Damping Actions of the Neuromuscular System With Inertial Loads: Soleus Muscle of the Decerebrate Cat

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Lin, David C. and W. Zev Rymer. Damping actions of the neuromuscular system with inertial loads: soleus muscle of the decerebrate cat. J. Neurophysiol. 83: 652–658, 2000. A transient perturbation applied to a limb held in a given posture can induce oscillations. To restore the initial posture, the neuromuscular system must provide damping, which is the dissipation of the mechanical energy imparted by such a perturbation. Despite their importance, damping properties of the neuromuscular system have been poorly characterized. Accordingly, this paper describes the damping characteristics of the neuromuscular system interacting with inertial loads. To quantitatively examine damping, we coupled simulated inertial loads to surgically isolated, reflexively active soleus muscles in decerebrate cats. A simulated force impulse was applied to the load, causing a muscle stretch, which elicited a reflex response. The resulting deviation from the initial position gave rise to oscillations, which decayed progressively. Damping provided by the neuromuscular system was then calculated from the load kinetics. To help interpret our experimental results, we compared our kinetic measurements with those of an analogous linear viscoelastic system and found that the experimental damping properties differed in two respects. First, the amount of damping was greater for large oscillation amplitudes than for small (damping is independent of amplitude in a linear system). Second, plots of force against length during the induced movements showed that damping was greater for shortening than lengthening movements, reflecting greater effective viscosity during shortening. This again is different from the behavior of a linear system, in which damping effects would be symmetrical. This asymmetric and nonlinear damping behavior appears to be related to both the intrinsic nonlinear mechanical properties of the soleus muscle and to stretch reflex properties. The muscle nonlinearities include a change in muscle force-generating capacity induced by forced lengthening, akin to muscle yield, and the nonlinear force-velocity property of muscle, which is different for lengthening versus shortening. Stretch reflex responses are also known to be asymmetric and amplitude dependent. The finding that damping is greater for larger amplitude motion represents a form of automatic gain adjustment to a larger perturbation. In contrast, because of reduced damping at small amplitudes, smaller oscillations would tend to persist, perhaps contributing to normal or “physiological” tremor. This lack of damping for small amplitudes may represent an acceptable compromise for postural regulation in that there is substantial damping for larger movements, where energy dissipation is more critical. Finally, the directional asymmetry in energy dissipation provided by muscle and reflex properties must be reflected in the neural mechanisms for a stable posture.

INTRODUCTION

Oscillatory behavior frequently occurs in mechanical systems that have a significant inertial component, including biological systems. During the maintenance of limb posture, for example, the combination of muscle and spinal reflexes (i.e., the neuromuscular system) has to counteract oscillations of limb inertia caused by perturbations arising from interactions with the external environment. The kinematics of a limb after an external perturbation are in part determined by muscle mechanical properties and by the modulation of those properties by reflex action. For this reason, neuromuscular mechanical properties have been widely studied, although their role in reducing oscillations arising from inertial interactions with the environment has not been as well studied (reviewed in Rack 1981).

Earlier studies of active muscle showed that the mechanical properties of muscle are broadly viscoelastic in character and are therefore critically involved in damping. However, the properties of active areflexive muscle differ greatly from those of muscle with intact reflexes (Bennett et al. 1996; Hoffer and Andreassen 1981; Lin and Rymer 1998; Nichols and Houk 1976). In particular, after an appreciable stretch, active areflexive muscle shows predominant viscous-like properties whereas reflexively active muscle shows predominant elastic behavior (Lin and Rymer 1993, 1998). In both cases, the mechanical responses are comparable to those of a linear viscoelastic system (Kirsch et al. 1994; Lin and Rymer 1998). An important idea that has emerged from these studies is that reflexes can potentially modulate the relative magnitudes of the elastic and viscous components of the overall mechanical impedance provided by muscle (Bennett et al. 1996; Lin and Rymer 1998).

Postural maintenance requires, implicitly, that mechanical oscillations be reduced after a perturbation. Damping, defined as the dissipation of mechanical energy, diminishes the amplitude of such oscillations. In mechanical systems, damping is often measured as the ratio of the magnitude of energy-dissipating components to the magnitude of energy-conserving components. For example, in a second-order linear system, the damping ratio is calculated from magnitude of viscosity and the product of mass and elasticity magnitudes. It follows that an examination of how the oscillations diminish after a perturbation will show the relative contributions of the viscosity and elasticity components of the neuromuscular system.

