Intrinsic Properties and Reflex Compensation in Reinnervated Triceps Surae Muscles of the Cat: Effect of Movement History

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Huyghues-Despointes, Clotilde M.J.I., Timothy C. Cope, and T. Richard Nichols. Intrinsic properties and reflex compensation in reinnervated triceps surae muscles of the cat: effect of movement history. J Neurophysiol 90: 1547–1555, 2003. First published May 7, 2003; 10.1152/jn.00719.2002. Effects of prior motion on ramp stretch responses of reflexive and areflexive muscles were measured in decerebrate cats. Soleus and gastrocnemius muscles were rendered areflexive by reinnervation a minimum of 9 mo before the terminal experiments. The introduction of a shortening phase prior to the ramp stretch increased the normalized initial stiffness of muscles and decreased the tendency to yield of the reinnervated muscles as compared with the case in which muscles contracted isometrically prior to stretch. Yielding was compensated by reflex action for all amplitudes of prior shortening in soleus and gastrocnemius muscles. The comparison of responses of untreated and reinnervated muscles indicated that the contribution of reflex action progressively declined with the amplitude of prior shortening as the extent of yielding diminished. In soleus muscle, during a variable delay period of isometric contraction interposed between shortening and lengthening force generation, initial stiffness and yielding returned to levels seen with isometric contractile history. However, these attributes recovered at different rates, suggesting that distinct processes are responsible for initial stiffness and yielding. Yielding was compensated for by reflex action regardless of the length of the interposed delay or of the amplitude of the prior shortening. These and previous findings indicate that the stretch reflex regulates muscular stiffness for a wide range of conditions. This regulation apparently arises from complementary mechanical properties of intrafusal and extrafusal muscle.

INTRODUCTION

The regulation of muscular stiffness by the stretch reflex, which comprises compensation for yielding and a reduction in the dependence of stiffness on background force (Nichols 1974; Nichols and Houk 1976; Nichols and Steeves 1986), was shown to apply to heterogeneous as well as homogeneous muscles (Huyghues-Despointes et al. 2003). This compensation can be attributed mainly to the robust dynamic response of the primary receptors of the muscle spindle (Houk et al. 1981).

In the studies referred to in the preceding text, stiffness and the responses of muscle receptors were measured by stretching muscles after a period of isometric contraction. Measurement of the responses of primary receptors to stretch after prior motion showed a reduction in the dynamic response (Gregory et al. 1987; Houk et al. 1992). These effects of prior motion as well as other conditioning stimuli have been attributed to the effects of the conditioning on the contractile mechanisms of intrafusal fibers (Proske et al. 1993). Prior motion is also known to alter (Campbell and Moss 2000, 2002; Herzog and Leonard 2000) and, in some cases, linearize the mechanical properties of electrically stimulated muscle (Kirsch et al. 1994; Lin and Rymer 1993) and chemically skinned muscle fibers (Huyghues-Despointes et al. 1998). This linearization has the effect of reducing the tendency of the muscle to yield although not causing a reduction in the dependence of muscular stiffness on background force (because stiffness depends on the number of contracting muscle units). Taken together, these studies suggest that prior movement can lead to a parallel reduction in yielding of the muscle and in reflex action. We investigated the influence of these parallel changes in muscles and spindle receptors on the regulation of the mechanical properties of muscle.

We employed the method of reinnervation (Cope and Clark 1993; Cope et al. 1994) to evaluate the effects of prior movement on the mechanical properties of areflexive muscles. This method was employed because it is usually not possible to recruit substantial contractile force from muscles other than soleus following an acute dorsal rhizotomy. The measurements on reinnervated muscles provided estimates of the effects of movement history on the intrinsic mechanical properties of areflexive muscles in which motor units were physiologically recruited. The comparison of mechanical responses between reinnervated and intact muscles allowed us to infer how movement history influenced reflex action. We chose shortening as prior motion because of its physiological relevance. Antigravity muscles of the feline ankle undergo shortening prior to the stretch associated with the E2 phase of locomotion (Goslow et al. 1973). Our study was motivated further by kinematic observations of the animals with reinnervated triceps surae muscles (Abelew et al. 2000; Nichols et al. 1999). During downhill walking, these animals showed a larger than normal dorsiflexion of the ankle of the treated limb during E2 even though the reinnervated muscles were capable of generating normal force levels (Cope and Clark 1993). Although ongoing motion might reduce the responsiveness of spindle receptors and linearize the properties of extrafusal muscle, reflex action is still apparently required for mechanical regulation during locomotion (Pearson et al. 1999). The investigation of the contributions of sensory feedback to stiffness regulation and coordination requires the use of realistic mechanical conditions.

