Damping Actions of the Neuromuscular System With Inertial Loads: Human Flexor Pollicis Longus Muscle

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Lin, David C. and W. Zev Rymer. Damping actions of the neuromuscular system with inertial loads: human flexor pollicis longus muscle. J Neurophysiol 85: 1059–1066, 2001. Our previous work in an animal model showed that neuromuscular damping properties help maintain limb posture by effectively dissipating mechanical energy arising from disturbances. The purpose of this study was to determine whether similar damping properties were expressed in intact, normal human muscles. To review briefly, when the reflexively active soleus muscle in a decerebrate cat is coupled to an inertial load, application of a force impulse to the load results in lightly damped oscillations. By calculating the logarithmic decrement in muscle velocity following the impulse (the decrement being related to the amount of energy dissipated from the inertia), we found that damping increased with oscillation amplitude, a nonlinear property. This nonlinearity represents an automatic compensation for larger perturbations. Our findings in parallel experiments on the interphalangeal joint of the human thumb were that the long thumb flexor, the flexor pollicis longus (FPL), displayed mechanical and reflex behavior closely comparable to that reported earlier for the cat soleus, despite differences in architectural and metabolic properties between these muscles. Specifically, by selecting experimental trials that did not include voluntary interventions, we observed amplitude-dependent differences in damping in which larger amplitude movements elicited larger damping than did smaller movements. In addition, even after accounting for amplitude-dependent differences in damping, damping was found to be larger in later cycles than in the first cycle. This nonlinearity indicates that both mechanical properties of muscle and reflex mechanisms are dependent on prior movement history. We propose that this history-dependent behavior arises from the effects of prior movement on stretch reflex gain, and these effects are mediated primarily via changes in muscle spindle properties. Recordings of electromyographic activity from the FPL, during the first and second cycles of oscillation supported this postulate of a reduced reflex gain following prior motion. The functional significance of these nonlinear damping properties is that during the initial muscle stretch, the stiffness is high, which helps to preserve the initial position (although at the expense of promoting oscillation). Subsequently, the ensuing increase in damping helps suppress continuing oscillation. This sequence of varying mechanical properties is broadly analogous to the features of a predictive, or feed-forward controller, designed to produce a response that initially maintains position, and subsequently damps oscillations. These results show that the intrinsic properties of muscle and spinal reflexes automatically provide a complex time-varying response, appropriate for maintenance of stable limb posture.

INTRODUCTION

In an earlier study, we examined the amount of damping provided by the neuromuscular system in a reduced animal preparation by recording oscillations induced when the reflexively intact soleus was coupled to a moving inertial load (Lin and Rymer 2000). The experimental paradigm was chosen for its functional relevance, which was reflected in two important attributes. First, it allowed for the normal interaction of force and length after a transient perturbation, as occurs routinely in the motor control of inertial (limb) segments. Second, oscillations are observed to arise naturally from neuromuscular viscoelasticity coupling to inertial loads, and they are also prevalent in the course of maintaining limb posture. Using the principle that damping is equivalent to the dissipation of mechanical energy, damping was shown to be highly nonlinear, in that energy dissipation increased with increasing oscillation amplitude. This nonlinearity could be attributed to intrinsic muscle mechanical properties and/or to nonlinear stretch reflex action.

The experimental model used in the earlier study was the isolated soleus muscle of the decerebrate cat. In the decerebrate cat preparation, underdamped oscillations occur readily in response to postural perturbations, a finding not necessarily replicated in an intact preparation (Hoffer et al. 1990). It could be argued that decerebration induces stretch reflex hyperexcitability, and that this hyperexcitability is both unphysiological and the primary cause of the oscillatory nonlinear response in this preparation. Therefore we thought it important to determine whether nonlinear damping properties are also expressed under more physiological conditions, such as those found in normal human subjects.

To date, human neuromuscular mechanical properties have been mainly evaluated using controlled positional perturbations applied across single joints. These human studies have replicated many of the nonlinear properties shown in isolated animal preparations, such as hyperbolic and asymmetric force-velocity relationships (Lehman and Calhoun 1990; Wickiewicz et al. 1984), yielding behavior and stretch reflex compensation (Carter et al. 1990; Crago et al. 1976; Sinkjaer et al. 1988), and amplitude-dependent mechanical properties (Joyce and Rack 1974; Kearney and Hunter 1982). One noteworthy variation to position-controlled perturbations was utilized by Stiles, who

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applied a force transient to the system. He lightly tapped the back of the outstretched hand and was able to elicit consistent oscillations. A comparison between the recorded hand oscillations and simulated linear system behavior demonstrated several nonlinear mechanical effects in the human records, including significant time-varying properties (Stiles 1980, 1983). However, the correspondence between the results of the positional perturbation studies and those of the Stiles studies remains unclear.

