Movement Reduces the Dynamic Response of Muscle Spindle Afferents and Motoneuron Synaptic Potentials in Rat

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Hafft, Valerie K., Edyta K. Bichler, T. Richard Nichols, Martin J. Pinter, and Timothy C. Cope. Movement reduces the dynamic response of muscle spindle afferents and motoneuron synaptic potentials in rat. J Neurophysiol 91: 2164–2171, 2004. First published December 24, 2003; 10.1152/jn.01147.2003. Among the mechanisms that may result in modulation of the stretch reflex by the recent history of muscle contraction is the history dependence observed under some conditions in the response properties of muscle spindles. The present study was designed to test one report that in successive trials of muscle stretch-release, spindle afferent firing during stretch, i.e., the dynamic response shows no history dependence beyond the initial burst of firing at stretch onset. Firing responses of spindle afferents were recorded during sets of three consecutive trials of triangular stretch-release applied to triceps surae muscles in barbiturate-anaesthetized rats. All 69 spindle afferents fired more action potentials (spikes) during the dynamic response of the first trial, excluding the initial burst, than in the following two trials. The reduced dynamic response (RDR) was nearly complete after trial 1 and amounted to an average of ~12 fewer spikes (16 pps slower firing rate) in trial 3 than in trial 1. RDR was sensitive to the interval between stretch sets but independent of stretch velocity (4–32 mm/s). RDR was reflected in the synaptic potentials recorded intracellularly from 16 triceps surae α-motoneurons: depolarization during muscle stretch was appreciably reduced after trial 1. These findings demonstrate history dependence of spindle afferent responses that extends throughout the dynamic response in successive muscle stretches and that is synaptically transmitted to motoneurons with the probable effect, unless otherwise compensated, of modulating the stretch reflex.

INTRODUCTION

The stretch reflex changes with motor task. For example, the strength of the stretch reflex modulates over different phases of a step cycle (Kearney et al. 1999; Misiaszek et al. 2000; see reviews by Sinkjaer et al. 2001; Zehr and Stein 1999). The stretch reflex is also modulated by movement history, with changes in strength resulting when the reflex is immediately preceded by muscle contraction or by changes in muscle length (Gregory et al. 1998; Hagbarth et al. 1995; Nakazawa et al. 1998; Ogiso et al. 2002; Wallace and Miles 1998; Wood et al. 1996; see review by Proske et al. 1993). Stretch reflex modulation is variously proposed in these reports to provide resistance to unexpected perturbations, compensation for ground irregularities, additional neural drive for muscle force, and stabilization of limb trajectory. Lin and Rymer (2000, 2001) show that successive stretch reflexes initiated by a single, brief perturbation of muscle length grow progressively smaller with the proposed consequence of reducing force oscillations and instability. Huyghues-Despointes et al. (2003) show that the reflex produced by stretching a contracting muscle is dramatically reduced or even eliminated when the stretch is preceded by muscle shortening, leading them to suggest that adjustments in reflex strength operate to hold muscle stiffness constant.

The exact mechanisms responsible for stretch reflex modulation are not yet established, although available evidence identifies some likely contributors. The stretch reflex can be modulated synaptically within the spinal cord by activation of the fusimotor system (e.g., Ellaway et al. 2002) and by circuits that mediate presynaptic inhibition (Misiaszek et al. 2000; see reviews by Brooke et al. 1997; Pierrot-Deseilligny and Meunier 1998; Stein 1995) and/or that generate rhythmic motor actions (Gosgnach et al. 2000; for review Clarac et al. 2000). Stretch reflex modulation may also derive from properties intrinsic to motoneurons because rapid repetition of muscle stretch can activate plateau potentials in motoneurons and enhance and prolong stretch reflexes (Bennett et al. 1998).

Modulation of the stretch reflex might also result from variability in the response properties of the sensory receptors/afferents themselves (see Brooke et al. 1997). Variability in spindle afferent responses is best characterized for the initial burst of high-frequency firing that is produced at stretch onset. Dependence of the initial burst on prior muscle movement (Kostyukov and Chekassky 1997; Wilson et al. 1995; reviews by Hunt 1990; Matthews 1972; Proske et al. 1993) is proposed to explain certain aspects of the dependence of the stretch reflex on prior muscle movement (Hagbarth et al. 1995; Lin and Rymer 2001). However, the brief duration of the initial burst seems insufficient to account for the full effect of prior movement on the stretch reflex. Instead, a peripheral mechanism for modulation of the stretch reflex would seem to require that the effect of prior movement extend over a larger portion of the afferent response to stretch, i.e., throughout the dynamic response. Although modified under some conditions (Hunt 1990; Matthews 1972; Proske et al. 1992), the postburst dynamic response is reportedly unchanged from the first through successive trials of muscle stretch-release (Houk et al. 1992). Given the potential importance to regulation of the stretch reflex, we sought to retest the aftereffects of repetitive muscle stretch on the dynamic response and, if present, to establish the magnitude of aftereffects for a broad sample of muscle spindles.