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The goals of this paper were to first verify that the effects of contractile history observed in the single muscle fibers (Huyghues-Despointes 1998) were apparent in intrinsic properties of whole muscles and to extend these observations to heterogeneous muscles. The second goal was to compare the mechanical properties of reinnervated, and therefore areflexive muscles (Huyghues-Despointes et al. 2003) to those of intact muscles to estimate the effects of prior motion on the stretch reflex. We found that prior shortening extended the linear range of the muscle progressively with increased amplitudes of shortening. As the linear range of the muscle was extended, the additional force due to reflex action became more delayed and reduced, resulting in stiffness regulation of the intact muscle for all amplitudes of release. These findings have been briefly reported in abstract form (Huyghues-Despointes et al. 1997) and in a dissertation (Huyghues-Despointes 1998).

METHODS

Eight neutered adult male cats were selected according to weight (4–7.25 kg, average: 5.5 kg) and normal motor coordination. Three of these animals did not undergo muscle reinnervation. The animals were housed in a large colony with other cats. After surgical intervention (see following text), the animals were first isolated for a recovery period that varied (1–3 mo) with individual cats prior to being reintroduced to the colony. Animals were monitored daily for general health. No stress was noted as a result of the surgery.

The reinnervation was performed on 5 of 8 cats as described in a previous paper (Huyghues-Despointes et al. 2003). With the animal deeply anesthetized, the nerve to medial gastrocnemius (MG) and the nerve that supplies soleus and the lateral gastrocnemius (LG-S) were sectioned one at a time and immediately resutured with 10-0 suture. Each animal was allowed to recover under the supervision of the veterinary staff and was reintroduced to the colony. Within 3–4 mo, the cats could climb the fences and jump. All experimental animals remained in the colony for >10 mo, during which their locomotion patterns on level and inclined surfaces were studied (Abelew et al. 2000).

In the terminal experiments, the animals were decerebrated while deeply anesthetized with isoflurane gas. After muscle dissection and intercollicular decerebration (all brain matter rostral to the transection was removed), gas anesthesia was terminated. Core temperature was maintained ~37°C and lactated Ringer solution was administered as needed. Steel rods were inserted from the knee into the shaft of the femur and tibia bilaterally, then rigidly clamped, fixing each knee at an approximate angle of 110°. In the stereotaxic frame, hip pins stabilized the pelvis. Dissection of the soleus (SOL) and gastrocnemius (G) muscle tendons followed. A suture was inserted through the intersosseous membrane around the fibula and secured as a reference marker for muscle lengths. At an approximate ankle angle of 90°, a suture was inserted through the desired muscle tendons and this length marked the L90 position. The posterior tibial nerve was dissected free for stimulation (twice threshold) during the experiment to generate crossed extension reflexes. Muscle temperature was maintained at 30–34°C either with streams of warm mineral oil or a heat lamp. Each muscle was linked to a myograph in series with a linear DC motor. Force was measured using myographs mounted on the linear slides through a universal joint to maintain alignment with the muscle. The set up was rigidly clamped to mechanical ground. Mechanical artifacts were carefully avoided, and they were always checked for during the data analysis phase. At the end of the experiment, the animal was killed by an overdose of pentobarbital sodium (Nembutal) injected intravenously or directly in the heart. A pneumothorax was also performed. Experimental protocols were approved by Emory University’s Institutional Animal Care and Use Committee.

A dorsal rhizotomy was performed on three untreated animals during the terminal experiment. These preparations served as controls for the reinnervated soleus muscles to verify that the reinnervated muscles behaved in a manner similar to those acutely deafferented. The L9, L7, and S1 dorsal roots were transected after a lumbar laminectomy.