In light of these uncertainties, the objectives of our current study are to characterize the damping of oscillations when the distal joint of the thumb, which is controlled (in part) by the flexor pollicis longus (FPL) muscle, is coupled to an inertial load. The FPL muscle is examined here using a protocol virtually identical to that used in the earlier cat soleus experiments. The protocol simulated the conditions of posture by testing a low level of muscle activation and low movement frequencies, which are in the range of frequencies that are elicited by perturbations during standing. To emulate the animal experiments, we asked subjects to activate a single muscle (no cocontraction) and hold its background activation constant throughout the trial. This implied that the only modulation of muscle activity was due to reflexes. We then used two criteria to identify trials with voluntary interventions and analyzed the remaining trials by tracking the velocity decrement following the application of a force impulse. We confirmed that damping was amplitude dependent (similar to the analogous animal experiments). In addition, damping was smaller in the first cycle of oscillation than in subsequent cycles, indicating the existence of history-dependent mechanical properties.

We postulate that the second nonlinearity is related primarily to the effects of earlier movement on muscle spindle properties. The functional significance of this finding is that an automatic modulation of system mechanical properties occurs following movement. Specifically, there is high stiffness initially (which potentially helps to regulate the initial position or posture), while the subsequent increase in damping helps suppress oscillations. Because this history-dependent variation arises from the intrinsic muscle and spindle properties, the neural control of posture is simplified because both position regulation and velocity reduction are accomplished without descending control. Preliminary results have been reported previously (Lin and Rymer 1997).

METHODS

Subjects

Experiments were performed on five male subjects, 25–35 yr old. Two of the subjects participated in the experiments on two different days for the two different experimental protocols (see Experimental protocol). All subjects had no physical or neurological impairments and provided informed consent.

Experimental setup

A torque motor (PMI model JR-16CH) controlled by a switching amplifier (PMI model AXA-180-90-12) was used for the experiments. The motor had a tachometer (output of 57 V per 1,000 rpm) and an amplifier (PMI model AXA-180-90-12) was used for the experiments.

The motor amplifier acted as a velocity servo. The input to the amplifier was digitally controlled by a PC and a 16-bit data acquisition card (Keithley Metabyte). The torque signal, \( T_s \), was sampled, integrated, and sent to the amplifier at a rate of 5 kHz, thus simulating an inertia according to

\[
v(i) = \frac{t_s}{I} \sum_{j=1}^{i} [T(j) - T_s] + V_o
\]

where \( i \) represents a sample time, \( t_s \) is the sampling interval, \( v \) is the velocity, \( V_o \) the initial velocity, and \( I \) is the moment of inertia simulated. Note that torque was referenced to initial torque, \( T_o \), similar to the cat study, so that positive and negative values could be achieved. This protocol is similar to the task of holding a weight against gravity (represented by the \( T_o \) term) and the weight being perturbed from a stationary position.

To compensate for any phase lags due to motor dynamics (i.e., mechanical response time and compliance), the position and torque were fed back, similar to adding integral and derivative control, respectively. The output equation for velocity became

\[
v(i) = \frac{t_s}{I} \sum_{j=1}^{i} [T(j) - T_s] + V_o + G_p \left[ t_s \sum_{j=1}^{i} v(j) - P(i) \right]
\]

where \( P \) was the measured position, \( G_p \) and \( G_T \) were the gains of the position and torque feedback, respectively. The position gain increased overall stiffness of the system and was adjusted to the maximum value, which caused only a small amplitude of vibration (\(<1\degree\) peak to peak; peak in power spectrum at 60 Hz). The torque gain affected the phase angle between torque and position, and the gain was adjusted so that oscillations with a spring remained at a constant amplitude.