In the present study, we demonstrate a systematic effect of...
prior movement on the dynamic response of spindle afferents in adult rats. The dynamic response, excluding the initial burst, was substantially reduced after the first of three successive triangular stretches. This reduction in dynamic response was typical of spindle afferents and expressed over a wide range of stretch velocities but depended strongly on the duration that the resting muscle was held at fixed length prior to stretch. Intracellular recording from motoneurons showed a parallel reduction in excitatory synaptic responses to successive stretches. Taken together, these findings identify response properties of spindle afferents that may modulate the stretch reflex during movement.

 Portions of this study were presented in abstract form (Haftel et al. 2002).

**METHODS**

**Experimental preparation**

Data were collected from 25 female Wistar rats (225–325 g) that were untreated prior to their use in terminal experiments. Experiments proceeded as approved by the Emory University Institutional Animal Care and Use Committee. Pentobarbital (Nembutal) was injected to induce (45 mg/kg ip) and maintain anesthesia throughout the experiment and to kill the rats by overdose at the end of data collection.

Surgical preparation of the anesthetized rats for electrophysiological recording was similar to that applied in our earlier studies, e.g., Seburn and Cope (1998). One or another of the triceps surae muscles, i.e., medial or lateral gastrocnemius (MG or LG, respectively) or soleus (SOL), and their nerves were dissected free of surrounding tissue in the left hindlimb. All other nerves in the left hindlimb were cut. Suture ties in the tendon of the selected muscle (MG, LG, or SOL) and on the uncut tendon of the plantaris muscle were positioned to line up at the resting muscle length (Lr) attained with knee and ankle joints at angles of ~90°. The tendon of the muscle selected for study was then cut at its insertion and attached to the lever arm of a length-servo motor (dual-mode lever arm system, Aurora Scientific) used to control muscle length and measure force. Initial muscle length was set at Lr. The tibial nerve and one dorsal root exposed by laminectomy were placed on separate bipolar electrodes.

**Data collection and analysis**

Rats were separated into two groups. In one group of 17 rats, action potentials were recorded from single muscle afferents in response to muscle stretch. For 3/17 rats in this first group, ventral roots L4–L6 were cut to de-efferent muscle spindles. In the second group of eight rats, synaptic potentials were recorded from spinal motoneurons in response to the same kind of muscle stretch.

**Muscle afferents**

Intra-axonal recording in dorsal roots from triceps surae afferents was performed as previously described (see Haftel et al. 2001). These records were used to measure afferent conduction velocity (CV) and to distinguish muscle spindle afferents identified by cessation or deceleration of firing rate during the rising phase of a stimulus-evoked muscle twitch. Next, afferent firing was measured in response to muscle stretch (see Fig. 1). The primary goal of this study was to determine whether there is a change from one stretch trial to the next during the dynamic response, i.e., afferent firing during constant velocity muscle stretch. The waveform used for this purpose was a symmetric triangular stretch and release. Sets of three successive stretch-release trials were presented based on observations that the dynamic response appeared to reach steady state by the third trial (see RESULTS). Between sets, the muscle was held at Lr for a minimum of 2 min to establish a resting state. In some cases, the rest interval between sets was adjusted (0.2–180 s) to examine its effect on the dynamic response. Stretches were 3 mm in amplitude, and each of three stretch-release trials occurred at the same velocity. A range of velocities was examined (typically 4–32 mm/s). Particular attention was given to stretch (and release) velocities of 4 mm/s because at this velocity over 3 mm the stretch phase lasted 750 ms and yielded a number of spikes, typically ≥20, sufficient to reliably characterize the dynamic response and its changes within a single set of triangular stretch-release. Sets of 4 mm/s stretch-release trials were repeated at least twice for several afferents. Post mortem measurements showed that at Lr, MG muscle length was 44.8 ± 1.4 (SD) mm (n = 9) and SOL muscle length was 34.0 ± 1.2 mm (n = 8). This means that the stretch applied to SOL or MG (and presumably LG) was ≤9% Lr and ≤0.12 Lr/s.