Data were sampled using a 486-based PC, at a rate ranging from 250 to 2,000 Hz, and saved to the hard disc. This wide range of sampling rates was dictated by limitations of the data acquisition system. However, even at the lower 250-Hz sampling rates, these rates more than doubled the expected frequency response of skeletal muscle for the moderate rates of stretch used here, thereby making aliasing unlikely. Muscle lengths were controlled with printed servo-motors. Force was measured using myographs mounted on the linear slides through a universal joint to maintain alignment with the muscle. The amplitude and velocities of stretch and release were chosen to reflect physiologically relevant length changes in the locomoting cat and were of sufficient magnitude to allow for the distinction of the short range effects described in the existing muscle literature.

With the muscles secured to the myographs, the tibial or sural nerve was stimulated at twice the reflex threshold at the rate of 40 Hz to activate the spinal circuitry that in turn activated the muscles in a physiological pattern of recruitment. The resultant contraction was monitored on the chart recorder, and stretches were manually triggered once the level of force had peaked. Whenever possible, the two hindlimbs underwent the same protocol in succession to compare responses obtained at the same initial force, while the reflex excitability of the animal was similar. A minimum of 4 min of rest was imposed between consecutive reflex activations to avoid muscle fatigue. In three animals, we directly stimulated SOL through its motor nerve at 20 Hz for a period of 4–6 s.

The force and length data collected were edited off-line with customized software to remove unstable or erroneous data. Less than 5–10% of the data was discarded during editing sessions. The data were not filtered. Analysis was accomplished using routines written in Matlab.

Assessment of whole muscle properties

Initial stiffness ($K_i$) was the magnitude of the stiffness generated by the muscle over the initial 10% of the stretch (see Fig. 1 in Huyghues-Despointes et al. 2003). The units of $K_i$ were expressed in N/mm. The data were analyzed as follows.

Initial force ($F_i$) is always defined as the force immediately prior to the start of the stretch, regardless of the contractile history. Therefore under certain circumstances, $F_i$ reflects force output but not necessarily activation level, as in the case of prior shortening preceding the stretch.

$K_i$ (incremental stiffness) was the measure of the force response obtained at the termination of the ramp stretch divided by the amplitude of stretch.

The quantity $K_i/K_o$ was a measure of the extent to which total muscular stiffness fell below $K_i$ at the termination of the ramp stretch (yield). If the neural pathways were intact, the force at the end of the stretch ($K_o$) was dependent on autogenic reflexes. However, the types
of active motor units also influenced the quantity $K_e$, making $K_e/K_i$ dependent on neural feedback as well as fiber type. A value of 1 for $K_e/K_i$ meant no change in the slope from the beginning of the stretch to the end of the stretch, and this was considered a linear response with no yielding. Smaller values of $K_e/K_i$ indicated larger extents of yielding.

RESULTS

When a muscle without sensory feedback is stretched after a period of isometric contraction, the force response consists of an initially elastic reaction, known as the short-range or initial yielding. If the reduction in stiffness is large enough, force will also decline with further stretch (Fig. 1A).

The data representing the effects of the delay interposed between the release and the subsequent stretch were collected in three reinnervated preparations and one dorsal rhizotomy preparation. The data representing the effects of amplitude were collected in seven reinnervated cat preparations and one dorsal rhizotomy preparation. The results from the reinnervated animals were identical to those from the dorsal rhizotomy preparation.

In the present experiments, the introduction of an episode of shortening prior to the 2-mm stretch reduced the yield and therefore tended to linearize the intrinsic responses of both G and SOL muscles. The reflex compensated for any remaining tendency to yield and thereby preserved nearly linear behavior of the muscle (Fig. 1, A and B, top left). The following patterns of responses were consistently observed for G in three reinnervated animals and for SOL in two reinnervated animals and one subjected to acute dorsal rhizotomy. As the amplitude of prior shortening was increased from 0.5 to 2 mm, the yield occurred later and to a smaller extent with a consequent increase in the linearity of the intrinsic responses. In both G and SOL, the contribution from autogenic reflexes, denoted in Fig. 1 (the difference between — and · · · within $\Theta$), was the greatest after a period of isometric contraction. As prior shortening increased, and the intrinsic response became more linear, the contribution from the stretch reflex diminished, becoming minimal with a 2-mm prior shortening history. For SOL, the intrinsic and total reflexive responses were indistinguishable for the 2-mm release (Fig. 1A). For G, the force fell below the intrinsic values during the release, and the stiffness during the subsequent stretch was greater for the reflexive response even for the largest releases (Fig. 1B). However, as shown previously (Fig. 4 in Huylghues-Despointes et al. 2003), the initial stiffness was in some cases greater for the untreated muscle. For both SOL and G, force declined during the isometric plateau after the stretch to a greater extent in the absence of the stretch reflex (Fig. 1, A and B, bottom right).