As in the cat experiments, accuracy of the inertial simulation was absolutely critical for the analysis and interpretation of the data. To help evaluate the accuracy of the inertial simulation, a spring (spring constant of 1.5 Nm/\( \text{rad} \)) was attached to the motor, and a torque impulse was applied. For a 10-fold range of moment of inertia magnitudes, the oscillations maintained a constant amplitude, indicating accurate mass-spring behavior for the resulting frequencies of 1.5–5 Hz and peak-to-peak amplitudes of 2–10°. The spring test was particularly sensitive for testing the accuracy of the simulations, as any deviation from inertial behavior would result in increasing or decreasing oscillations. To provide further checks of the inertial simulation, all experimental torque records were doubly integrated, and the difference between the integrated signal and the recorded position compared. This difference was routinely very small, such that the variance accounted for by the mass simulation was always \( >98\% \).

A final check of the simulation accuracy was that velocity was maintained after a force was applied to and then removed from the system, implying that any frictional forces were compensated by our feedback system.

For recording purposes, the position, velocity, and torque signals were low-pass filtered at 500 Hz and sampled at 1,000 Hz using a Macintosh computer and data acquisition card (National Instruments). Intramuscular electromyographic (EMG) activity was recorded using insulated bilateral stainless steel 50-\( \mu \)m wires, inserted into the appropriate muscle. The correct placement of the wire was checked by electrical stimulation of the muscle via the wire. EMG signals were amplified, low-pass filtered at 500 Hz, and recorded at 1,000 Hz. All trials were checked after the experiment for simulation accuracy and moment of inertia and initial velocity magnitude.

The interphalangeal (IP) joint of the thumb was used in all experiments. This joint provides advantages for testing mechanical prop-
properties of muscle because the joint is controlled by just two antagonistic muscles, the FPL and extensor pollicis longus (EPL), and the inertia of the terminal phalangeal segment is small, on the order of 0.003 g · m² (Brown et al. 1982). The distal portion of the thumb was fastened with a plastic cable tie to a fixture, which was in turn attached to the shaft of the motor (Fig. 1). The proximal portion of the thumb was held securely by a test tube clamp. The forearm of the subject was pronated and supported in a cradle such that the dorsal aspect of the proximal portion of the thumb and the radial edge of the forearm formed a straight line. The musculotendon length of the FPL is longest in this forearm position (Rack and Ross 1984), so that muscle would be operating beyond the slack length of the tendon.

The center of rotation of the thumb had to be aligned accurately with the axis of rotation of the motor shaft, otherwise erroneous torques would be recorded due to the misalignment. It was difficult to visually locate the joint center, so the alignment was done by systematic trial and error. The thumb was placed in several different positions with respect to the motor axis, and the subject was asked to move the limb into extreme flexion and extension. The position with the least amount of perceived resistance was taken to be the best alignment. This alignment was also checked by measuring the passive torque at full extension and 60° of flexion; extremely large torques (>0.2 Nm) meant that the alignment was inaccurate, and the thumb was repositioned.

At the experiment start, maximum flexion and extension torque for each subject was recorded at 35° of flexion. (All thumb IP joint angles defined relative to the IP segments forming a straight line, so that 0° reflects full joint extension.)

Experimental protocol

Before the start of the trial, the thumb was positioned in 35° of flexion. The torque signal was displayed on an oscilloscope, and the subject was asked to produce a flexion torque by matching a reference line, set to approximately 10–15% of the subject’s maximum isometric flexion torque. This torque level was chosen because subjects were able to maintain that level of muscle activation throughout the 3-s long trial, and fatigue did not occur during the experimental session.

The instruction, “do not intervene,” was given. This instruction has been used frequently in many studies requiring that the descending command to the muscle remain constant (see, for example, Asatryan and Fel’dman 1965; Carter et al. 1990; Gielen and Houk 1984). The consequence of maintaining the same level of voluntary activation was that in the final steady state (i.e., isometric condition), the length-tension relationship of muscle properties, moment arm characteristics, and passive joint properties would promote return of the joint to the original position. Assuming that the static torque-angle relationship does not change over time also assumes that factors such as fatigue or the nonlinear properties of spindles or motoneurons would not be significant.

Thus the initial joint position is preserved as the equilibrium position, but only as an outcome of the subject’s constant effort and because of the short-term constancy of intrinsic mechanical properties. The assumption that the final equilibrium position is the same as the initial position is an important one for our analysis (see next section).

