Damping in Reflexively Active and Areflexive Lengthening Muscle Evaluated With Inertial Loads

DAVID C. LIN1 AND W. ZEV RYMER1,2
1 Departments of Biomedical Engineering and Physiology, Northwestern University; and 2 Veterans Administration Lakeside Medical Center, Chicago, Illinois 60611

Lin, David C. and W. Zev Rymer. Damping in reflexively active and areflexive lengthening muscle evaluated with inertial loads. J. Neurophysiol. 80: 3369–3372, 1998. Studies of active areflexive muscle have shown that during a constant velocity stretch the increment in force elicited by an incremental length change falls dramatically after a few hundred micrometers of stretch, a finding labeled as “muscle yield.” The mechanical behavior after the yield was like a viscous damper, in that force varied only with velocity. In light of these observations, our aims were to determine whether viscous properties are also evident under more physiological conditions, specifically under inertial loading, and to evaluate the damping action of reflexively intact compared with that of deafferented muscle. The active soleus muscle in a decerebrate cat was forcibly stretched by a simulated inertia with a specified initial velocity. We compared muscle length changes when afferent pathways were intact with those recorded after cutting the dorsal roots. Our findings were that areflexive muscle showed highly damped responses, with large changes in mean muscle length, indicative of high viscosity relative to stiffness. In contrast, reflexively active muscle produced lightly damped oscillations, with minimal changes in mean length, reflecting low viscosity and high stiffness. It appears that the stretch reflects modifies the relative contributions of elastic and viscous-like forces, maintaining elasticity, which in turn sustains oscillations. These differences highlight tradeoffs between positional and velocity regulation, in that elastic properties of reflexively active muscle promote oscillations with modest change in mean muscle length, whereas viscous-like properties of areflexive muscle produce damped responses, with poor positional regulation.

INTRODUCTION

The mechanical properties of muscle are widely studied to understand the roles of intrinsic muscle mechanics and of reflex action in the maintenance of posture. These mechanical properties determine the motion caused by perturbations from the initial posture. By examining oscillatory behavior of muscle under physiologically relevant conditions, the damping behavior and stability of the neuromuscular system can be systematically evaluated.

The classic study of Joyce et al. (1969) demonstrated that the intrinsic mechanical properties of areflexive cat soleus muscle were highly nonlinear. Specifically, during a constant velocity stretch, the change in force caused by a change in length during a stretch decreased sharply after the stretch amplitude exceeded a fraction of a millimeter, a property called “muscle yield.” Lin and Rymer (1993) further showed that, if the deafferented soleus was activated by physiological means (the crossed extensor reflex), postyield behavior was dominated by viscous-like properties. In earlier experiments (Nichols and Houk 1976), the stretch reflex was shown to compensate for muscle yield, preserving an elastic-like response throughout the imposed stretch. Taken together, these findings led us to postulate that the stretch reflex transforms muscle mechanical properties from predominant viscosity to predominant elasticity, the latter comparable with the initial high stiffness of muscle.

One concern with these earlier studies is that the perturbations were position controlled, representing a nonphysiological intervention. To rectify this deficit, we chose to apply inertial loads that approximate physiological loads in two ways. First, the common occurrence of oscillations during limb or whole animal posture suggests a significant inertial component. Second, the inertial load allows the physiological interaction of force and length, in contrast to standard length or force controlled experiments. The hypothesis of Lin and Rymer that viscous-like properties dominate after yielding can also be tested readily with inertial loads. For example, the response of active muscle to a force impulse applied to the inertia should be highly damped, with a large change in position after the yield related to the reduction in stiffness.

Our results show that, when an inertial load is given a force impulse, leading to the stretch of active areflexive muscle, there are minimal oscillations in muscle length, but there is a clear and progressive increase in mean muscle length (i.e., the length at which the oscillations are centered). In contrast, for identical perturbations, reflexively active muscle demonstrates lightly damped oscillatory behavior, and the mean muscle length is much closer to the initial position. These contrasting responses highlight the tradeoff between length regulation (i.e., the maintenance of initial length), which is mediated by high stiffness in conjunction with the stretch reflex, and velocity regulation (the minimization of velocity transients), which is mediated by high viscosity of areflexive muscle. Portions of this work were presented previously (Lin and Rymer 1996).