Records of afferent action potentials, muscle length, and muscle force were collected, digitized (22 kHz), and stored on computer for later analysis using a CED 1401plus and Spike 2 software (Cambridge Electronics). Figure 1 illustrates the parameters that were measured. The maximum values for instantaneous firing rate (IFR) were measured during the initial burst and at or near the peak of triangular stretch (IFR peak). Of primary interest was the difference in dynamic response that is readily apparent between stretch-release trials in Fig. 1. A discreet initial burst, typically fewer than three spikes, appeared for some spindle afferents, e.g., Fig. 1, in trial 1 but not in the subsequent two trials as expected based on previous reports (see INTRODUCTION). The postburst dynamic response, hereafter referred to simply as the dynamic response, was measured from the afferent firing that occurred over the remaining portion of muscle stretch. Various measures were used to characterize firing during the dynamic re-

**FIG. 1.** Dynamic response reduced by prior movement. Instantaneous firing rate (IFR) for 1 spindles afferent (A) and force of the passive medial gastrocnemius muscle of a rat (C) in response to 1 set of 3 triangular stretch-release trials (B). Muscle length (L) was electrophysiologically controlled to increase (upward direction) by 3 mm from resting length (LR: length at ankle angle: 90°) and to return to LR at constant velocity (4 mm/s) for both stretch and release. Dynamic response measured here as increment in afferent firing from stretch onset to peak stretch, excluding the initial burst.
Motoneurons

Glass micropipettes (5–15 MΩ, 2 mM K-acetate) were driven into the spinal cord until antidromic action potentials were recorded from motoneurons in response to electrical stimulation of the MG and LG-SOL nerves (0.04-ms pulses, >2.5 times threshold at 1 pps). Data collection proceeded when action potential amplitude exceeded 65 mV and membrane potential varied by no more than 2 mV. Sets of three triangular stretch-release trials of 3 mm in amplitude and 4 mm/s velocity identical to those used to study afferent responses (see preceding text) were applied to the common tendon of all three triceps surae muscles. Sets were separated by 20 s, or by 0.2 s in a few cases, during which time the muscles were held at Lr. These stretch-release sets were repeated as many times as stable recording permitted. Records of motoneuron membrane potential and dorsal root volleys (recorded with bipolar electrodes) were collected, digitized (22 kHz), and stored on computer for later analysis using the CED 1401plus and Spike 2 software. The synaptic responses to as many sets of triangular stretch-release trials had Pearson correlation coefficients, $r > 0.9$, *significant differences with trial 1 (ANOVA, $P < 0.00025$); there were no significant differences between trials 2 and 3 (ANOVA, $P > 0.5$).

Results

Sample

The axonal conduction velocities of stretch-activated afferents ranged from 40 to 75 m/s, comparable to values reported earlier for adult Wistar rats (Andrew et al. 1973; Hnik and Lessler 1973; Leslie 1973; Lewin and McMahon 1991). Afferents were readily classifiable as muscle spindle afferents ($n = 69$) based on firing rates that decelerated during the rising phase of isometric twitch force. Most afferents were sampled from the MG muscle ($n = 36$). Data from MG afferents were similar to, and therefore pooled together with, data taken from spindle afferents that supplied either the SOL ($n = 4$) or LG ($n = 4$) muscle. Additional data were sampled from 20 MG spindle afferents in rats with ventral roots sectioned at the time of data collection.

Spindle responses depend on prior movement

All spindle afferents exhibited a conspicuous change in the dynamic response after stretch-release trial 1 (see Fig. 1). The instantaneous firing rates were higher in trial 1 relative to trials 2 and 3, and these higher rates extended throughout most of the dynamic response. These unique features in dynamic response for trial 1 emerged whether plotted against the imposed change in muscle length (Fig. 2A) or the resultant change in passive muscle force (Fig. 2B).

Quantitative comparisons across successive 3-mm stretch-release trials are made in Table 1 for various measures of spindle afferent firing. Table 1 shows that afferent firing converged to approximately the same maximum rate at peak muscle stretch (IFR peak) for all three trials, and that trials 2 and 3 were similar by all measures. By contrast, firing rates began and remained higher throughout most of the stretch phase in trial 1 as compared with trials 2 and 3. These differences are expressed in the linear regression of afferent firing rate on muscle length, for which the y intercept was relatively higher and slope shallower for trial 1. Note the substantial difference in magnitude of the average y intercepts, which for trial 1 was ~30 pps greater than for trials 2 and 3.