After the subject achieved a steady torque, the oscilloscope screen was blanked, so that the subject would not be influenced by the changing torque display, and the perturbation was then applied. The perturbation was given in the form of a torque impulse, which extended the joint and created an initial stretch velocity in the FPL muscle (Fig. 1). At the end of the trial, the position record was scanned for any obvious voluntary reactions, which usually took the form of a shift in the mean position of oscillation (see preceding paragraph). Trials with obvious voluntary reactions were not recorded.

Both the initial velocity and inertial load were varied systematically. For three subjects, velocities of 20, 40, and 60°/s and loads of 0.008 and 0.012 kg · m² were used. In addition, for four subjects, velocities of 30 and 60°/s and three to five different loads ranging between 0.008 and 0.024 kg · m² were used. The data recorded from the second protocol, obtained primarily for another study, showed similar results, although statistical significance was not achieved as consistently (see RESULTS). Twenty trials at each initial velocity and inertia were recorded in sets of five trials. No obvious differences were found between the four sets. To avoid fatigue, trials were performed at a minimum interval of 20 s between trials, with longer rest periods given when necessary.

In three of the subjects, intramuscular electrodes were inserted into the FPL and EPL muscles to verify their role in the reflex responses. For display purposes, EMG records had the mean removed, and the signals were then rectified and low-pass filtered at 50 Hz, and normalized to the values recorded at maximal flexion and extension torques.

Analysis of data

Mechanical responses elicited from human subjects during protocols that use “do not intervene” as an instruction have the potential to be highly variable due to subject intervention (Crago et al. 1976; Gielen et al. 1984). Since the main purpose of this study was to characterize the damping properties of neuromuscular system alone (i.e., muscle and reflexes without voluntary intervention), we needed to develop criteria for distinguishing between trials that have voluntary interventions from those that did not. The data from all 20 trials for each load and initial velocity were judged using two criteria, and those trials passing the criteria were used for subsequent analysis.

The first criterion allowed no more than a shift of 1° in mean joint position during the oscillation, which is the position about which the oscillations were centered. The mean position was estimated by the position at the last local velocity maximum and minimum recorded. The probable cause of a shift in mean position was a change in the baseline activation of the muscle, otherwise intrinsic joint and muscle properties would maintain an equilibrium position (see previous section). Hence, only trials with a small range of mean oscillation baselines were accepted. Applying this criterion eliminated 10–60% of the trials for a given velocity condition, depending on the subject.

The second criterion examined the variability of the data, namely inter-trial differences in recorded torques and positions. The criterion assumed that the variability of the trials with no voluntary interventions (those with only reflex variability) was less than that of trials with voluntary interventions (e.g., Crago et al. 1976). Therefore the majority of trials should be separable from the trials with the larger voluntary intervention variability.
In addition, we assumed either that voluntary reactions were expressed as muscle co-contraction; or that the subject changed the activation of the flexor in response to the extension. We saw no evidence for cocontraction. Specifically, none of the EMG records showed prolonged periods of high agonist-antagonist activity, and the integrated EMGs during the initial isometric period were not statistically significantly different ($P < 0.05$) from those recorded at the end of the trial. For the case of flexor activation, this could either be a prolonged or temporary change (increase or decrease). A prolonged change would result in a shift in final equilibrium position, causing the trial to be (appropriately) excluded by criterion 1. A temporary change in flexor activity followed by a resumption of baseline activity would produce extraneous torques generated by voluntary interventions and result in variations in amplitude and/or time of the peak displacements, especially in the early portion of the trial.

The second criterion was implemented by selecting trials in which the magnitude and time-of-peak displacement amplitude of the second half-cycle lay within 1.3 times standard deviation of the mean of the accepted trials (i.e., those accepted under the 1st criterion). This criterion is equivalent to assuming that most trials are within normal reflex variability, and that only “outliers” reflect voluntary interventions. Moreover, the second half-cycle was used because it was more sensitive than the characteristics of the first half-cycle (i.e., an extraneous voluntary torque may not have enough time to affect the kinematics of the mass until the 2nd half-cycle).

