us now consider the somewhat unexpected behavior of the second coefficient  $k_2$  during slow movements. It has the units of stiffness and according to eq. 5, depends only on the coactivation component  $c$ . Its apparent changes during the slow movements (Fig. 4) suggest a significant initial drop in the stiffness after which it is constant. This seems to contradict demonstrations of muscle coactivation

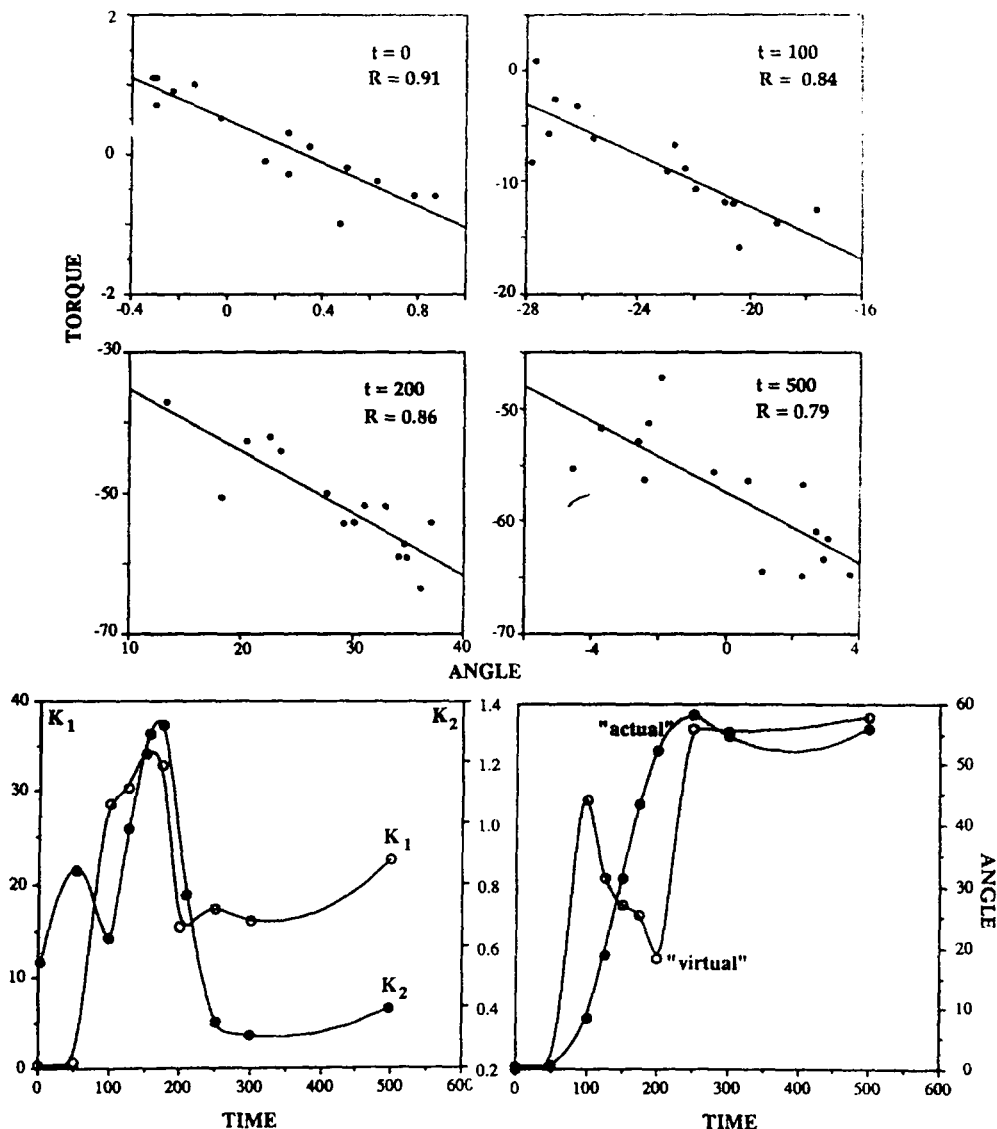


Fig. 5. Above: examples of the sets of datapoints for a series of fast movements performed by one of the subjects. Note different angle and torque scales for different graphs. Torque scale is in Nm, angle scale is in degrees. Below left: time changes in the coefficients of the regression equation  $T = k_1 - k_2\alpha$  for the same subject. Time scale is in ms,  $k_1$  scale is in Nm,  $k_2$  scale is in Nm/°. Below right: the virtual trajectory represents a ratio  $k_1/k_2$  derived from the regression equations. The actual trajectory was calculated by averaging angle values for the unperturbed trials. Time scale is in ms, angle scale is in degrees.

(which implies greater stiffness) during isotonic movements.<sup>26,43,49</sup> Note, however, that although joint movements in our experiments were deliberately restricted to low speeds, inertial forces were not zero and would have played their most significant role during the initial phase of movement. For example, at the moment of peak acceleration (100–200 ms after  $t_0$ ), inertial torque was comparable to the externally applied torque (about 3 Nm in the example shown in Fig. 2).

The existence of a significant inertial torque component implies that the measured torque is smaller than the total torque and therefore the actual stiffness is less than estimated by the extrapolated regression lines. This effect was likely to be most pronounced

during the initial phase of the movements when absolute values of joint angle changes are small and the inertial components of torque are relatively high. We think that the initial drop in  $k_2$  represents an artifact of the experiment due to inertial torques during the initial phase of the movements.

To check this assumption, we reprocessed the data for one of the subjects with and without taking into account the inertial torque component (Fig. 9). Including the inertial torque into analysis has led to a smaller initial drop in  $k_2$  and a slightly N-shaped virtual trajectory even for those slow movements (cf. thin solid and dashed lines in Fig. 9). The new virtual trajectory is very similar to the one modeled by Hogan for movements of similar duration (cf.