One difficulty in comparing the neuromuscular system with a viscoelastic analogue is that the neuromuscular system is a high-ordered, nonlinear feedback system (Kearney and Hunter 1990). This makes the analysis of mechanical responses difficult and severely limits the application of standard second-order linear system analogues to a small range of conditions. Nevertheless, comparing experimental measures with second-order system behavior is useful in identifying gross nonlinear
properties as well as pointing out possible functional consequences.

It is especially noteworthy that almost all prior studies of neuromuscular contributions to postural maintenance were performed under either length- or force-controlled conditions. In the present study, we chose to apply inertial loads because they are physiologically relevant in two respects. First, inertial loads allow for the physiological interaction of length and force. Second, virtually all normal movements are likely to involve significant inertial elements because limb segments have mass.

Moreover, the application of a transient perturbation, such as a force impulse applied to the load, is representative of many naturally occurring postural disturbances (such as a brief push), as compared with the persistent isovelocity or isotonic protocols.

In light of these deficits, the primary objective of this study was to extend our previous study (Lin and Rymer 1998) by characterizing the damping of oscillations when the neuromuscular system is coupled to inertial loads and when stretch reflexes are intact. When these experimental data were contrasted with the behavior of a linear second-order system, we determined that damping was nonlinear in two respects. First, the amount of energy dissipated from the load by the neuromuscular system increased with oscillation amplitude and second, the damping was asymmetric, displaying predominantly an elastic-like response in lengthening and a viscoelastic-like response in shortening. These nonlinearities are potentially advantageous for the maintenance of posture in the limiting of unwanted excursions. Preliminary results were reported previously (Lin and Rymer 1996).

METHODS

Experimental setup

Our electromechanical actuator and servo were designed to simulate a pure inertial load. To achieve this objective, we combined a linear motor configured as a position servo with an analog circuit for force feedback. The analog circuit implemented the following equation:

\[ x(t) = \frac{1}{m} \int \int F(t) dt + \int V_0 dt \]

where \( x \) is the displacement, \( m \) is the mass, \( F \) is the force, and \( V_0 \) is the initial velocity of the mass. In addition, a phase lead network (Franklin et al. 1991) was necessary to compensate for phase delays in the servo system. Note that force was referenced to the initial force to obtain positive and negative forces such that:

\[ F(t) = F_a(t) - F_o \]

where \( F_a \) is the force measured by the load cell in series with the tendon and \( F_o \) is the force at the start of the perturbation. The subtraction of \( F_o \) simulated the posture of supporting limb inertia against gravity (see DISCUSSION).

It was important to verify the fidelity of the inertial simulations because any added compliance or phase delays in the servo would lead to inaccurate simulations. Moreover, our analysis critically depended on accurate simulation of the inertia (see Analysis of damping behavior).

Two methods were used to test the simulations. The first test was to attach a stiff spring (stiffness = 0.95 N/mm) to the servo. The phase compensation was adjusted so that the oscillations after a velocity step remained constant for a fourfold range of simulated masses (see Fig. 1). The spring load was a very sensitive test that assured that the phase relationship between force (input to servo) and length (output of the servo) remained at 180°, consistent with the behavior of an inertia. It was possible to maintain constant oscillation amplitudes over a range of frequencies (determined by simulated mass) for a single setting of the lead compensation network. Moreover, the change of oscillation amplitude varied proportionally with the square root of mass magnitude, corresponding to a mass-spring system.

The second test was to doubly integrate the force record, scale the result with the magnitude of inertia, and compare this to the experimental record of length. There was no visible difference between the doubly integrated record and recorded length for all the experimental data used in the analysis.

Protocol

Four adult cats were used in the experiments. The preparation of the soleus muscle and supracollicular decerebration followed the protocol of Lin and Rymer (1993).