This criterion usually excluded another 20% of trials, leaving about 30–70% of the original 20 trials for a given velocity condition. For the most variable subject, the two criteria excluded about 50% of the trials across all velocity conditions, and about 20–30% of the trials for the other two subjects used in the primary protocol. The factor of 1.3 times the standard deviation was chosen arbitrarily but seemed adequate in separating the no intervention trials in that the trials not accepted were randomly scattered about the accepted trials (see Fig. 3), which would be expected in trials with voluntary intervention. In addition, our reduced animal preparations (Lin and Rymer 2000) had small variability relative to the criterion we used to exclude trials with supposed voluntary interventions, further supporting our contention that our second criterion kept trials with only normal reflex variability.

It is also possible that the “set” of a subject, which is the intention of the subject, can vary within a set of trials and between subjects and affect the mechanical response (Prochazka 1989). We are assuming that the two criteria used to identify the nonintervention trials also discriminated between different sets within an experimental session. We further have to assume that the set between subjects is similar (i.e., that they interpret “do not intervene” the same way).

Analysis of the data from the trials selected paralleled that performed in our earlier decerebrate cat experiments. In the cat study, the logarithmic decrement (LD) in velocity (which is the logarithm of the ratio between velocities at the beginning and end of each cycle of oscillation) was used as a measure of system damping. It is important to note that the analysis assumes that the oscillations take place about an equilibrium position. The LD is related to the total energy in the load, and is valuable as an indicator of changes in the mechanical properties during the entire oscillation period. In addition, the chosen damping measure, LD, is a function of the ratio between energy dissipative and conservative forces, similar to the damping ratio in a linear system (the ratio of viscosity to inertia and elasticity). Last, cycles with the peak velocities <2°/s were not analyzed because the signal was often degraded by noise at those small velocities.

**RESULTS**

**Response of reflexively active muscle to a torque impulse**

The goal of our study was to elicit the mechanical impulse response of the neuromuscular system while in a state resembling posture. The torque impulse created a step in the velocity of the simulated moment of inertia, extending the joint from its initial position and resulting in underdamped oscillations (Fig. 2). The FPL EMG (recorded with intramuscular electrodes) increased as the joint was extended and muscle was stretched, indicating the presence of a stretch reflex response. EMG from the antagonist muscle, the EPL, did not change from passive muscle baseline, indicating that cocontraction was not evoked by the perturbation.

The application of the criteria distinguished trials with voluntary intervention as described in METHODS. As shown in Fig. 3, this process identified the set of most consistent trials. The data from these trials were used in the subsequent analyses.

**Amplitude-dependent damping properties**

Measurements of the LD for joint angular velocity for successive cycles of oscillation showed nonlinear dependence of damping on velocity amplitude, much like the response of the reflexively active cat soleus muscle subjected to similar inertial loading conditions (Fig. 4). The data shown in Fig. 4 were then separated into data obtained from the first cycle of oscillations and data obtained from subsequent cycles (this separation will be justified in the next section). The slope of the LD in velocity plotted against velocity oscillation amplitude was significantly greater than zero ($P < 0.05$) for both first and subsequent cycles, indicating a relationship between the amount of damping and oscillation amplitude. A significant relationship existed between LD and both the displacement and velocity amplitude, which is not surprising since the two quantities covary in our experimental protocol. Thus we could not determine whether damping depended more on displacement or velocity amplitude.

The summary for the three subjects exposed to three initial velocities shows that dependence of damping on oscillation amplitude was significant for all velocity conditions ($P < 0.05$; Fig. 5). Data from experiments using 2 initial velocities and multiple loads protocol (in 4 subjects) also showed positive
slopes, which were statistically significant \((P < 0.05)\) for all but 3 of the 14 loads used on the 4 subjects (Table 1). The statistical significance of the damping dependence on amplitude for these four subjects was not as consistent due to the limited range of initial velocities used. In total, data from five different subjects (2 of the same subjects were used in both protocols) support the conclusions of amplitude-dependent damping.

Differences between first and subsequent cycles

As stated in the introduction, damping has been shown to be time varying in earlier human experiments (Stiles 1983). In our current study, for trials where a large initial velocity was applied, the peak velocity of the second cycle of oscillation was sometimes similar to the initial velocity of another trial where the initial velocity was smaller. For example, the data for a velocity amplitude equal to \(20°/s\) in Fig. 4 reflect this overlap in velocities. These data demonstrate that the amount of damping during the second cycle was greater than that of the first cycle, and that this was not simply an amplitude-dependent phenomenon (because amplitudes of oscillation were not the same for all trials). The error estimates are the 95% confidence interval for the slope. In all subjects, the slopes were significantly greater than zero, and the 1st and subsequent cycle slopes were significantly different.