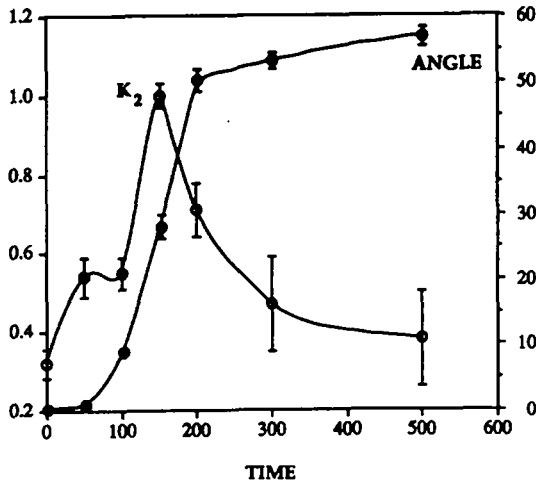


Fig. 6. Values of the  $k_2$  (related to joint stiffness) for different  $t_i$  were measured across the subjects. The average across the subjects actual trajectory is also shown. Standard errors are shown by vertical bars. Note a considerable increase in  $k_2$  in the middle of the movement. Angle scale is in degrees,  $k_2$  scale is in  $\text{Nm}/^\circ$ , time scale is in ms.

Fig. 3 in Ref. 30). There is still an initial drop in  $k_2$  which may be due to the crudeness of our estimation of the inertial torque, ignoring viscous torque component, and/or other factors. This unexplained behavior of  $k_2$  during slow movements was observed only during the first phase of the movement (20–25% of the total movement time). The factors responsible for it presumably affected the assessed values of  $k_1$  as well; therefore, the values of  $k_1$  and the virtual trajectories for times less than 150 ms must be treated with caution.

#### Static experiments

The proposed explanation of the changes in  $k_2$  over time should also apply to the static experiments. In

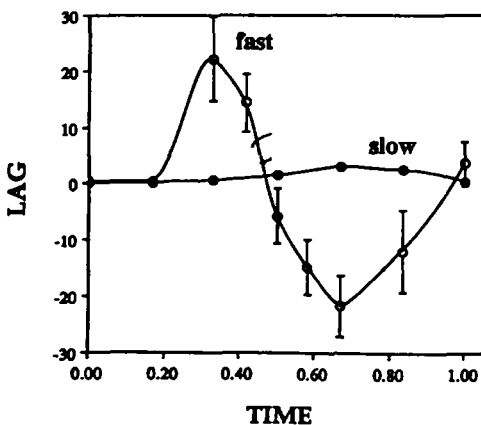
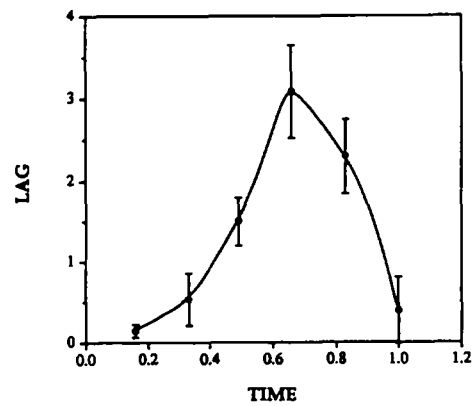


Fig. 7. The lag between the virtual and actual trajectories for fast (open circles, fast) and slow (closed circles, slow) movements was averaged for different  $t_i$  across the subjects. Note that an increase in movement speed leads to a 10-fold increase in the absolute values of the lag and a reversal of its sign. The data were normalized by the movement time. Lag scale is in degrees.



TIME	0.16	0.33	0.49	0.67	0.83	1
t	1.98	1.78	4.68	5.53	4.97	0.96
p	0.1	0.13	0.003	0.0015	0.0025	0.38

Fig. 8. The lag between the virtual and actual trajectories for slow movements averaged for different  $t_i$  across the subjects shown at a different scale (cf. Fig. 7). The Table shows  $t$ - and  $P$ -values for a two-tailed Student's  $t$ -test comparing the lag values with zero.

the static experiments, the same measurements were made without voluntary changes in the motor command. Limb movements were induced by load changes, and their duration was similar to that of slow voluntary movements. Coefficients of correlation for the linear regression lines were typically higher than those obtained in the dynamic experiments, and were all over the limit of statistical significance ( $P < 0.01$  for most of the datasets). Typical examples of time-varying changes in the coefficients  $k_1$  and  $k_2$  are shown in Fig. 10. The same figure shows  $k_1$  and  $k_2$  changes during a slow movement for the same subject. Since arm position changed during the tests with voluntary movements, we performed the static experiments in three different initial positions corresponding approximately to the initial, final, and intermediate ( $90^\circ$ ) joint angles (three subjects). The coefficients calculated at the three different positions were not different (Fig. 8), so, in three additional subjects, these experiments were performed only in the intermediate position ( $90^\circ$ ).

Note that the changes in  $k_1$  were much smaller in the static than in the dynamic experiments, but the time-course of  $k_2$  was very similar in both.

#### Changing the bias

In three of the subjects, the slow movement series was repeated with a smaller bias. Qualitatively, the results with a lower bias were similar (Fig. 11) but the magnitudes of the changes in  $k_1$  were significantly smaller. Since  $k_1$  was measured in the units of torque, this finding reflects that moving the same distance against a lower bias requires smaller torque changes. Values of  $k_2$  before and after reaching the plateau

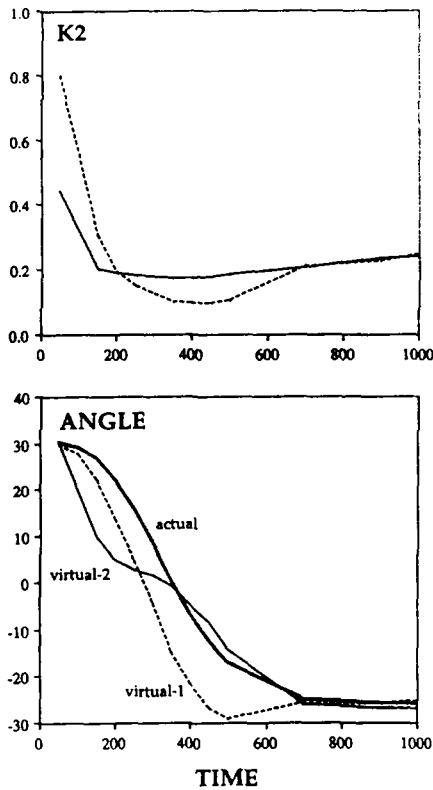


Fig. 9. Time changes of  $k_2$  (above) and virtual trajectories (below) calculated for the same set of slow movements with (thin solid lines, virtual-2) and without (dashed lines, virtual-1) taking into account the inertial torque component. The lower graph also shows the actual trajectory (thick line) which was calculated by averaging angle values for the unperturbed trials. Taking inertial component into account leads to attenuation of the initial drop in  $k_2$ , and emergence of a point of inflection somewhere in the middle of the movement. Time scale is in ms, angle scale is in degrees,  $k_2$  scale is in  $\text{Nm}/^\circ$ .