The primary experimental objective was to obtain the force impulse response of reflexively active muscle coupled to an inertial load. As in an earlier experiment of Lin and Rymer (1998), the crossed-extension reflex was elicited by manipulating the contralateral leg, providing natural activation to the soleus while it was isometrically held 10 mm short of maximum physiological length (the muscle length at full ankle flexion). When a steady force output of 5 N was achieved, the simulated mass was given an initial velocity that always acted to stretch the muscle. Providing the mass with an initial velocity was equivalent to applying a force impulse, i.e., a transient perturbation, to the simulated mass.

To fully characterize the neuromuscular properties, initial velocity and simulated mass were varied. Initial velocities ranged from 10 to 30 mm/s. Mass magnitude ranged from 10 to 80 kg. Two to six trials of each condition were recorded, depending on the state of the preparation.

The ranges of the masses and of velocities were chosen because the frequency and displacements of the induced oscillations corresponded to motions described after postural perturbations during standing. For example, in one study, a transient downward push in the lumbar area of a standing decerebrated cat elicited oscillations with frequencies in the range of 3 to 4 Hz (cf. Fig. 8 in Hoffer et al. 1990). In another study, externally imposed anterior-posterior displacements of a standing cat induced slow oscillations in vertical force in roughly the same frequency range (Rushmer et al. 1983). The muscle velocities im-
posed by a transient perturbation are also significantly less than those seen in locomotion because the inertia of the segments acts as a mechanical filter; 50 mm/s was the approximate upper limit for velocities in Hoffer et al. (1990).

Data analysis

Position and force records were low-pass filtered at 50 Hz using a 40th order finite impulse response filter in MATLAB. To calculate the velocity of the muscle, the position signal was differentiated by taking the difference of successive points and the record was then low-pass filtered at 20 Hz. The mass and initial velocity were determined after the experiment by fitting the best values of mass and initial velocity to the data.

In many trials, muscle length ended with an offset in displacement from the original starting length, mostly caused by the variability in reflex response (see RESULTS). The amount of this offset, which amounts to a steady-state error in position, was estimated by assuming that the mean oscillation length occurred at the local maxima or minima of velocity. The lengths at which the maximum and minimum velocity occurred for the last two recorded half-cycles were averaged and the average was taken to be an estimate of the offset in mean oscillation length. This offset was variable and had large effects on the analysis of data. Hence only trials that had a final mean oscillation length ±0.3 mm of the initial length were analyzed.

Analysis of damping behavior

The fundamental principle used as the basis for our analysis is that damping is an energy dissipating process. Calculating the amount of energy in mechanical systems is a generalized method for examining system dynamics (Arnold 1989). By using this general definition, we avoid restricting the measure of damping to the assumption of a linear viscoelasticity (i.e., a second-order system). Furthermore, it is important that the measure be a ratio of the energy at the beginning of a cycle of oscillation to the energy at the end of the cycle. This is because the absolute amount of energy lost in a mechanical system often depends on the amount of initial energy.

Our chosen measure of damping was the logarithmic decrement (LD) in velocity, calculated for every cycle of oscillation within a trial. Because the simulated load was pure inertia, the maximal velocity squared was proportional to the maximal energy of the load for each cycle of oscillation. This means that LD was also proportional to the ratio of maximum kinetic energy of the load from one cycle to the next. The kinetic energy lost by the load is either dissipated (lost forever) or stored in the neuromuscular system, e.g., in its elasticity. However, because maximal velocity always occurs near the initial position, we assumed that the energy is dissipated. Therefore LD measured the normalized energy dissipated by the muscle from the load for each cycle of oscillation. The LD was calculated by

\[ LD(n) = \ln \left( \frac{V(n)}{V(n+1)} \right) \]  

where \( V(n) \) is the velocity at the beginning of cycle \( n \) \( (n = 1, 2, 3, \ldots) \). Because the trials started with an initial stretch velocity, the velocity at the beginning of the first cycle was the initial velocity imparted to the mass.

In addition, comparing the energy dissipation measure, the LD, with the behavior of a linear system was straightforward because the decline in oscillation amplitude for a second order linear system follows an exponential time course. Thus LD is a constant and equal to:

\[ LD = -\frac{2\pi \xi}{\sqrt{1-\xi^2}} \]  

where \( \xi \) is the damping ratio of the second-order system. Furthermore, the LD is a function of the damping ratio, a measure of the ratio between the energy-dissipating and energy-conserving elements.