TABLE 1. Summary data for experiments with two initial velocities

<table>
<thead>
<tr>
<th>Subject</th>
<th>Moment of Inertia, kg (\cdot) m(^2)</th>
<th>Slope for First Cycles, s/deg</th>
<th>Slope for Subsequent Cycles, s/deg</th>
</tr>
</thead>
<tbody>
<tr>
<td>DL</td>
<td>0.008</td>
<td>0.011 ± 0.005</td>
<td>0.032 ± 0.012</td>
</tr>
<tr>
<td></td>
<td>0.012</td>
<td>0.009 ± 0.007</td>
<td>0.024 ± 0.017</td>
</tr>
<tr>
<td></td>
<td>0.016</td>
<td>0.018 ± 0.006</td>
<td>0.032 ± 0.045*</td>
</tr>
<tr>
<td></td>
<td>0.020</td>
<td>0.006 ± 0.0046</td>
<td>0.040 ± 0.051</td>
</tr>
<tr>
<td></td>
<td>0.024</td>
<td>0.017 ± 0.009</td>
<td>0.072 ± 0.118*</td>
</tr>
<tr>
<td></td>
<td>0.010</td>
<td>0.011 ± 0.007</td>
<td>0.027 ± 0.022</td>
</tr>
<tr>
<td></td>
<td>0.015</td>
<td>0.012 ± 0.009</td>
<td>0.065 ± 0.035</td>
</tr>
<tr>
<td></td>
<td>0.02</td>
<td>0.013 ± 0.008</td>
<td>0.025 ± 0.038*</td>
</tr>
<tr>
<td>MC</td>
<td>0.016</td>
<td>0.011 ± 0.007</td>
<td>0.027 ± 0.022</td>
</tr>
<tr>
<td></td>
<td>0.02</td>
<td>0.013 ± 0.008</td>
<td>0.025 ± 0.038*</td>
</tr>
<tr>
<td></td>
<td>0.015</td>
<td>0.007 ± 0.005</td>
<td>0.029 ± 0.021</td>
</tr>
<tr>
<td></td>
<td>0.010</td>
<td>0.009 ± 0.0055</td>
<td>0.023 ± 0.011</td>
</tr>
<tr>
<td>AK</td>
<td>0.010</td>
<td>0.004 ± 0.0029</td>
<td>0.023 ± 0.010</td>
</tr>
<tr>
<td></td>
<td>0.015</td>
<td>0.003 ± 0.0025</td>
<td>0.024 ± 0.006</td>
</tr>
<tr>
<td></td>
<td>0.02</td>
<td>0.002 ± 0.0025</td>
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<tr>
<td></td>
<td>0.02</td>
<td>0.004 ± 0.0033</td>
<td>0.009 ± 0.0321*</td>
</tr>
</tbody>
</table>

The dependence of logarithmic decrement on oscillation amplitude. The slopes were estimated from plots similar to Fig. 5 of data taken from the 2nd experimental protocol, where only 2 different initial velocities were utilized. The error estimates are the 95% confidence interval. * Not significantly different from zero.
subsequent cycles were significantly greater (of Fig. 4) for each set of data (3 subjects). The slopes for the dependence of damping on velocity amplitude (i.e., the slopes and subsequent cycles was further assessed by calculating the SION).

The apparent difference in damping properties for the first and subsequent cycles was further assessed by calculating the dependence of damping on velocity amplitude (i.e., the slopes of Fig. 4) for each set of data (3 subjects). The slopes for the subsequent cycles were significantly greater ($P < 0.05$) than those calculated for the first cycle of oscillation (Fig. 5). The data from the second protocol were not as consistent, but the subsequent cycles slopes were greater than the first cycle slopes for all the mass conditions from all the subjects. These results show that the damping properties provided by the neuromuscular system varied during the oscillations, indicating that prior movement appeared to have a significant effect. In summary, when amplitude-dependent effects were accounted for, system damping increased as the oscillations progressed.