were also lower. Changes in the ratio  $k_1/k_2$ , corresponding to the reciprocal parameter shift, were very similar in movements against the two biases (Fig. 11). The movements against the lower bias were performed by the subject somewhat slower in the illustrated experiments. This is evident in both virtual and actual trajectories.

#### DISCUSSION

These experiments demonstrate that shifting JCCs can be recorded (or reconstructed) experimentally. Thus, the notion of the shifting JCCs during a movement ceases to be an abstraction. This also corroborates some of the basic ideas of the EP hypothesis and the model describing the emergence of the EMG patterns during movements performed under different strategies.<sup>36,40,41</sup>

According to the mass-spring models of muscle behavior and, in particular, to the EP hypothesis, voluntary movements arise from centrally specified shifts in the spring parameters.<sup>6,14</sup> To perform an isotonic movement, spring parameters change so

that the final EP corresponds to a desired joint position (Fig. 12). If there is a capability to control both the spring's rest length and stiffness (intercept and slope of the JCC), there are infinitely many combinations for achieving this task illustrated by three possible JCCs running through final EP B in Fig. 12.

Let us suppose that the control system "knows" the final values of its control variables  $r$  and  $c$ . There is still an infinite number of temporal patterns leading from initial values  $r_0$  and  $c_0$  to final values  $r_1$  and  $c_1$ . Among them are two patterns illustrated in Fig. 1. The simplest one (A), advocated by Feldman and colleagues, has an advantage of simplicity. The second pattern (B) is more complex, but offers

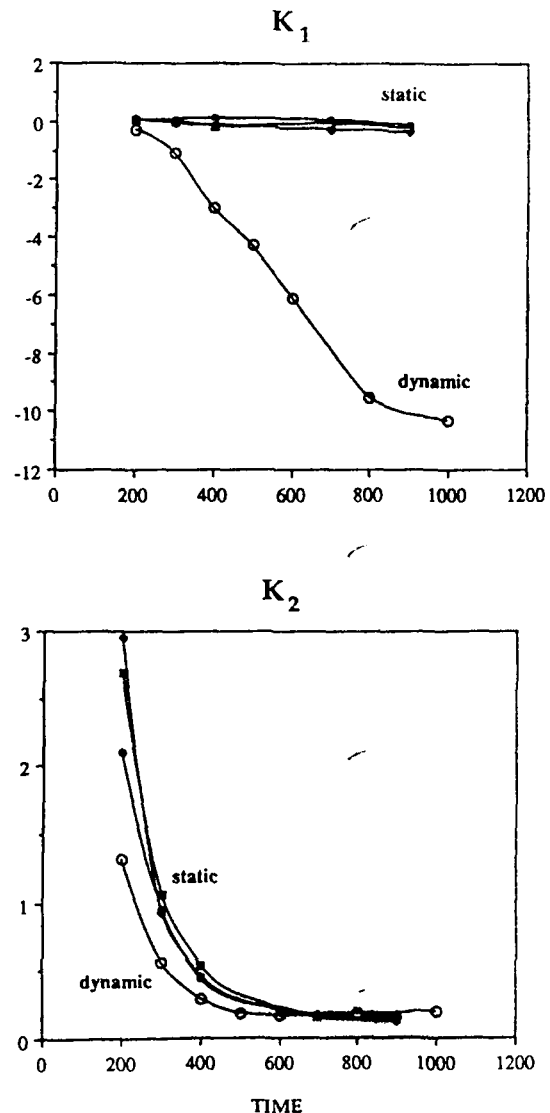


Fig. 10. Time changes in  $k_1$  and  $k_2$  values for the static experiments for three different initial elbow positions, and dynamic experiments. Note similar shifts of  $k_2$  in the static and dynamic experiments with virtually no changes in  $k_1$  in the static experiments as compared with the dynamic experiments. Time scale is in ms,  $k_1$  scale is in  $\text{Nm}$ ,  $k_2$  is in  $\text{Nm}/^\circ$ .

