Reflex Compensation for Variations in the Mechanical Properties of a Muscle

Abstract. *Soleus muscles of anesthetized cats were stretched and released by different amounts while their motor axons were stimulated. Muscle force increased, then gave way in response to large stretch. In the presence of active stretch reflexes in decerebrate cats, the give in force was absent. We demonstrate that autogenetic reflexes can compensate for variations in muscular stiffness revealed when responses to stretch and release are compared.*

The stretch reflex is traditionally presented as a mechanism for regulating the length of a muscle as the load on it varies. An index of this regulation is the stiffness (*1*) of the reflex. If the stiffness is large, the variation in length resulting from a variation in load will be small. Two factors which increase the stiffness of the stretch reflex are length feedback from spindle receptors and the mechanical properties of the muscle (muscular stiffness); force feedback from Golgi tendon organs decreases reflex stiffness (*2, 3*).

The presumption that the stretch reflex serves to regulate muscle length can be challenged both on experimental and on theoretical grounds. For example, it has been observed that the stiffness of the stretch reflex in some situations is no greater than the stiffness of the muscle (*4, 5*). Furthermore, one can deduce that force feedback, by decreasing the stiffness of the stretch reflex, interferes with the regulation of muscle length (*3*). If the main function of autogenetic reflexes is to regulate length, it seems inappropriate to have tendon organ reflexes. Although length and force feedback are antagonistic in regulating against variations in load, they are synergistic in regulating against variations in the mechanical properties of a muscle (*3*). Fatigue and nonlinearity are examples of this type of variation. Perhaps the primary contribution of autogenetic reflexes to muscular control is one of compensating for variations in muscle properties. The experiments described here, and in an earlier abstract (*6*), support this hypothesis by demonstrating that autogenetic reflexes, presumed to originate in spindle receptors and Golgi tendon organs, can compensate rather effectively for the give in muscular force which can occur when a contracting muscle is stretched.

Cats were anesthetized with sodium pentobarbitol. A hind limb was denervated except for the nerve to the soleus muscle, an extensor of the ankle. The soleus was dissected, bathed in mineral oil (37°C), and attached to an electromechanical stretching device having an overall stiffness of 18 kg/mm. After laminectomy the ventral spinal roots L7 and S1 were cut proximally and dissociated into five portions, each of which when stimulated resulted in approximately the same force. Each portion was stimulated eight times per second, but by spacing the stimuli to the different portions by 25-msec intervals, a relatively smooth force was developed (*7*). This method of stimulation approximates the asynchronous activation of motor units during the tonic stretch reflex (*5, 7*). Essentially the same results were obtained from synchronously stimulated muscle, except for the presence of ripple in the force record due to the unfused contraction.

Approximately 5 seconds after initiating stimulation, the force developed by the soleus reached a plateau. The muscle was then either stretched or released; the change in length followed the time course shown in Fig. 1A (lower traces); and the change in force was monitored with a strain gauge myograph (Fig. 1A, upper traces). The responses to small (0.2 mm) changes in length were quite symmetrical about the initial force (traces b and c). Each consisted of a dynamic response during the ramp, followed by a slow approach to the isometric force corresponding to the new length.

In contrast, the responses to large (3.4 mm) changes in length were highly asymmetrical (traces a and d), as we had anticipated from the results of earlier studies (*7, 8*). When muscle length was decreased the force dropped steeply, then more slowly (trace d). At the completion of the ramp the force recovered progressively and reached the isometric value corresponding to the new length after about 10 seconds (not shown). The response to a large increase in length consisted of several distinct phases (trace a). Initially the force rose steeply. After the muscle was stretched approximately 0.4 mm, the force gave way and then began to recover partially, all while the constant velocity phase of the stretch continued. The force dipped again when the ramp was terminated and then slowly approached the isometric value corresponding to the new length. In trace a of Fig. 1A the dip at the termination of the ramp actually brought the force below the isometric value corresponding to the initial muscle length.