METHODS

Animal preparation and experimental setup

Two adult cats were principally used in the experiments. Additional data were drawn from four similar experimental preparations. The soleus preparation and supracollicular decerebration followed...
FIG. 1. Comparison between reflexively active (—) and areflexive (---) trials with the same load and initial velocity. The perturbation in the form of a force impulse was applied at time \( t = 300 \text{ ms} \), which initially stretched the muscle from its postural position. The rectified, unfiltered electromyogram displayed was recorded from the reflexively active trial. The arrow indicates the time at which deviation of the 2 trials started to occur. Lin and Rymer (1993). To test areflexive responses, dorsal roots (L2–S2) were sectioned, and the absence of reflex innervation was verified by tendon vibration.

The linear motor was configured as a position controlled feedback system (compliance of \( \sim 0.0015 \text{ mm/N} \)). The shaft position was regulated by a circuit designed to simulate pure inertial loads by the equation

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

where \( x \) was the displacement, \( m \) was the mass, \( F \) was the force, and \( V_0 \) was the initial velocity of the mass. Note that force was referenced to initial force to obtain positive and negative forces, such that

\[
F(t) = F_m(t) - F_0
\]

where \( F_m \) was the force measured by the load cell placed in series with the tendon and \( F_0 \) was the initial force before the perturbation.

The accuracy of the simulations was checked by two methods. First, a stiff spring (\( k = 2.3 \text{ N/mm} \)) was attached to the motor. An analog lead compensator, connected to the output of the inertial simulating circuit and necessary to counteract servo phase lags, was adjusted such that the oscillations remained at a constant amplitude. Second, the recorded force was integrated twice and fitted with mass and initial velocity values to obtain the least squared error with the experimental position record. The difference between the doubly integrated force and recorded position was always minimal.

An electromyogram (EMG) was recorded by 75 \( \mu \text{m} \) intramuscular stainless steel wires placed several millimeters apart in the muscle belly. Length was recorded by a linear variable differential transformer (LVDT) located in parallel with the motor shaft. Length and EMG recordings were low-pass filtered at 400 Hz. Force was low-pass filtered at 1,000 Hz to avoid generating phase lags in the inertial simulation. Signals were sampled at 1,000 Hz with a Macintosh computer and data acquisition card (National Instruments).

Protocol

The crossed-extension reflex was used to activate the soleus while it was held isometrically 10 mm short of maximum physiological length. Once a steady force output of 5 N was achieved, the simulated mass was given an initial velocity to stretch the muscle, equivalent to a force impulse. Both initial velocity and simulated mass were varied in a range from 10 to 20 mm/s and from 20 to 40 kg, respectively. The loads were applied to the muscle with reflexes intact and abolished. Two to six trials of each condition were recorded depending on the state of the animal.

It should be noted that the physiological range of inertial loads imposed on the cat soleus under normal physiological conditions is currently not known. The masses simulated in this study were quite large (20–40 kg) and were associated with oscillation frequencies from 1 to 3 Hz when the reflex was active. This frequency range was less than the 3- to 4-Hz oscillations in the soleus muscle produced by a small downward push on the lumbar position of a cat (cf. Fig. 8 of Hoffer et al. 1990). However, movements of the entire body, such as perturbations in the anterior–posterior direction, are probably associated with even larger inertias and therefore with lower frequencies. Thus the results presented here are primarily relevant to postural perturbations involved with whole body movements and are less relevant to situations where the soleus is interacting primarily with the inertia of the foot.

Results

A comparison between reflexively active and areflexive muscle responses is shown in Fig. 1. In both records, the
DAMPING IN REFLEXIVELY ACTIVE AND AREFLEXIVE MUSCLE

Reflexively active and areflexive muscle reveals that areflexive muscle was much more damped (smaller $X_{\text{max}}$) but did not maintain the initial length (larger $\Delta X_{\text{mean}}$). In contrast, reflexively active trials maintained the initial length but at the cost of a marked increase in oscillations. The other loads showed similar results as Fig. 1, with an obvious separation between the reflexively active and areflexive muscle for the two measures. The second animal displayed similar results. Data obtained from four other reflexively active experimental preparations also showed lightly damped oscillations about the initial length under comparable inertial loading.

DISCUSSION

Modulation of mechanical states by the stretch reflex

We found that the response of areflexive muscle after yield is qualitatively similar to that of a viscous-like element coupled to a moving inertia, in that force does not oscillate and declines slowly back to its steady-state value. Although only two areflexive experimental preparations were used, it is noteworthy that these results concur with our earlier study (Lin and Rymer 1993), in which viscous properties emerged after yield was induced. It is important to note that the magnitudes of the inertia used always caused relatively large amplitude stretches and that perturbations using smaller masses may not produce “yielding” stretches.