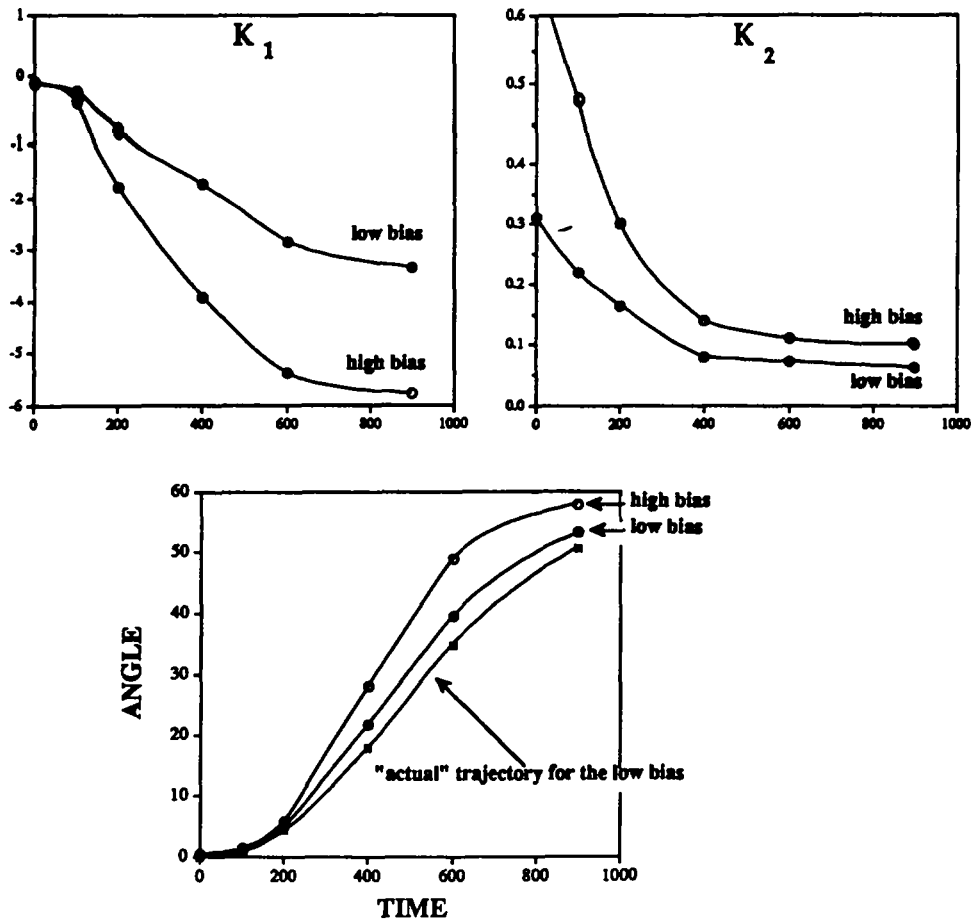


Fig. 11. Time changes in  $k_1$  and  $k_2$  (above) in two experimental series with movements performed against different initial bias torques. Note smaller range of  $k_1$  changes and lower plateau values of  $k_2$  for the movements performed against the smaller bias. The lower graph shows virtual trajectories for the two sets of movements and the actual trajectory for the series performed against the smaller bias. Time scales are in ms, angle scale is in degrees,  $k_1$  scale is in Nm,  $k_2$  scale is in Nm/°.

independent control of the braking process (antagonist burst, see Introduction) that is likely to play a crucial role in successful damping of oscillations in the final state.

#### *Virtual trajectory of slow movements*

The ratio  $k_1/k_2$  reflects the instantaneous position of the JCC in angle units. During isotonic movements, this ratio may be considered a reflection of the central representation of the intended instantaneous arm position, i.e. the equilibrium position to which the arm would come to rest if there were no subsequent changes in the central motor command. Changes of this ratio may be considered a virtual trajectory of a single-joint movement analogous to a similar notion introduced for multi-joint movements.<sup>20,52</sup>

Overplotting virtual and actual trajectories for slow movements demonstrates a time lag with the actual trajectory trailing behind the central one. This time lag is likely to be due to a number of factors including inertial properties of the limb and the movement speed which is defined, according to the

models,<sup>2,40</sup> by the rate of control parameter shift ( $\omega$  in eq. 2).

#### *The N-shaped virtual trajectories*

The experimental reconstruction of virtual trajectories during fast movements (Fig. 5) shows the second of the two patterns, the N-shaped virtual trajectories for smooth, fast single-joint movements ( $r$  changes in Fig. 1B). These results are consistent with our speculations on central motor control processes for fast single-joint movements, advanced in a model of EMG emergence.<sup>40,41</sup> For slower movements, the delayed shift in  $\lambda_{\text{act}}$  (Fig. 1B) becomes smaller and eventually disappears leading to a control pattern similar to the one illustrated in Fig. 1A and to a monotonic virtual trajectory (cf. Figs 4, 5 and 9).

In the experiments with slow movements explicitly accounting for inertial torque component, the virtual trajectory demonstrates a slight inflection which resembles N-shaped curves reconstructed for fast movements. The change from monotonic to N-shaped virtual trajectory develops gradually as the amplitude of the delayed shift in  $\lambda_{\text{act}}$  increases. This

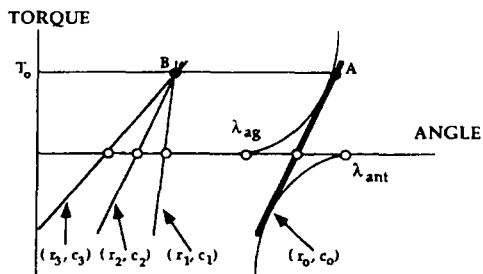


Fig. 12. According to the EP hypothesis, there is an infinite number of final  $(r, c)$  combinations leading to an isotonic movement from an initial joint position A to a desired final position B. If the final pair  $(r, c)$  is chosen, there is still an infinite number of time patterns  $r(t)$  and  $c(t)$  leading to them from initial values  $(r_0, c_0)$ .

is an evolutionary change rather than a qualitative change in strategy between slow and fast movements. This point requires, however, additional experiments reconstructing JCCs during movements at a variety of velocities.

The virtual trajectories shown in Fig. 5 are similar to those proposed by Hogan<sup>30</sup> and Hasan<sup>29</sup> basing on theoretical optimization criteria. However, they are consistent with a wide variety of other control strategies as well.

#### Stiffness changes

In slow movement experiments, we have not recorded what we consider reliable changes in the coefficient  $k_2$  related to the joint stiffness, and therefore, to the coactivation parameter  $c$ . The apparent "stiffness" dropped dramatically during the first 150–200 ms in both dynamic and control static exper-

iments. Since in the static experiments the subjects were not performing voluntary movements, the  $k_2$  changes cannot be attributed to central motor programming associated with voluntary movement initiation. Therefore, we suggest that the changes in  $k_2$  can be most parsimoniously explained as an artifact due to the inertial properties of the limb and design of the experiments. Taking into account inertial torque component during slow movements considerably attenuated the initial drop in  $k_2$  (Fig. 9). Since those movements were slow, and the muscle coactivation decreases with a decrease in movement speed<sup>7,49</sup> the actual changes in  $k_2$  in our experiments might be too small to be detected by our methods.

The experiments with fast movements have demonstrated a transient three-fold increase in the JCC slope (joint stiffness) peaking somewhere in the middle of the movement corresponding to our version of the central control patterns (cf. Fig. 6 with  $c$  changes in Fig. 1B). The apparent difference of the  $k_2$  between fast and slow movements may reflect the difference in the timing and amplitude of the delayed shift in  $\lambda_{ant}$  (Fig. 1B) with a decrease in movement velocity. This interpretation is similar to the one advanced for the differences in the virtual trajectories (above). It implies a transient increase in joint stiffness patterns that is monotonic with movement velocity due to changes in the degree of muscle activation rather than a change in the control pattern.