The responses of the muscle to large changes in length were markedly altered by autogenetic reflexes. To demonstrate this, cats were decerebrated by midcollicular transection, a hind limb was denervated except for the nerve to the soleus, and the soleus muscle was mounted as described earlier. The muscle was extended to an initial length which yielded a tonic stretch reflex. Ramp stretches or releases, identical to those described earlier, were then applied to elicit the reflex responses shown in Fig. 1B. The responses to small changes in length (traces b and c) were similar to the responses of a muscle deprived of reflexes (compare with Fig. 1A). When the muscle was stretched by larger amounts, however, the give present in muscle responses was absent in the reflex responses. Other differences are apparent from a comparison of the muscle and reflex responses to large increases (traces a) and decreases (traces d) in length.

Conditions which influence these responses include the initial length of the muscle, the initial force, which depends on the initial length and on the number of muscle fibers contracting, the temperature at which the muscle is maintained (37°C in these experiments), and the rate at which individual motor units are activated. Since Grillner and Udo (*5*) have reported that all motor units are activated approximately eight times per second during a tonic stretch reflex, we have used this rate of stimulation in muscle experiments. Our observations with nine cats ranging from 2.5 to 3.5 kg indicated that there was little variation among animals.

Comparisons between individual reflex responses and responses of a stimulated muscle can be made provided the initial conditions are matched. From the results of the nine experiments on muscle and eight reflex experiments, 15 comparisons have been made. Two of these are illustrated in Fig. 2.

The reflex response shown in Fig. 2A began from an initial length 4 mm short of maximal physiologic extension and from an operating force of 700 g.

Chosen for comparison was a muscle response to an identical stretch which began from the same initial length. The initial force was larger, since the entire muscle was stimulated. The muscle response was therefore scaled by the factor 700 g/1670 g so that the initial forces became identical. Since tetanic forces developed by muscle fibers which are functionally in parallel are additive (*3*), this scaling procedure should yield a response of a stimulated muscle which can be compared with the reflex response. The near perfect superposition of the responses just following the initiation of stretch indicates that this portion of the reflex response is accounted for by the mechanical response of the muscle. When the stretch exceeded 0.4 mm, the force developed by the muscle with intact reflexes continued to rise. We see no alternative but to attribute this difference to reflex compensation. The compensation continues to be appreciable for the duration of the record.

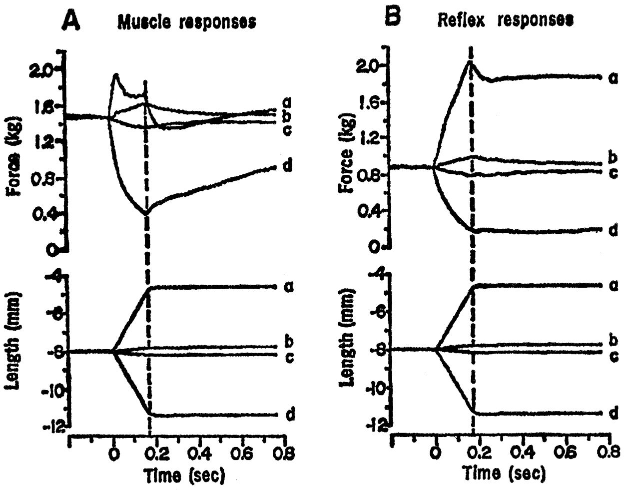
At the end of four reflex experiments the dorsal roots were cut and a crossed-extensor reflex was elicited by stimulating the contralateral peroneal nerve. The responses of a muscle activated in this way were essentially the same as the responses of a stimulated muscle in anesthetized animals. In addition, different initial forces could be produced by varying the strength of the crossed-extensor reflex. With this technique, the procedure for scaling muscle responses was shown to be valid.

The extent of compensation varied among animals and, in the same animal, with initial conditions. A comparison of Fig. 2, A and B, illustrates a variation with initial force. In Fig. 2B the initial force, at the same initial length, was augmented with a crossed-extensor reflex. The contralateral peroneal nerve was stimulated (2 volts; 20 times per second) before and during the application of stretch. In contrast with the other examples, the point at which the muscle gives is not masked completely by autogenetic reflexes. The superimposed muscle response is the same as in Fig. 2A except here the scaling factor is larger, corresponding to the larger initial force. The lesser compensation is to be expected. Most of the motoneurons innervating the muscle must have been recruited prior to stretching, since the initial force was near to the force developed by a stimulated muscle at that length. Hence, the number of motor units which could be recruited to compensate for the give in muscular force was probably small.