It should be noted that LDs were not calculated for velocities <2 mm/s because noise, introduced to the velocity record by taking the derivative of position, corrupted the calculation of LD for these ranges (i.e., the ratio of small numbers with added noise). In addition, at these smaller amplitudes oscillation amplitude actually increased in some cases. This possibly indicates negative damping, which Rack (1981) also demonstrated during small perturbation amplitudes.

RESULTS

Response of reflexively active muscle to a force impulse

Using the crossed-extension reflex, we first established a background force in the soleus muscle. At the point that isometric muscle force reached a constant level, we applied a...
step in the velocity of the simulated mass, which subsequently was allowed to freely oscillate (Fig. 2). The velocity step was akin to applying a force impulse and initially stretched the muscle an appreciable amount. This lengthening also caused muscle force to increase above the background level, and this initial mechanical response of muscle produced an acceleration in the opposite direction of the stretch. The recorded electromyographic activity (EMG) also increased from the baseline level as the muscle was stretched, indicating the onset of a stretch reflex response. Subsequently, EMG was modulated broadly according to the associated change in muscle length, although the extent of this modulation was not analyzed in detail. The force fluctuations around the background force induced underdamped oscillations around a position close to the initial muscle length, which is similar to the behavior of a mechanical system with components of elasticity, viscosity, and inertia.

If we increased the initial velocity for a given mass in the same preparation, the size of the oscillations increased and their frequency changed slightly (Fig. 3). Increasing the magnitude of the mass load for a constant initial velocity produced larger movement amplitudes and greatly altered the frequency of oscillation (Fig. 4). Both of these results were expected because both the impulse magnitude and the natural frequency of the entire system vary with inertia magnitude.

Depending on the preparation, the mean oscillation length in some trials was not centered around the original position, but was sometimes greater than and sometimes less than the initial posi-
tion, reflecting a steady-state positional error. For instance, if the
initial reflex response was reduced (which sometimes occurred as
the preparation deteriorated near the end of the experiment), the
final oscillations were centered around longer lengths. As de-
scribed in METHODS, final mean oscillation lengths differing >0.3
mm from the initial position were not analyzed.

Analysis of damping properties

The LD in velocity was calculated for each cycle of oscil-
lation and across all initial velocity conditions for a constant
load in each preparation. By plotting the LD against the am-
plitude of oscillation, we found that damping increased with
oscillation amplitude (Fig. 5). The amplitude shown in Fig. 5 is
the velocity amplitude, but the relationship between LD and
displacement amplitude was similar to that for velocity ampli-
tude. Compared with second-order linear system behavior
where the LD is always constant, amplitude-dependent damp-
ing is indicative of nonlinear behavior.

Data collected across different masses in all four prepara-
tions are summarized in Fig. 6 by plotting the slopes of LD
versus velocity amplitude (as in Fig. 5) for different mass
loads. The rank ordering of the preparations was chosen so as
to begin with the preparation displaying the most consistent
reflex responses and/or with the largest sample size to the smallest
sample size. The 95% confidence intervals for $r^2$ values are for the best fit lines
(based on least squared error) for the lengthening and shortening directions. Values are shown in
Fig. 7 and are consistent with observed asymmetry. Hence the
lengthening and shortening responses are asymmetric with
regard to the relative contributions of viscous and elastic be-
behavior to the overall mechanical properties.

DISCUSSION

Relevance to the physiological maintenance of posture

The functional significance of this study was to assess the
capacity of the neuromuscular system to maintain its initial
posture when the muscle was subjected to a transient pertur-
bation applied to a simulated in-series inertial load. For our
study, we assumed that for preservation of posture the neu-
romuscular system was required to maintain an initial position
with small amounts of continuing motion (i.e., minimal veloc-
ities). To assess the relevance of our preparation to more
realistic physiological conditions, we next examine the as-
sumptions underlying our experimental protocol.