#### Static joint compliant characteristics

The static experiments have demonstrated nearly constant values of the  $k_1$  parameter, as compared to the changes observed during the movements. Since  $k_1$  is directly related to  $r$ , this observation is consistent with the interpretation that the subjects are able to comply with the instruction "not to react" used in all the earlier experiments which recorded JCCs.<sup>4,9,12,24,53</sup>

#### Possible consequences of ignoring viscosity

The effects of adding viscous forces to our analysis can be qualitatively assessed. Viscous forces oppose the motion which implies that our estimates of  $T$  on the left-hand side of eq. 6 are low. The external torque has a small effect on the velocity of the movement, so low estimates of  $T$  imply the trajectories of  $k_1$  in Figs 4 and 5 rise too slowly. The effect of this is that we tend to underestimate the lag of the actual trajectory in the first half of fast movements and overestimate its lead for the second half of fast movements.

Let us consider  $v$ , a parameter characterizing a "lumped" viscosity of the system. Viscosity can change during movements and should be considered a time function  $v(t)$ . Estimates of  $v$  for a static elbow joint with the muscles activated against a small constant external torque give values of about 0.6 Nm/rad per s.<sup>25</sup> There are no adequate assessments of  $v(t)$  during movements. However, our unpublished observations suggest that  $v$  does not

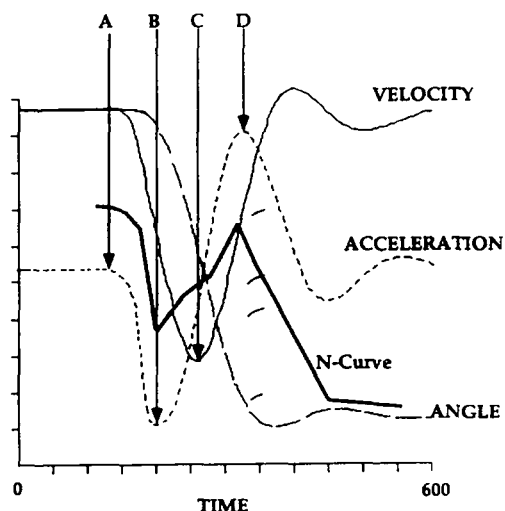


Fig. 13. A typical N-curve (thick line) is superimposed over nominal patterns of joint angle, velocity and acceleration for a fast elbow flexion. At point A, the external torque component dominates. In the vicinities of points B and D, the inertial torque component is much higher than external and viscous torques. In the vicinity of point C, the viscous torque component is likely to play a significant role. Time scale is in ms.

increase during fast movements. So, let us use this value and hope that we are not significantly underestimating the viscous component of the total torque.

Nominal profiles of angle, velocity, and acceleration changes during fast movements and a superimposed N-shaped virtual trajectory are illustrated in Fig. 13 (cf. Fig. 5 and Refs 26, 27). To account for one of the effects of reflex delays (see Appendix), the N-shaped curve is shifted by 25 ms (our assessment of a half of the delay in the hypothetical reflex loop) to the left along the time axis. At the beginning of the movement (point A), the external torque in our experiments was 3 Nm. At the time of peak acceleration (point B), the inertial torques are of the order of 30 Nm (using a peak acceleration of  $10,000^\circ/\text{s}^2$ ). Slightly lower values are observed at the time of peak deceleration (point D). At the time of peak speed (point C), the inertial component is zero while the viscous component is maximal and about 5 Nm (using a peak speed of  $500^\circ/\text{s}$ ). At the beginning of the movement, when both speed and acceleration are relatively low, the external torque will dominate. In the vicinity of points B and D, the inertial torque component is much higher than the external and viscous components. Only in the vicinity of point C, the viscous component is likely to play a dominant role.

These very qualitative assessments suggest that our results may be corrupted in the vicinity of point C. However, it seems that we may be rather confident in the vicinities of points A, B, and D which are the crucial points characterizing the N-shape, and at the moment of movement termination when both inertial and viscous components are zero.

For slow movements, similar assessments suggest peak values of viscous torques of about 1.5 Nm. This is smaller than the external torque in most of the trials. Therefore, we think that ignoring viscous torque component did not corrupt our data qualitatively for slow movement as well.

#### *Are the results self-evident?*

The method we have used for reconstructing JCCs will yield regression lines for any mechanical mass-spring system. However, a passive mechanical mass-spring system would demonstrate close to linear torque-angle relations without changes in stiffness and zero length. One of the basic questions of applicability of mass-spring models of motor behavior, including the EP hypothesis is: does the motor system behave as a mass-spring with controlled spring parameters? Our affirmative answer to this question supports the mass-spring modeling for single-joint motor control. Secondly, one might expect that a possibly highly variable signal (the central command

for a voluntary movement) would lead to a significant drop in the coefficients of correlation when compared with the classical static experiments (cf. Figs 3 and 5). This is not the case. Thirdly, we do not think one can assume that coefficients of the regression equations, emerging as a result of a rather complicated analysis of the data, must behave according to any of the theoretically postulated patterns or even in any orderly manner. Therefore, the data presented in this paper were a surprise rather than confirmation of self-evident consequences of elementary physics.

#### *Possible future applications*

The method described here has many potential applications for testing different aspects of motor control processes if it is appropriately developed.

(1) Recording movements with different speeds would reveal the dependence of the time lag between the virtual and actual trajectories upon the speed. The hypothesis that this lag is due to dynamics of the peripheral apparatus suggests that the lag should increase with increase in either movement speed or external load. Quantitative assessment of this lag might be helpful for analysing results of the studies with targets that jump during or just prior to a movement,<sup>31,35,47,52</sup> when reprogramming is likely to take place.

(2) This method might be helpful in analysing differences in central programming of movements of different accuracy. The  $\lambda$ -model provides a natural basis for analysis of relations between speed and accuracy.<sup>31</sup> It suggests that the speed-accuracy trade-off and other relations between different measures of performance may be results of different, task- (or strategy)-dependent processes of central programming. One may try to reveal these differences with the described method.