The comparison of muscle and reflex responses to a large stretch also demonstrates that reflex stiffness can greatly exceed muscular stiffness. For the 3.4-mm stretch in Fig. 2A, the increment in force measured 0.6 second after initiating the ramp is 1390 g for the reflex and 55 g for the muscle, yielding values of 410 and 16 g/mm, respectively, for reflex stiffness and muscular stiffness. Applying slower stretches, Grillner and Udo (*5*) found lower values for reflex stiffness and higher values for muscular stiffness. Our results were similar to theirs when we used lower velocities of stretch.

Values for stiffness were also calculated from responses to shortening. When these values were compared with the ones derived from stretch responses, we consistently found that muscular stiffness for shortening was much greater than for lengthening, if the amplitude of the length transient was large. The same comparison of reflex responses revealed much smaller differences. More generally, a greater symmetry of the reflex responses, as compared with the muscle responses, is apparent in Fig. 1. This result is interpreted to exemplify an ability of autogenetic reflexes to compensate for variations in muscle properties, in this case a difference in the stiffness of the muscle depending on whether it is stretched or released.

The present results were obtained in decerebrate cats, a preparation in which transmission from tendon organ afferents to motoneurons is thought to be depressed (*9*). The gain of this pathway is higher in spinal cats (*9*), but its value in normal animals is not known. A higher gain of force feed-



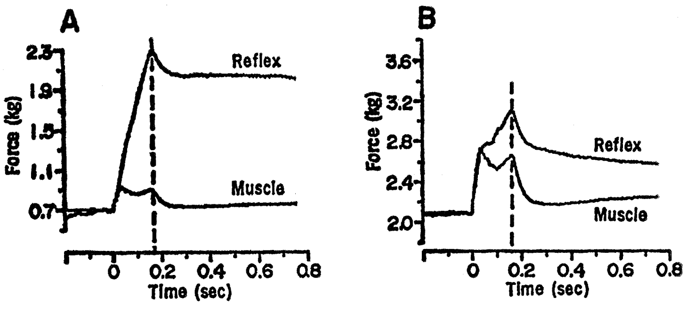


Fig. 1 (left). Comparison of muscle and reflex responses to large and small stretches and releases. Traces a, b, c, and d show the changes in force and length for large stretch, small stretch, small release, and large release, respectively. The family of muscle responses demonstrates that the mechanical properties of the soleus muscle depend on the amplitude and direction of the imposed change in length. The family of reflex responses shows less dependence on these input parameters. The reduction in variation is attributed to feedback via autogenetic reflexes. In (A) the cat was anesthetized and ventral roots were stimulated eight times per second; in (B) the preparation was decerebrate. Length is expressed with reference to maximal physiologic extension. Passive forces accounted for less than 4 percent of the increment in force at the completion of the ramp (vertical dashed lines). Fig. 2 (right). Superimposed comparisons of reflex and muscle responses at two initial forces. For all records the initial length was 4 mm short of maximum and the ramp stretch was 3.4 mm starting at time zero and ending at the vertical dashed line. At a moderate initial force (A), the give in muscle force appears to be entirely masked by the reflex. The larger initial force in (B) was produced by a crossed-extensor reflex. Here reflex compensation for the give in muscle force is less effective. Since the initial length was longer than in Fig. 1, passive forces account for about 15 percent (in the reflex responses) and 45 percent in the muscle responses) of the increment in force at the completion of the ramp (vertical dashed line). In Figs. 1 and 2 reflex responses were from different decerebrate preparations; muscle responses were from the same anesthetized cat.

back is important to consider, since it might account for the apparent absence of stretch reflexes at expected latencies in human subjects reported by several investigators (*10*). The pause between a monosynaptic response to stretch and a later increase in electromyographic activity may be due to a preponderance of inhibition from Golgi organs, as has been suggested for the respiratory system (*11*). Preliminary results with standing human subjects have shown a definite inhibitory period in the electromyogram recorded from ankle extensors when these muscles are stretched by rotating a platform (*12*).