Both intrinsic and reflexive responses were quantified by measuring $K_e$ (initial stiffness), $K_i$, and $K_e/K_i$, our index of yielding. $K_e$ increased with initial force ($F_i$) in all cases, where $F_i$ is the force immediately prior to stretch, but the increase became less rapid at high $F_i$ (Fig. 2). We attributed this lack of proportionality of initial stiffness and force to the effects of in-series elastic structures. This series compliance becomes limiting at higher forces where internal muscular stiffness becomes large (Houk et al. 1970; Sandercoc and Heckman 1997). For SOL at matched initial forces immediately preceding the stretch, prior shortening resulted in an increase in $K_i$ for both reflexive and intrinsic responses (Fig. 2B). This difference was more pronounced at higher initial forces. In the case of G (Fig. 2A), the values of $K_i$ for the reflexive muscles were not significantly influenced by prior release.

The $K_e$ measured at the termination of the ramp included both intrinsic and reflex components in the intact muscles. For ramp responses after isometric contractions, the dependence of $K_e$ on force is markedly reduced in the presence of the stretch reflex, as shown previously (Huylghues-Despointes et al. 2003) and in Fig. 3. The data shown in Fig. 3 were drawn from an experiment using a dorsal rhizotomy to achieve deafferentation. These data indicate that the $K_e$ of areflexive muscles after isometric contraction were nearly proportional to initial force, while the $K_e$ of intact muscles were larger and less dependent on force. In this example, the responses of reflexive muscles
reflexive muscles tended to reduce the values of $K_f/K_i$, but not below the values obtained for reinnervated muscles (○, ■, ◊, ▲ lie above ○, □, ◊, △). At low to moderate forces in SOL and G, reflex action increased the values of $K_f/K_i$ beyond the magnitudes provoked by prior shortening. At higher forces, values of $K_f/K_i$ converged as the total response became dominated by the intrinsic properties of muscle, particularly for large amplitudes of prior shortening (○, ■, ◊, ▲ vs. ○, □, ◊, △ in Fig. 4). These data indicate that both reflex action and prior shortening can increase the value of $K_f/K_i$, but the closest approximation to a value of 1 (ideal linearity) was achieved in the presence of reflex action with prior shortening. The results also show that the reduction in apparent contribution of reflex action for the larger amplitudes of prior shortening (Fig. 1) could not be explained by any dependence of reflex gain on activation level because reflex action for the isometric condition was effective in influencing the value of $K_f/K_i$ at low activation levels. We therefore attributed the influence of prior shortening on both intrinsic responses and reflex action to the movement itself and not to the change in activation level per se.

The introduction of a delay between the end of shortening and the initiation of stretch promoted the return to the nonlinear behavior of the reinnervated SOL as had been shown for slow twitch single muscle fibers (Huyghues-Despointes 1998). The results shown in Fig. 5 are from experiments performed in a decerebrate preparation with an acute dorsal rhizotomy (Huyghues-Despointes 1998). Eight to 12 trials were obtained from one animal for each delay over a range of initial forces. Similar results were obtained from reinnervated SOL muscles. During the isometric interval between shortening and subsequent stretch, the force in the deafferented muscle showed a rapid but short-lived initial regeneration followed by a much slower rate of force redevelopment (Fig. 5, delay 2000). In the presence of the stretch reflex, the force followed an initially rapid but small recovery and achieved a plateau at a level substantially below that attained by the areflexive muscle. The tendency to yield of the areflexive muscle recovered after several hundred milliseconds of delay were allowed. The stretch reflex compensated for the yield for all delay times. Because the yield was effectively compensated by reflex action and because the force did not increase substantially following the release, the force response of the reflexive muscle closely approximated the trajectory of the imposed length change. In other words, the response of the muscle was more spring-like in the presence of the stretch reflex.