We were also interested in determining whether the reflex response had changed between the first and subsequent movement cycles, because the reflex magnitude influences the mechanical properties (Rack 1981). To evaluate this, similar kinematic states were compared. This was necessary because the reflex response magnitude depends on stretch amplitude and velocity. As previously discussed, Fig. 4 shows data from first cycles of oscillation that have the same velocity at the start of the cycle as data from second cycles of oscillation that had a greater initial velocity. When the EMG responses from these two cases are compared (Fig. 6), the integrated EMG activity from the first cycle of oscillation is significantly greater than that of the second cycle ($P < 0.05$). Data taken from the other two subjects also showed statistically significant differences for the integrated FPL EMG activity for matched velocities.

**DISCUSSION**

Our major finding is that the FPL muscle, which provides flexion of the IP joint of the thumb, displays systematic nonlinear damping properties when it is stretched by a simulated inertial load to which a torque impulse has been imparted. Specifically, the LD in velocity, which is used as a quantitative measure of system damping (and which is related to the ratio of dissipative to conservative forces), increases for the second and later cycles, indicating a change in mechanical behavior of the neuromuscular system. It is important to note that our conclusions are limited to the restricted conditions of our experimental objectives, namely the “no intervention” condition, low levels of muscle activation, and lower frequencies of movement.

We will review the parallels between these findings and those from other preparations and consider the potential sources of these nonlinear behaviors in some detail. Last, we will evaluate the potential importance of the observed nonlinearities for the neural control of posture.

**Comparison to cat experiment results**

The experimental conditions for these human experiments were chosen to closely match those of a parallel series of decerebrate cat experiments. First, the range of moments of inertia was chosen so as to elicit a similar oscillation frequency range to that seen in the cat experiments (1–3 Hz). It should be noted that the inertias utilized were 3–4 orders of magnitude than the inertia of the segment alone, and the damping properties can differ significantly in the higher frequency range associated with the smaller inertial loads (Rack 1981). The range of loads was further constrained by the experimental finding that subjects had trouble not intervening for loads outside the range used (i.e., very large or very small moments of inertia). To fully characterize the velocity dependence of damping, we needed to use a wide velocity range. Thus at the extremes of the range where a subject would feel comfortable, the variability would tend to be higher, contributing to the large number of trials excluded from the analysis (see METHODS).

The results from both cat and human experiments show that the logarithmic decrement in velocity provided by the neuromuscular system increases with displacement and velocity amplitude, a nonlinear property. The proposed physiological mechanism for this nonlinearity is that muscle lengthening decreases neuromuscular stiffness progressively with increasing amplitudes of movement (Lin and Rymer 2000). This reduction in stiffness appears to take place without concurrent changes in viscosity, so that the ratio of spring-like forces to viscous-like forces (which is related to the logarithmic velocity decrement), decreases. Moreover, the finding that a normal human muscle shows similar amplitude-dependent nonlinearities to those recorded in the cat preparation indicates that the damping behavior is not simply attributable to the hyperreflexive decerebrate state.

To reveal any movement history effects, the human data were separated into first and subsequent cycles, and it was shown that there was a statistically significant difference in damping properties for these categories. Unfortunately, the data from the decerebrate cat could not be separated in a similar manner, due to the difficulties in obtaining data for later cycles (cf. Fig. 4 of Lin and Rymer 2000).
Movement-dependent damping

Movement-dependent damping properties could determine how a perturbation is resisted initially and then how subsequent motion is later controlled. To address these potentially different roles, damping in the first and in subsequent cycles was examined by two different means. First, the slope of the damping measure (LD) was plotted against oscillation velocity amplitude and was shown to be larger for later cycles than for the first cycle. Second, the damping measure (LD) was greater in the second cycle than in the first cycle, for comparable velocity amplitudes.

A broadly similar result was described in an earlier study of induced oscillatory motion in the human wrist joint (Stiles 1983). In this study, the relationship between frequency and the damping ratio of the best fitting second-order linear model was shown to change for each progressive cycle of oscillation. The phase relationship of EMG to kinematic variables was also different in the first cycle when compared with later cycles. This phase difference was hypothesized to cause the observed damping ratio variations by changing the lag of the feedback signal. However, since the wrist study did not consider amplitude-dependent effects, it was unclear whether the change in damping ratio could be attributed solely to the preceding movement history.