In conclusion, we demonstrate that autogenetic reflexes can compensate for variations in muscular stiffness revealed when responses to large stretches and releases are compared. Our data also show that the stiffness in response to large stretches can be greatly increased by autogenetic reflexes. The former observation supports the hypothesis that these reflexes compensate for variations in the mechanical properties of a muscle, whereas the latter supports the hypothesis that they compensate for variations in load. Our data do not allow us to distinguish which function is more important. The evidence reviewed in the preceding paragraph favors a higher gain of force feedback in normal animals. If this is true, compensation for variations in muscle properties would be greater, whereas compensation for variations in load would be less.

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References and Notes

1. Reflex stiffness is defined as the slope of the relation between reflex force and muscle length, or by the ratio, change in force/change in length, when incremental inputs are used (*2, 3*).
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Perspectives on Linear Heat Transfer

A simple linear equation relating heat flow to a temperature difference is frequently useful in describing heat exchange. Confusion exists because there are basically three different linear equations that pertain to three different situations, and the three equations are used in different ways by biologists and engineers. The origin of the difficulty seems to be a lack of agreement among biologists on a consistent set of conditions under which the particular linear equations should be applied. With a little care and more critical thought much of the confusion could be resolved (*1–3*).

Kleiber (*4*) has not helped to clarify the situation because he dealt with only two of the three linear equations and confused the substance of my earlier analysis (*1*). I think the way to gain a reasonable perspective now is to examine all three equations together, spell out their limitations, and indicate their application. The equations are:

$$dQ/dt = h_c A(T_s - T_a) \qquad (1)$$

$$dQ/dt = kA/d(T - T_a) \qquad (2)$$

$$M = C(T - T_a) \qquad (3)$$

where dQ/dt is the total rate of heat flow; h_c is the convective surface conductance; k is the thermal conductivity; A is the heat transfer area; d is the thickness over which a temperature gradient exists; T_s, T, and T_a are, respectively, surface temperature, "bulk" core or body temperature, and ambient temperature; M is the metabolic heat production rate; and C is a coefficient.

Equation 1 is called, in modern engineering heat transfer, Newton's law of cooling (*5*) and Newtonian cooling (*6*). It is used to describe convective heat flow. In heat convection the boundary layer heat flux (from the surface of an object to the surroundings) is described by a set of partial differential equations. For mathematical simplicity, Eq. 1 is often assumed, instead, to adequately describe this heat flux. It is generally agreed that the equation is not a phenomenological law of heat convection but rather a definition of h_c. Equation 1, as it stands, does not describe cooling of an object but rather the heat transfer from its surface to the environment. To describe cooling, one must equate this to the time rate of change of internal energy of the object, whereupon the solution for T as a function of time yields the cooling equation (*1*, *6*). For Eq. 1 to describe the loss or gain of heat by the entire object, the object must have a very large thermal conductivity so that only very tiny thermal gradients occur within it (the "bulk" temperature of the object and its surface temperature are then virtually equal), and the time-temperature history is controlled by the surface resistance, to which Eq. 1 applies. This is called Newtonian heating or cooling because the object is now similar to the red-hot block that Newton used in his experiments. I suggested (*1*) the following origin for Eq. 1: Use Newton's original proportionality (determined under the simultaneous conditions of conduction, convection, and radiation)

$$d(T_s - T_a)/dt \propto (T_s - T_a) \qquad (4)$$

and the first law of thermodynamics for a closed system

$$dQ = dH - VdP$$

(H, V, and P are, respectively, enthalpy, volume, and pressure). Then, after the time derivative of the first law at constant P is taken,

$$dQ/dt = C_p dT/dt$$

(C_p is the total heat capacity of the system) substitution of Newton's proportionality for dT/dt would, with a few assumptions, lead to Eq. 1, the total heat exchange between the system and the surroundings across the system's surface area A. I called this the contemporary Newtonian law of cooling to distinguish it from Eq. 4 and relate it to modern engineering usage. My choice of semantics may have caused Kleiber (*4*) to think I tried to develop some "new Newtonian cooling law,"