CHOICE OF LOAD CONDITIONS. The rationale for our choice
of inertial load magnitudes and their physiological relevance
have already been discussed in INTRODUCTION and METHODS.
In our experiments, the force acting on the simulated inertia
was superimposed on a background force such that oscilla-
tions occurred around the initial force and position. Under
physiological postural conditions, a muscle often has to
support a gravitational load, e.g., holding the weight of a
body segment. Our experimental protocol mimics this situ-
ation because movement of a limb segment is determined by
the net force on the limb, which is equal to the muscular
force minus the gravitational force, which we have simply
mimicked by a constant force offset (Eq. 2). In addition,
activation of an antagonist is unnecessary because of the
presence of the simulated gravitational load. Thus our ex-
perimental design corresponds to a simplified single muscle/

APPLICABILITY OF THE DECEREBRATE ANIMAL MODEL. Al-
though the decerebrate cat preparation has been used fre-
cently for postural experiments, differences between the nor-
mal and decerebrate states, especially hyperexcitable stretch
reflexes (Hoffer et al. 1990), could potentially give rise to
misleading results. Specifically, it is conceivable that our two
major findings, amplitude-dependent damping and directional
asymmetry, could be features unique to the preparation or at
least could appear there in exaggerated form. Although we
cannot exclude this possibility entirely, parallel experiments on
the flexor pollicis longus muscle in humans also showed non-linear, amplitude-dependent mechanical properties (Lin and Rymer 1997), indicating that a normal system behaves similarly. In the next section, we will discuss further how the hyperreflexive state could influence each of our findings.

Amplitude-dependent damping

Our measurement of energy dissipation shows that system damping increases with displacement and velocity amplitude, which is behavior distinctly different from that of a linear system. It is predictable that both displacement and velocity are correlated with damping because they are not independent (i.e., both vary with force impulse magnitude). Hence, we cannot ascertain from these studies if damping depends primarily on displacement or velocity, but only that damping is amplitude-dependent.

Dependence of damping behavior on perturbation amplitude can also be seen in several earlier studies in animal and human preparations. Studies of amplitude-dependent mechanical properties in humans (Kearney and Hunter 1982; Milner and Cloutier 1998) and in areflexive cat muscle (Kirsch et al. 1994) show that within the context of a second-order model, values of stiffness decrease and viscosity remains constant as displacement amplitude is increased. Others studies also show that the resonant frequency of a human limb decreases with increasing amplitude during perturbations (Agarwal and Gottlieb 1977; Joyce and Rack 1974). Because our measure of system damping is comparable with more standard measures of the relative contributions of viscosity and stiffness for a given inertia, it seems that increased system damping with increased oscillation amplitude likely originates from a preferential reduction of the stiffness component.

A reduction in stiffness is also consistent with the results of Lin and Rymer (1998). Lengthening in areflexive muscle, forced by a moving inertia, produces a disruption in the force-generating capacity of muscle, sometimes called muscle "yield." The net result is that a muscle loses the ability to restore its initial position and the inertia quickly comes to a rest (i.e., the kinematics are overdamped). Moreover, as the amplitude of the perturbation becomes larger, the resultant disruption in force-generating capacity also becomes larger, thus further reducing a muscle’s ability to restore its initial position. Therefore our hypothesis is that amplitude dependence arises from a greater disruption of a muscle’s ability to generate force as the amplitude is increased, resulting in a more overdamped response.

Although the stretch reflex response becomes larger with increasing stretch amplitude (see also Houk and Rymer 1981), the adverse effects of increasing stretch velocity on muscle mechanical behavior may not totally be offset by the parallel increase in stretch reflex response. Even in reflexively intact muscle, the underlying muscle yield becomes more visible as velocity increases, such that the derivative of the force with respect to time displays increasingly well-defined discontinuities (reflecting incomplete compensation for yield) as the stretch velocity is increased (Boskov 1990).

In addition, it is well known that primary muscle spindle endings are more sensitive at smaller amplitudes of movement (Matthews and Stein 1969) and may enhance system damping via their velocity sensitivity (Wu et al. 1990). However, we believe that the efficacy of the velocity-dependent contribution is counteracted by the nonlinear lengthening effects on muscle intrinsic properties (as described in the previous paragraph). Hence, the net effect of increased spindle output is to enhance elastic stiffness (Nichols and Houk 1976), thereby decreasing system damping.