A comparison of the two measures, $X_{\text{max}}$ and $\Delta X_{\text{mean}}$, for reflexively active and areflexive muscle reveals that areflexive muscle was much more damped (smaller $X_{\text{max}}$) but did not maintain the initial length (larger $\Delta X_{\text{mean}}$). In contrast, reflexively active trials maintained the initial length but at the cost of a marked increase in oscillations. The other loads showed similar results as Fig. 1, with an obvious separation between the reflexively active and areflexive muscle for the two measures. The second animal displayed similar results. Data obtained from four other reflexively active experimental preparations also showed lightly damped oscillations about the initial length under comparable inertial loading.

FIG. 2. Changes in mean oscillation length ($\Delta X_{\text{mean}}$) and maximum length overshoot ($X_{\text{max}}$) for reflexively active (○) and areflexive (×) muscle. Shown are individual trials with different inertial loads with the same initial velocity. The lines are drawn through the means at each load level. The same 2 measures from the other initial velocities and in the 2nd animal also showed a clear separation for reflexively active and areflexive trials.

Initial response to the force impulse reflected muscle “short-range stiffness,” which is the early high stiffness recorded before the onset of yield. The point of departure between the two records occurred at the time that reflex action became effective. This reflex action evidently compensated for muscle yield because the yield was not discernible in reflexively active muscle. However, in areflexive muscle, force after the yield declined steadily as velocity decreased, although the muscle continued to lengthen, as would be expected for a viscous element. Thus the response of areflexive muscle was highly damped and associated with a large change in final muscle length. Qualitatively, EMG activity from the reflexively intact muscle in Fig. 1 increased during muscle lengthening and decreased during shortening.

Postural maintenance requires that the established postural length be maintained and that oscillations be minimal. To assess these requirements, two empiric measures of the system response were derived; change in mean length about which the oscillations were centered, $\Delta X_{\text{mean}}$, and length overshoot, $X_{\text{max}}$ (Fig. 2). $\Delta X_{\text{mean}}$ was estimated by calculating the difference between the initial muscle length and the length where the velocity was at its local minimum, the end of the first half cycle. $X_{\text{max}}$ was the difference between the peak displacement and the new mean length of oscillation (at the end of 1st half cycle). Shown are measurements made from multiple trials in one animal, for several masses and a constant initial velocity.

A comparison of the two measures, $X_{\text{max}}$ and $\Delta X_{\text{mean}}$, for...
the stiffness of the elastic element after lengthening varies with these additional factors. Similarly, the magnitude of the stretch reflex effects depends on sensitivity of the reflex, on muscle state, and on kinematic conditions (Houk and Rymer 1981).

An important implication of Figs. 1 and 3 is that stretch reflexes degrade system damping, which is a function of the relative amounts of elasticity and viscosity. This contradicts the view that the stretch reflex can promote damping, presumably because of the velocity sensitive feedback from muscle spindles (Wu et al. 1990). In retrospect, the effect on system damping can also be predicted from earlier work by Nichols and Houk (1976) and their idea that the stretch reflex acts to preserve stiffness, which is at the expense of system damping. It may be that higher-oscillation frequencies, associated with smaller inertial loads, benefit more from the phase advance of velocity feedback provided by muscle spindle primary endings, especially if the amplitudes of stretch are small enough to prevent yielding behavior, but this conclusion is beyond the scope of our limited data.

Maintenance of posture

Postural maintenance often requires that a perturbed joint return to its initial position (length regulation) and that velocity transients be quickly damped out (velocity regulation). Areflexive muscle does not satisfy the first of these requirements but is very effective at satisfying the second requirement (Fig. 1). In contrast, reflexively active muscle is more effective at position regulation, allowing minimal change of mean length, but not velocity regulation because of the emergence of high stiffness.

The tradeoff between positional and velocity regulation is also common for analogous mechanical systems, in which a compromise between the stiffness and viscosity components is often made to achieve an “optimal” system response. This study shows two very different responses, varying from predominately elastic to predominately viscous, each of which could be optimal for a particular task. Furthermore, in the neuromuscular system, reflex action can be modulated during natural movement (Stein and Capaday 1988). It is conceivable then that the CNS can vary system properties between these extremes to generate an optimal mechanical impedance to satisfy the postural length and velocity requirements of the chosen task.

We thank K. Paul, J. Miller, and C. J. Heckman for assistance in the experiments.

Support of the work was provided by National Institute of Health Grants T32-HD-07418 and RO1-NS-28076.

Address for reprint requests: D. C. Lin, 1648 Pierce Dr., Emory University, Atlanta, GA 30322.

Received 9 February 1998; accepted in final form 10 August 1998.

REFERENCES