(3) Analysis of movements performed on the background of changing external force does not have to be confined to single-joint movements. A similar paradigm may be used for reconstructing individual JCC shifts and virtual trajectory during multi-joint movements.

We believe that the method of reconstruction of the JCC used in this work has considerable potential for both single- and multi-joint movement studies. Future plans include using it for reconstructing JCCs during single-joint movements at a variety of speeds, over a variety of distances, and against a variety of loads, as well as generalizing it for free three-dimensional movements.

*Acknowledgements*—The authors are grateful to Mr Om Paul for his excellent programming support. This work was supported by NIH grant AR 33189 and American Paralysis Association grant LA1-8901-01.

#### REFERENCES

1. Abdusamatov R. M. and Feldman A. G. (1986) Description of the electromyograms with the aid of a mathematical model for single joint movements. *Biophysics* 31, 549–552.

2. Abdusamatov R. M., Adamovich S. V. and Feldman A. G. (1987) A model for one-joint motor control in man. In: *Motor Control* (eds Gantchev G. N., Dimitrov B. and Gatev P.), pp. 183–187. Plenum Press, New York.
3. Allum J. H. J. (1975) Response to load disturbances in human shoulder muscles: the hypothesis that one component is a pulse test information signal. *Expl Brain Res.* **22**, 307–326.
4. Asatryan D. G. and Feldman A. G. (1965) Functional tuning of the nervous system with control of movements or maintenance of a steady posture. I. Mechanographic analysis of the work of the limb on execution of a postural task. *Biophysics* **10**, 925–935.
5. Bennett D. J., Xu Y., Hollerbach J. M. and Hunter I. W. (1989) Identifying the mechanical impedance of the elbow joint during posture and movement. *Abstr. Soc. Neurosci.* **15**, 396.
6. Bizzi E. (1980) Central and peripheral mechanisms in motor control. In *Tutorials in Motor Behavior* (eds Stelmach G. E. and Requin J.), pp. 131–143. Elsevier, North Holland, Amsterdam.
7. Corcos D. M., Gottlieb G. L. and Agarwal G. C. (1989) Organizing principles for single-joint movements. II. A speed-sensitive strategy. *J. Neurophysiol.* **62**, 358–368.
8. Darling W. G. and Cooke J. D. (1987) A linked muscular activation model for movement generation and control. *J. Mot. Behav.* **19**, 333–354.
9. Davis W. R. and Kelso J. A. S. (1982) Analysis of "invariant characteristics" in the motor control of Down's syndrome and normal subjects. *J. Mot. Behav.* **14**, 194–212.
10. Day B. L. and Marsden C. D. (1982) Accurate repositioning of the human thumb against unpredictable dynamic loads is dependent upon peripheral feedback. *J. Physiol.* **327**, 393–407.
11. Enoka R. M. (1983) Muscular control of a learned movement: the speed control system hypothesis. *Expl Brain Res.* **51**, 135–145.
12. Feldman A. G. (1966) Functional tuning of the nervous system with control of movement or maintenance of a steady posture. II. Controllable parameters of the muscle. *Biophysics* **11**, 565–578.
13. Feldman A. G. (1966) Functional tuning of the nervous system with control of movement or maintenance of a steady posture. III. Mechanographic analysis of execution by man of the simplest motor task. *Biophysics* **11**, 667–675.
14. Feldman A. G. (1974) Control of the length of a muscle. *Biophysics* **19**, 776–771.
15. Feldman A. G. (1980) Superposition of motor programs. I. Rhythmic forearm movements in man. *Neuroscience* **5**, 81–90.
16. Feldman A. G. (1980) Superposition of motor programs. II. Rapid flexion of forearm in man. *Neuroscience* **5**, 91–95.
17. Feldman A. G. (1986) Once more on the equilibrium-point hypothesis ( $\lambda$  model) for motor control. *J. Mot. Behav.* **18**, 17–54.
18. Feldman A. G. and Latash M. L. (1982) Afferent and efferent components of joint position sense: interpretation of kinaesthetic illusions. *Biol. Cybern.* **42**, 205–214.
19. Feldman A. G. and Orlovsky G. N. (1972) The influence of different descending systems on the tonic stretch reflex in the cat. *Expl Neurol.* **37**, 481–494.
20. Flash T. (1987) The control of hand equilibrium trajectories in multi-joint arm movements. *Biol. Cybern.* **57**, 257–274.
21. Gielen C. C. A. M. and Houk J. C. (1984) Nonlinear viscosity of human wrist. *J. Neurophysiol.* **52**, 553–569.
22. Gottlieb G. L. and Agarwal G. C. (1980) Response to sudden torque about ankle in man. II. Postmyotatic reactions. *J. Neurophysiol.* **43**, 86–101.
23. Gottlieb G. L. and Agarwal G. C. (1980) Response to sudden torque about ankle in man. III. Suppression of stretch-evoked responses during phasic contraction. *J. Neurophysiol.* **44**, 233–246.
24. Gottlieb G. L. and Agarwal G. C. (1988) Compliance of single joints: elastic and plastic characteristics. *J. Neurophysiol.* **59**, 937–951.
25. Gottlieb G. L., Agarwal G. C. and Tanavde A. S. (1986) A method of estimating human joint compliance which is insensitive to reflex, triggered or voluntary reactions. *Abstr. Soc. Neurosci.* **12**, 468.
26. Gottlieb G. L., Corcos D. M. and Agarwal G. C. (1989) Strategies for the control of voluntary movements with one mechanical degree of freedom. *Behav. Brain Sci.* **12**, 189–250.
27. Gottlieb G. L., Corcos D. M., Agarwal G. C. and Latash M. L. (1990) Organizing principles for single-joint movements. III. Speed-Insensitive Strategy as a default. *J. Neurophysiol.* **63**, 625–636.
28. Granit R. (1970) *The Basis of Motor Control*. Academic Press, London.
29. Hasan Z. (1986) Optimized movement trajectories and joint stiffness in unperturbed, inertially loaded movements. *Biol. Cybern.* **53**, 373–382.
30. Hogan N. (1984) An organizational principle for a class of voluntary movements. *J. Neurosci.* **4**, 2745–2754.
31. Houk J. C. (1976) An assessment of stretch reflex function. *Prog. Brain Res.* **44**, 303–314.
32. Houk J. C. (1979) Regulation of stiffness by skeletomotor reflexes. *A. Rev. Physiol.* **41**, 99–114.
33. Houk J. C. and Rymer W. Z. (1981) Neural control of muscle length and tension. In *The Nervous System. Handbook of Physiology* (ed. Brooks V. B.), Vol. II, part 1, pp. 257–324. American Physiological Society, Bethesda.
34. Iles J. F. (1977) Responses in human pretibial muscle to sudden stretch and to nerve stimulation. *Expl Brain Res.* **30**, 451–470.
35. Lacquaniti F., Licata F. and Soechting J. F. (1982) The mechanical behavior of the human forearm in response to transient perturbations. *Biol. Cybern.* **44**, 67–77.
36. Latash M. L. (1989) Direct pattern-imposing control or dynamic regulation? *Behav. Brain Sci.* **12**, 226–227.
37. Latash M. L. (1989) Implications of the equilibrium-point hypothesis for the variability of aimed hand movements. In *Spatial, Temporal and Electromyographical Variability in Human Motor Control* (ed. Worringham C. J.), pp. 16–17. Ann Arbor, MI.
38. Latash M. L. and Gottlieb G. L. (1989) Reconstruction of shifting joint compliant characteristics during slow movements. *Abstr. Soc. Neurosci.* **15**, 51.
39. Latash M. L. and Gottlieb G. L. (1990) Compliant characteristics of single joints: preservation of equifinality with phasic reactions. *Biol. Cybern.* **62**, 331–336.
40. Latash M. L. and Gottlieb G. L. (1991) An equilibrium-point model of dynamic regulation for fast single-joint movements: I. Emergence of strategy-dependent EMG patterns. *J. Mot. Behav.* (in press).
41. Latash M. L. and Gottlieb G. L. (1991) An equilibrium-point model of dynamic regulation for fast single-joint movements: II. Similarity of isometric and isotonic programs. *J. Mot. Behav.* (in press).