It is also conceivable that hyperexcitable stretch reflexes of the decerebrate preparation could qualitatively influence damping, as compared with intact preparations. However, amplitude-dependent mechanical properties are seen in both areflexive (zero reflex gain) preparations (Kirsch et al. 1994) and in hyperreflexive (high reflex gain) preparations (this study). Moreover, amplitude-dependent damping was observed in a parallel study in humans in whom reflex action was normal (Lin and Rymer 1997).

Asymmetry in damping properties

The qualitative result, that neuromuscular mechanical properties depend on the direction of motion, is shown in the force-length trajectories (Fig. 7). Asymmetry in the mechanical response can also be anticipated from the asymmetric force-velocity (F-V) relationship of muscle, which has been well documented in many isolated muscle experiments. These data show that during stretch the force evoked by increasing stretch velocities quickly reaches a maximal value, as compared with the shortening direction (Joyce et al. 1969; Krylow and Sandercocck 1997). In other words, the shortening F-V relationship modulates force over a greater range and exhibits a greater viscous-like effect, in agreement with our results.

The stretch reflex contribution to neuromuscular properties is asymmetric as well. The change in spindle afferent discharge has been shown to be much greater in lengthening than in shortening (Houk et al. 1981), and its contribution has even been modeled as a half-wave velocity rectifier (Kearney et al. 1997). The increased spindle discharge in lengthening would act to maintain stiffness by recruiting more motor units (Cordo and Rymer 1982).

Asymmetry in muscle mechanical behavior must also be examined in the context of the other described nonlinearity, namely amplitude-dependent damping. The F-V slope is greater for smaller velocities, both in shortening and lengthening, and accordingly should emulate a larger viscosity when the amplitude is small (Krylow and Sandercocck 1997). However, our experimental results show the opposite, that the damping is larger for larger amplitudes. This discrepancy indicates that the effects of forced lengthening on the mechanical properties of reflexively intact muscle, which may not be reflected in the F-V curve, must be important for amplitude-dependent damping and the dissipation of energy.

Implications of nonlinear amplitude-dependent mechanical properties

In our experimental protocol, larger oscillations were induced either by applying larger masses or by higher initial velocities, which means more mechanical energy was imparted to the system. In both cases, amplitude-dependent damping provided by the neuromuscular system automatically compensated for this increase in energy. Thus the functional significance of amplitude-dependent damping is that larger perturba-
tions are opposed by more damping and the initial posture is better maintained.

For smaller amplitude oscillations, we also observed damping to be smaller. Functionally, less damping means that small motions are more persistent, an observation previously made in humans, especially when they hold a background force (Joyce and Rack 1974; Stiles 1980). Tremor and sway are two additional examples of small-amplitude oscillations that persist under physiological conditions [reviewed in Stein and Lee (1981)]. The possible causes of this persistent motion are asynchronous contractions of motor units, internal disturbances (e.g., fatigue), and reflex loop delays (Stiles 1980).

The contrast between large damping for large amplitudes and small damping for small amplitudes further indicates that the neuromuscular system provides more stability for larger perturbations, which are potentially more troublesome with respect to maintaining posture. Movements of a smaller amplitude may be “allowed” to persist because they pose less severe effects on function.

Implications of nonlinear directional dependent mechanical properties

We have shown that lengthening muscle, even when assisted by stretch reflex activation, does not provide as much damping as in the shortening direction. This asymmetry is important because it is potentially destabilizing, in that damping may be needed in both directions of motion, depending on the perturbation applied. Therefore the nervous system may have to adopt additional strategies to maintain a stable posture during unknown perturbations.

In posture, the use of cocontraction as a control strategy is commonly thought of as a means to increase joint stiffness (Carter et al. 1993). In addition, because antagonistic muscles of a single joint change length in opposite directions, the joint properties are more symmetric than if one muscle were active, providing elastic and damping properties in response to perturbations in both directions of motion. Thus cocontraction is a frequently used strategy when the direction of the perturbation is unknown (Milner and Cloutier 1998), possibly because it not only increases joint stiffness as commonly believed but also makes joint damping properties more symmetric and enhances system stability.

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