The rates of recovery of initial stiffness ($K_f$) and yielding ($K_f/K_i$) after release were different (Figs. 6 and 7). Prior shortening caused an elevation of initial stiffness at matched forces in SOL (Fig. 6; see also Fig. 2B) for both areflexive muscle (○, △, □, ◊, and △) and reflexive muscles (○, ▲, ■, ◊, and △). Within ~100 ms, the effect of the prior release resulting in an elevation of initial stiffness disappeared. This occurred within a similar time course as the initial force recovery (Fig. 5). There was no significant difference between the deafferented and the intact responses because these measures were taken prior to the time when the stretch reflex begins to affect the force output. In the case of yielding (Fig. 7), the ratio $K_f/K_i$ was highest across the force range for the responses of reflexive muscle. Except at low forces, the ratio was also high (the muscle did not yield much) in areflexive

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**Fig. 2.** Relationship between initial stiffness ($K_i$) and initial force ($F_i$) for intrinsic and reflex responses. + (intrinsic responses) and * (reflexive responses), measurements made after isometric conditions. A: G. B: SOL. Data obtained from a reinnervated preparation. Prior shortening amplitudes displayed: 2.0, 1.5, 1.0, and 0.5 mm. ○, □, ◊, △, and ◊, intrinsic responses. ■, ▲, and ●, reflex responses. SOL data were from an acute unilateral dorsal rhizotomy preparation. In both muscles, while the points from the isometric contractile history tend to lie lower than after a prior shortening, the differences in $K_i$ are small.

were obtained only for initial forces above ~8 N due to the presence of a tonic stretch reflex. In other cases, the magnitudes of the $K_i$ obtained at the termination of the ramp remained approximately constant down to low initial forces (see Fig. 3 dynamic responses in Huyghues-Despointes et al. 2003). After a 2-mm release, the $K_i$ of both intact and reinnervated muscles were similar and increased steeply with initial force to achieve a constant value at higher initial forces. These results and those shown in Fig. 1 indicate that the responses of the intact muscles become dominated by intrinsic properties with sufficient prior shortening.

Our measure of yielding was the ratio $K_f/K_i$. Values of $K_f/K_i$ for treated muscles were not strongly dependent on $F_i$ and converged toward the value of 1 with greater amplitudes of prior shortening (Fig. 4). For reflexive muscles stretched after isometric contraction, values of $K_f/K_i$ were > 1 at lower forces and declined as initial force increased. Prior shortening of reflexive muscles tended to reduce the values of $K_f/K_i$, but not below the values obtained for reinnervated muscles (○, ■, ◊, ▲ lie above ○, □, ◊, △). At low to moderate forces in SOL and G, reflex action increased the values of $K_f/K_i$ beyond the magnitudes provoked by prior shortening. At higher forces, values of $K_f/K_i$ converged as the total response became dominated by the intrinsic properties of muscle, particularly for large amplitudes of prior shortening (○, ■, ◊, ▲ vs. ○, □, ◊, △ in Fig. 4). These data indicate that both reflex action and prior shortening can increase the value of $K_f/K_i$, but the closest approximation to a value of 1 (ideal linearity) was achieved in the presence of reflex action with prior shortening. The results also show that the reduction in apparent contribution of reflex action for the larger amplitudes of prior shortening (Fig. 1) could not be explained by any dependence of reflex gain on activation level because reflex action for the isometric condition was effective in influencing the value of $K_f/K_i$ at low activation levels. We therefore attributed the influence of prior shortening on both intrinsic responses and reflex action to the movement itself and not to the change in activation level per se.