42. Lee R. G. and Tatton W. G. (1982) Long latency reflexes to imposed displacement of the human wrist: dependence on duration of movement. *Expl Brain Res.* **45**, 207–216.
43. Lestienne F. (1979) Effects of inertial loads and velocity on the braking process of voluntary limb movements. *Expl Brain Res.* **35**, 407–418.
44. Marsden C. D., Merton R. A. and Morton H. B. (1976) Stretch reflex and servo action in a variety of human muscles. *J. Physiol.* **259**, 531–560.
45. Marsden C. D., Obeso J. A. and Rothwell J. C. (1983) The function of the antagonist muscle during fast limb movements in man. *J. Physiol.* **335**, 1–13.
46. Matthews P. B. C. (1959) The dependence of tension upon extension in the stretch reflex of the soleus of the decerebrate cat. *J. Physiol.* **47**, 521–546.
47. Megaw E. D. (1974) Possible modification to a rapid on-going programmed manual response. *Brain Res.* **71**, 425–441.
48. Miller D. I. and Nelson R. C. (1976) *Biomechanics of Sport*. Lea & Febiger, Philadelphia.
49. Mustard B. E. and Lee R. G. (1987) Relationship between EMG patterns and kinematic properties for flexion movements at the human wrist. *Expl Brain Res.* **66**, 247–256.
50. Partridge L. D. and Benton L. A. (1981) Muscle, the motor. In *The Nervous System. Handbook of Physiology* (ed. Brooks V. B.), Vol. II, part 1, pp. 43–106. American Physiological Society, Bethesda.
51. Rack P. M. H. and Westbury D. R. (1969) The effects of length and stimulus rate on tension in the isometric cat soleus muscle. *J. Physiol.* **204**, 443–460.
52. van Sonderen J. F., Denier van der Gon J. J. and Gielen C. C. A. M. (1988) Conditions determining early modification of motor programmes in response to changes in target location. *Expl Brain Res.* **71**, 320–328.
53. Vincken M. H., Gielen C. C. A. M. and Denier van der Gon J. J. (1983) Intrinsic and afferent components in apparent muscle stiffness in man. *Neuroscience* **9**, 529–534.

(Accepted 4 February 1991)

## APPENDIX

### Methodological aspects of measuring joint compliance

It seems helpful to clarify our use of the terms stiffness and zero length and how they relate to other measures of stiffnesses, e.g. measured with phasic randomized perturbations.<sup>5,35</sup> Single-joint behavior can be modeled with a second-order differential equation like:

$$T_e(t) = m(t) \frac{d^2\alpha(t)}{dt^2} + b(t) \frac{d\alpha(t)}{dt} + k(t)[r(t) - \alpha(t)], \quad (A1)$$

where  $m$ ,  $b$ ,  $k$ , and  $r$  are time functions,  $T_e$  is external torque, and  $\alpha$  is joint angle. Functions  $m(t)$ ,  $b(t)$ ,  $k(t)$ , and  $r(t)$  are related to moment of inertia, coefficient of viscosity, coefficient of stiffness, and “zero length” of the spring correspondingly. According to the EP hypothesis,  $k(t)$  [which is related to  $c(t)$ ] and  $r(t)$  are control signals.

There are numerous ways to measure coefficients of such an equation including application of small torque perturbations at certain times and measuring the length changes,<sup>25</sup> or using randomized perturbations with subsequent correlation of torque and angle changes.<sup>5,35</sup> Note, however, that eq. A1 models a damped spring with an instantaneous reaction to external load or central command changes.