Mechanism for movement-dependent damping

It has long been recognized that the damping properties of the neuromuscular system vary with the phase and magnitude of the reflex response (reviewed by Rack 1981). Furthermore, the reflex response can counteract the effects of muscle lengthening, by promoting essentially elastic behavior, with minimal velocity dependence (Nichols and Houk 1976). Consequently the magnitude of the reflex determines the ratio of elastic-like to viscous-like forces (Lin and Rymer 1998). Therefore our hypothesis for the mechanism of history-dependent damping is that the reflex response diminishes in later oscillatory cycles as a result of the effects of movement occurring in the first cycle of oscillation. As a consequence, the diminished reflex response does not compensate for muscle lengthening, reducing stiffness, and increasing system damping.

EMG recordings support the first premise of our hypothesis, that the reflex response is diminished with prior movement (Fig. 6). For the second premise, that movement history influences stretch reflex responses, evidence comes from previous experiments in both reduced preparations and man. Houk and colleagues used continuous constant velocity stretches and releases in a reduced muscle preparation and recorded from primary muscle spindle afferents (Houk et al. 1992). In the first stretch following the initial isometric state, the Ia afferent recordings displayed a large initial burst followed by the steady-state dynamic response, but the second stretch (and subsequent stretches), which was initiated without muscle ever returning to a state of zero velocity, had a much smaller burst. In fact, any amplitude of prior stretch reduced the initial afferent burst. One explanation for this result is that intrasural fibers have similar nonlinear properties to extrafusal muscle, i.e., short-range stiffness followed by yielding, and the intrasural fibers can also fall slack during the shortening (Houk et al. 1992; Proske et al. 1992). Stein and Kearney also showed that prior movement at the human ankle reduced the soleus stretch reflex gain, and that the reflex response was modulated by the amplitude of the preceding movement (Stein and Kearney 1995).

The stretch reflex effects could be mediated by short-latency (spinal) or long-latency (cortical) pathways. We were not able to distinguish between the two possibilities with our EMG data. However, this still does not negate our hypothesis that a change in spindle properties due to prior movement is the primary reason for the change in the reflex response, whether it is short or long latency, or both.

Interaction of nonlinearities

The analyses used in this study independently characterized damping dependence on amplitude and movement history. However, the two nonlinearities are simultaneously expressed during the time course of the oscillations of the limb. As the oscillation progressed, the amplitude of movement diminished, causing a decrease in damping. In contrast, there is the competing increase in damping attributable to the prior movement. The combination of the two nonlinearities means that movement-related increases in damping are functionally important because they offset the decreases attributable to amplitude effects. In fact, the data in Fig. 4 suggest that the damping does not change appreciably between the first and second cycles of oscillation. This result corresponds to the reported finding that the estimated damping ratio increases only slightly during the time course of oscillations occurring at the end of a single-joint voluntary movement (Milner and Cloutier 1998). Thus damping properties exhibited during posture may also be expressed during the termination of voluntary movements.

Implications for postural maintenance

We have pointed out in an earlier study that a significant problem the neuromuscular system must resolve is that high stiffness is necessary to maintain positional stability, but this may come at the cost of increased oscillation (Lin and Rymer 1998). Furthermore, a large reflex response preserves stiffness but can cause additional oscillations (Hoffer et al. 1990). A potential solution to the problem is to modulate stiffness (and thus overall system damping) in such a way as to initially prevent a large displacement excursion and then later increase damping to help dissipate energy, possibly by decreasing stiffness.

This strategy is analogous to hybrid control, which can modulate system properties in time according to the change in demand (also known as “gain scheduling”). It has been postulated that hybrid control can be physiologically implemented via descending neural control of the gamma fibers innervating muscle spindles, thus controlling feedback gain and representing a type of feed-forward control (Prochazka 1989).

The aforementioned movement-related modulation in reflex gain acts in a way that is similar to the actions of an hybrid control system. High reflex gain initially (i.e., the 1st cycle) preserves high stiffness, but the movement subsequently reduces the reflex gain by changing spindle properties, thereby allowing the viscous-like properties of muscle to become more prevalent. A solution to the tradeoffs between having high
stiffness and high damping is provided by automatic modulation of reflexes (and in turn mechanical properties) by prior movement, and both positional and velocity aspects of postural maintenance can be satisfied.

In summary, intrinsic peripheral properties present the appropriate variation in mechanical properties during oscillations induced from posture, similar to a hybrid system (or gain scheduling), without the need for additional explicit feed-forward control.

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