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SOL with the prior shortening (see also Fig. 4B). As the delay between the release and the stretch increased, the ratio progressively declined (muscles yielded more) over several hundred milliseconds for areflexive muscle. The longer time course of recovery of the ratio $K_f/K_i$ than initial stiffness was also observed for chemically skinned muscle fibers from SOL (Huyghues-Despointes 1998; Huyghues-Despointes et al. 1997). We computed the $t_{1/2}$ for six values of initial force. The $t_{1/2}$ values were computed as the time taken for $K_f/K_i$ to decay to one half the difference between the maximum and minimum values. The values for different initial forces were similar and averaged to 477 ms. Although the stretch reflex and prior shortening both reduced the tendency to yield, the stretch reflex compensated for yielding over a wider range of forces and over all delay periods.

**DISCUSSION**

We have documented the complementary effects of movement history on the mechanical responses of reflexive and areflexive (reinnervated or deafferented) muscles in decerebrate cats. By comparing the responses of the two preparations, we have inferred the effects of prior movement on the contribution of the stretch reflex to the mechanical properties of the muscles. The responses of reflexive muscles showed an absence of yielding over a wide range of initial forces and extents of prior shortening and an approximately constant magnitude of $K_e$ over a wide range of initial forces as predicted by the hypothesis of stiffness regulation. The contributions of intrinsic properties varied considerably over these conditions so that the contributions of the stretch reflex must have varied in a complementary fashion to regulate $K_e$. Prior movement tended to increase the linearity of intrinsic properties but not at low forces or for long delays before the test stretch. These results suggest that reflex action provides mechanical regulation over a wide range of motor behaviors.

The reduction in reflex action with prior shortening was unlikely to have been due to an effect of lowered background force on reflex gain because the reflex was substantial at lower forces when stretch was preceded by an isometric contraction. We therefore attribute the reduction in the reflex component to the effects of movement history. Prior shortening also had the effect of slightly increasing initial stiffness ($K_i$), the stiffness of the muscle measured over the first 10% of stretch when normalized to $F_i$. That is, a prior shortening caused a larger decrease in force than in stiffness, thereby dissociating $K_i$ from $F_i$. By interposing a 100-ms delay between the end of the prior shortening and the subsequent stretch, we observed that the values of initial stiffness were undistinguishable from those obtained when the prestretch conditions were isometric. On the other hand, the extent of yielding was slower to return and did so only after 600–700 ms of delay were introduced between the shortening and stretching phases. Therefore initial stiffness and yielding recovered with distinct time constants.

**Intrinsic properties**

We observed two distinct effects of a prior release on the responses to stretch of the reinnervated muscles, namely, a small disproportionate decrease in initial stiffness and force, as well as a reduction in the extent of yield. Similar results were obtained using chemically skinned muscle fibers from SOL, indicating that these dynamic properties result from the contractile apparatus itself (Huyghues-Despointes 1998; Huyghues-Despointes et al. 1997). These effects were also predicted by Kirsch et al. (1994) and Lin and Rymer (1993). We termed the stiffness measured during the initial 10% of muscle stretch “initial stiffness” rather than short-range stiffness because the latter term has been used mainly to refer to initial stiffness for the isometric prestretch condition (Hill 1968; Proske et al. 1993).

Short-range stiffness is thought to arise from slowly cycling
produce a disproportionate decrease in stiffness. However, the stretches were delivered over a substantial time interval, so the force recovery would have contributed to the measurement of apparent stiffness as well, leading to a greater than expected stiffness for matched initial force. The rapid dissociation may have recovered quickly (within 100 ms) as well, leading to a rapid return to the control stiffness-force relationship (Fig. 6). An increase in the ratio of stiffness to force could also result from a change in the ratio of strongly-bound, nonforce producing cross-bridges to force-producing cross-bridges (Martyn and Gordon 1992). However, the conditions of rapid dissociation for shortening muscle (Huxley 1957) favor the former hypothesis.

The more gradual recovery of yielding than initial stiffness suggests that reattachment rate remains elevated for a considerable time after shortening. This interpretation is supported by the continued force recovery observed during longer delays (Fig. 5). As reattachment rate slows, mechanically disrupted cross-bridges take longer to reattach and yielding increases.