This is certainly not a complete description of actual limbs and their reactions. One can identify at least two different kinds of mechanism with different characteristic time delays mediating muscle reaction to length changes and therefore contributing to the muscle spring properties. The first one, whose reaction can be considered instantaneous, is defined by mechanical properties of the peripheral apparatus including the muscle itself. An innervated deafferented muscle would demonstrate pure properties of this loop.<sup>33,51</sup> Reflex connections bring about a delayed muscle reaction to a perturbation which is attributed in animal experiments to the tonic stretch reflex.<sup>19,46</sup> The latter component is observed in humans as well and forms the basis of the  $\lambda$ -model.<sup>12,13,17</sup>

Let us suppose that the characteristic delay in the hypothetical reflex loop is  $t_1$ . Then, if one applies a load perturbation and measures joint angle, the kinematics will be influenced by different physiological factors at different times after the moment of perturbation. A measurement at

a time  $t$  ( $0 < t < t_1$ ) is equivalent to testing a deafferented muscle. A measurement at a time  $t'$  ( $t_1 < t'$ ) would also supply information on the muscle with intact reflex connections.

According to the EP hypothesis, motor control is based on central regulation of parameters of the hypothetical reflex loop. From this view, eq. A1 must be interpreted with great care because its parameters can reflect the properties of very different neuromuscular mechanisms depending on how and when angle and torque are measured. In particular, ignoring time delays makes extraction of information relevant to the reflex loop problematic, especially when step-like external perturbations are used. This approach, however, might be useful for analysing issues dealing with mechanical properties of the peripheral apparatus under different states of muscle activation.

Latency of any reflex loop is a sum of three components: transmission in the afferent path, central delay, and transmission in the efferent path. We do not have reliable methods for assessing the central delay time for the hypothetical reflex loop. For the present purposes, let us assume that this time is negligible and the whole delay consists of two equal parts, afferent and efferent,  $t_{af} = t_{ee} = t_1/2$ . If at a moment of time  $t_0$ , instantaneous position and slope of the JCC is described by central parameters  $c_0$  and  $r_0$ , the generated efferent signal will reflect the position of the JCC and an afferent volley that was in fact generated  $t_1/2$  ago. When the efferent signal comes to the muscles, it will convey outdated information reflecting the position of the JCC which was centrally generated  $t_1/2$  ago and afferent information which was generated by the peripheral receptors  $t_1$  ago.

Let us assume the moment of inertia to be constant and that there are no acceleration-dependent force-generators. In his original work, Feldman<sup>12,13</sup> recorded force-length characteristics of passive muscles and showed that they represented a small fraction of the reactions activated through the reflex loop muscles. Although the “peripheral” elastic component for an activated muscle is higher,<sup>28,50</sup> one may, in a first approximation, write:

$$T_e(t + t_1) = M \frac{d^2\alpha(t + t_1)}{dt^2} - v(t + t_1) \frac{d\alpha(t + t_1)}{dt} = k_1 \left( t + \frac{t_1}{2} \right) \left[ \alpha(t) - \alpha_0 \left( t + \frac{t_1}{2} \right) \right], \quad (A2)$$

where  $T_e$  is an externally applied torque,  $v(t)$  is a function describing the viscous torque component,  $x_{01}$  is "zero" length and  $k_1$  is stiffness for the hypothetical reflex mechanism that forms the basis of the EP hypothesis. Comparing with eq. 1 one can see that the left side of eq. A2 is total torque  $T(t + t_1)$ , and  $k_1(t)$  and  $x_{01}(t)$  are analogous to  $c(t)$  and  $r(t)$ , correspondingly.

Equation A2 can be simplified so that it would describe the "static" do-not-intervene-voluntarily paradigm. Firstly, at the equilibrium  $dx/dt = 0$  and  $d^2x/dt^2 = 0$ . Secondly, at the final equilibrium state, joint torque and angle are constants, and since we assume that the central command is constant, all the other coefficients are not changing with time either. So, the differences in the time arguments do not matter in this case. Note, however, that the fact that  $k_0$  and  $k_1$  are independent of time does not mean that they are constants since they may depend on joint angle (a non-linear spring). Then, one gets:

$$T = k_1[x - x_{01}]. \quad (\text{A3})$$

This equation is simple enough to allow experimental reconstruction of the torque-angle dependencies and assessing values of the coefficients  $x_{01}$  and  $k_1$ .

In the framework of the present study, we do not analyse possible contribution of viscosity, i.e. ignore the second member of the right side of eq. A2. According to existing assessments,<sup>25</sup> viscous torques for slow movements are small as compared with elastic torques, and for fast movements are small as compared with inertial torques. This might not be true for certain moments during a movement, e.g. when the speed is maximal and acceleration is zero. However, we decided to ignore this component and analyse the following

expression:

$$T(t + t_1) = M \frac{d^2x(t + t_1)}{dt^2} = k_1 \left( t + \frac{t_1}{2} \right) \left[ x(t) - x_{01} \left( t + \frac{t_1}{2} \right) \right]. \quad (\text{A4})$$

We did not include the delay  $t_1$  in the analysis because its value is unknown. However, our method of reconstructing JCCs is based on reproducing a standard motor program, i.e. fixed functions  $k(t)$  and  $r(t)$  on the background of slow ramp external torque changes. As such, it becomes relatively insensitive to  $t_1$ , at least at times bigger than  $t_1$ . If spring characteristics of a system described by eq. A4 are analysed by corresponding joint angle external torques measured at the same time, the errors will be introduced because of using  $T(t)$  rather than  $T(t + t_1)$ . These errors will be proportional to the ratio  $T(t) - T(t + t_1)/T(t + t_1)$  which is in turn proportional to  $t_1/t$ .

The following considerations justify our usage of  $T(t)$ . Firstly, since ramp torque changes were used, these errors proportionally affected all the measurements. Secondly, since  $t_1$  is likely to be of the order of 50–70 ms,<sup>31,32,46</sup> and the time of ramp torque changes during slow movements was 800 ms, and during fast movements was 300 ms, these errors are likely to be of a considerable magnitude only for relatively short times (initial phases of the movements). Thirdly, during fast movements, the inertial component (second member at the left side of eq. A4) dominated over the externally applied force for most of the times of measurement. Note that using step-like perturbations may lead to dramatic effects of ignoring  $t_1$ , since the ratio  $T(t) - T(t + t_1)/T(t + t_1)$  can be very high because  $T(t + t_1)$  can be much lower than  $T(t)$ .

On the other hand, ignoring the  $t_1/2$  delay in the right side of eq. A2 leads to a shift of the virtual trajectories "to the right" along the angle axis by  $t_1/2$ . This consistent error has been of no importance in the framework of present study.