**Autogenic reflex properties**

In both G and SOL, the reflex linearized the force response to stretch. The main difference between these muscles was that, in G, the reflex seemed to have a noticeable effect throughout the release as well as the stretch phase, whereas for the SOL, the reflex action became apparent only at the point at which a yield would occur in the absence of autogenic feedback. Primary receptors respond more vigorously to stretch than release (Houk et al. 1981), so we did not expect to find substantial contributions of the stretch reflex during release. The differences in responses between the two muscles likely resulted from differences in passive connective tissue elements. The force measurements included both active and passive components. Every attempt was made to dissect the intact and reinnervated muscles similarly and to perform measurements at similar initial lengths, but some differences were unavoidable. A greater passive stiffness, presumably parallel, of the intact muscle may also have contributed to the greater than expected stiffness in response to stretch.

![Gastrocnemius (G) Cross-bridges in extrafusal fibers that can be disrupted by prior movement (Proske et al. 1993). The determinants of initial stiffness after release are probably quite complex because the muscle is not in a steady state. The property of muscular stiffness reflects the number of attached cross-bridges, the time course of attachment, and the rate of cross-bridge detachment (see Huyghues-Despointes 1998; Huyghues-Despointes et al. 1997). This hypothesis is supported by the observation of a higher short-range stiffness in type I (slow twitch) than in type II (fast twitch) muscle fibers for a given background force (Malamud et al. 1996) due to the lower rate of detachment in type I fibers. Shortening prior to stretch is likely to lead to a transient increase in the rate of turnover of cross-bridges through increased detachment (Campbell and Moss 2000; Huxley 1957). The latter effect would cause a reduction in both force and stiffness, but the increase in detachment rate would produce a disproportionate decrease in stiffness. However, the stretches were delivered over a substantial time interval, so the force recovery would have contributed to the measurement of apparent stiffness as well, leading to a greater than expected stiffness for matched initial force. The rapid dissociation may have recovered quickly (within 100 ms) as well, leading to a rapid return to the control stiffness-force relationship (Fig. 6). An increase in the ratio of stiffness to force could also result from a change in the ratio of strongly-bound, nonforce producing cross-bridges to force-producing cross-bridges (Martyn and Gordon 1992). However, the conditions of rapid dissociation for shortening muscle (Huxley 1957) favor the former hypothesis.

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muscle would have resulted in a greater decrease in force during both shortening and lengthening. Because passive stiffness is greater for G than for SOL, differences between muscles in the two legs would be accentuated in the former. Another factor was that the fiber lengths are shorter in G than in SOL. Because both muscles were stretched by the same amount, the stretch per fiber length was greater in G. The stiffness and magnitude of the stretch reflex might therefore be greater in G than in SOL and consequently both intrinsic and reflex responses would be greater for a given length input. Evidence supporting a contribution from this factor is the substantially larger reflex responses in G compared with SOL (Fig. 1). An additional factor contributing to the greater reflex in G is the combined homonymous feedback, as well as the effects of heteronymous Ia feedback that exists between the lateral and medial portions of this muscle group (Eccles et al. 1957; Scott and Mendell 1976).

It is likely that the effect of prior movement on the contributions of the stretch reflex was due at least in part to a reduction in the initial burst of the primary receptors of the muscles spindles. Prochazka et al. (1989) reported firing rates of Ia afferents in the cat G during locomotion. Their results showed that the firing rate gradually increased from the time of paw contact, throughout the lengthening of the muscle, with little sign of an initial (dynamic) burst. Later it was shown that the response of a primary afferent was dependent on the prior movement history (Houk et al. 1992). After an isometric contraction the initial burst was present, but after a period of shortening, the initial burst was diminished or no longer expressed. The postburst dynamic responses of the receptors were little altered, however, suggesting that changes in the magnitude of the initial burst may have played a major role in the history dependence of the reflex. A reduction in initial burst of muscle spindle receptors and the increased turnover rate of...
cross-bridges in the extrafusal muscle may therefore have led to the parallel effects on intrinsic mechanical properties and reflex action.

The progressive delay in the reflex response with amplitude of prior shortening (Fig. 1) may have resulted from slackness in the intrafusal fibers due to cross-bridges that cycle slowly or not at all (Proske et al. 1993). The slackness would increase with amplitude of release, leading to a greater delay. The reduction in initial burst (Houk et al. 1992) and in the reflex component that we observed suggested that the release also caused some dissociation of cross-bridges because the magnitude of the subsequent reflex response was also reduced. Because intrafusal cross-bridges would take some time to reform, the initial burst would have been reduced in the more compliant intrafusal fibers.

The lack of force recovery after shortening in the presence of the stretch reflex contrasts strikingly with the progressive recovery of force that occurred in the absence of reflex action (Fig. 5). The force recovery of the reinnervated muscles represented a fixed population of motor units and resembled the responses of electrically stimulated muscle (Nichols and Houk 1976) at rates of stimulation between 8 and 20 pps. Comparison with the rates of recovery of electrically stimulated muscle suggests that motor units were firing on average faster than 8 pps (see Nichols and Houk 1976) in the reinnervated muscles. The reduced force recovery in the presence of the stretch reflex agrees with previous data (Nichols and Houk 1976) and was most likely due to a sustained de-recruitment of motor units in response to the reduced drive from muscle spindle receptors brought about by the shortening. The de-recruitment was not enough to bring the force in the muscle to zero. The responses of de-effferented primary receptors decline precipitously on rapid stretch (Appenteng et al. 1982) but do not decline to zero for the amplitude of 2 mm in the presence of activity of γ-motoneurons that is characteristic of the decerebrate preparation (Houk et al. 1973).

Functional implications

During locomotion in cats, the triceps surae muscles become activated during the shortening of the E1 and the subsequent stretch of the E2 phases of the step cycle (Engberg and Lundberg 1969). As locomotion speed increases, the extents of the length changes during these periods increase substantially (Goslow et al. 1973). The present experiments suggest that, when standing and locomotion are compared, the linear range of muscles is extended during stepping and may be further extended at more rapid velocities of locomotion. Because the triceps surae muscles are lengthened increasingly rapidly with locomotion speed (Goslow et al. 1973), the extended linear range provides additional time for any reflex action required to regulate stiffness.

On the basis of the results presented here and in previous publications (Houk et al. 1981; Nichols and Houk 1976), one would predict that reflex action would be particularly important for movements in which active lengthening is prominent. Kinesiological studies have indicated that compensation by autogenic reflexes is modest during stance for level walking (Abelew et al. 2000), when active lengthening may be partially accounted for by stretching of the tendon (Hoffer et al. 1989). In this case, the shortening during the E1 phase may have been sufficient to linearize the intrinsic properties of the triceps surae muscles and reduce the contribution of the stretch reflex. During walking down a ramp, however, when active lengthening is large, reflex action plays a large role in regulating ankle stiffness and in interjoint coordination (Abelew et al. 2000). The stretch reflex therefore appears to act conditionally to regulate stiffness. The compatibility of these results from decerebrate preparations and intact animals shows that such reflex measurements in reduced preparations can reveal mechanisms underlying normal motor coordination and provide important insights into the manner in which these mechanisms are adaptive.

An important functional implication of these results is that reflex modulation, both in time and strength, can occur as the result of prior mechanical effects on muscle receptors and extrafusal muscle in addition to what are assumed to be centrally generated changes in synaptic strength (Capaday and Stein 1986; Menard et al. 1999; Nichols et al. 1999a). Reflex action can adapt in part to the changing requirements of motor behavior in a manner that does not require central commands (Lin and Rymer 2000; Nichols et al. 1999b). Although $K_e$ is apparently regulated in the short term by reflex action, the relative increase in the contributions of intrinsic stiffness over that of reflex action that results from prior movement should lead to changes in the proportions of viscous and elastic components of muscular stiffness (see RESULTS). This ascendency of viscous-like properties would be expected to enhance the stability of the musculoskeletal system during ongoing movement (Lin and Rymer 2000).

Reflex action reduces the dependence of muscular stiffness on the level of recruitment of motoneurons and on the influence of movement history. At the same time, the automatic adjustments in reflex action that result from prior movement allow the intrinsic stabilizing properties of skeletal muscles to be expressed. In addition, the changes in response properties of muscle spindle receptors may be detected at cortical levels and may affect kinesthesia under different behavioral conditions (Gandevia and Burke 1992).

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DISCLOSURES

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REFERENCES