RDR

The number of spikes during the dynamic response, excluding initial burst spikes, was significantly greater for all spindle

<table>
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<tr>
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<th>Trial 1</th>
<th>Trial 2</th>
<th>Trial 3</th>
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<tbody>
<tr>
<td>IFR peak, pps</td>
<td>102.1 ± 38.4</td>
<td>100.8 ± 37.6</td>
<td>99.1 ± 36.9</td>
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<tr>
<td>Slope IFR vs. length, pps/mm</td>
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<td>*29.8 ± 8.5</td>
<td>*30.0 ± 12.1</td>
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<tr>
<td>y intercept, pps</td>
<td>45.1 ± 13.5</td>
<td>*15.6 ± 14.9</td>
<td>*13.5 ± 15.8</td>
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<tr>
<td>DR spike number</td>
<td>53.9 ± 18.9</td>
<td>*43.2 ± 17.0</td>
<td>*41.9 ± 16.8</td>
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Values are means ± SD for parameters measured during 3 successive trials of muscle stretch-release at 3-mm amplitude and 4-mm/s velocity (see Fig. 1). Spike number during dynamic response (DR) and IFR peak reported for all 69 spindles; remaining 2 parameters measured from 49/69 spindle afferents for which the linear regression of all 3 stretch-release trials had Pearson correlation coefficients, $r > 0.9$; *significant differences with trial 1 (ANOVA, $P < 0.00025$); there were no significant differences between trials 2 and 3 (ANOVA, $P > 0.5$).

FIG. 2. Dynamic response decreased by prior movement independently of muscle length and passive muscle force. Data taken from 1 spindle afferent from the medial gastrocnemius in rat. Instantaneous firing rates were higher in trial 1 than in succeeding trials over most of the dynamic response. Dynamic response was greater for trial 1 whether plotted against (A) muscle length or (B) passive muscle force. Linear regression was performed on the relation between instantaneous firing rate and muscle length during the dynamic response. For the majority of spindle afferents (48/69), the Pearson correlation coefficient ($r$) for the regression line exceeded 0.9 in all three stretch-release trials in a set. The slope and y intercept of the regression lines were obtained from these regressions to represent dynamic response. In addition, spike number ($N$) was measured from the dynamic response, excluding the initial burst, for each of the three trials ($N_1$, $N_2$, and $N_3$). This parameter avoids the assumptions of curve fitting and allows precise characterization of firing during the dynamic response for all afferents. Another advantage of spike number is its independence of temporal variation in firing rate typically observed during the course of muscle lengthening. The reduction in dynamic response (RDR) that is the focus of this report was calculated as the difference in number of spikes between trials 1 and 3, i.e., $N_1 - N_3$. Values for these various parameters are reported as means ± SD. Differences between sample means were tested statistically by one-way ANOVA.
afferents on average in the first compared with the following two trials in a set (Table 1). Statistical comparisons of trials 2 and 3 revealed no differences. From this point forward, the RDR is reported as the difference in number of spikes between trials 1 and 3 with initial burst spikes excluded, i.e., \( N1 - N3 \). Whether measured by RDR or the change in linear slope or y intercept, Table 1 demonstrates that the dynamic response fell significantly and substantially after one stretch-release trial. 

The magnitude of RDR for all afferents is illustrated in Fig. 3. The rightward shift of points off the line of identity in Fig. 3A indicates that all spindle afferents produced fewer spikes during the dynamic response in trial 3 than in trial 1. For all 69 spindle afferents, there were \( 12.0 \pm 4.7 \) (SD) spikes fewer on average in trial 3 than in trial 1, amounting to a decrease in firing rate of \( \approx 16 \) pps averaged over the 0.75-s stretch duration at 4 mm/s. Figure 3A also shows that acute ventral root section had a small yet significant \( (P = 0.041) \) effect on RDR: the mean value of \( N1 - N3 \) for afferents with ventral roots intact \( (n = 49) \) was \( 12.8 \pm 4.8 \) spikes and with ventral roots sectioned \( (n = 20) \) was \( 10.2 \pm 4.1 \) spikes. Figure 3B shows that the number of spikes in trials 2 and 3 were nearly the same for all spindle afferents with only a slight rightward shift (average \( N2 - N3 = 1.4 \pm 0.9 \) spikes). No appreciable changes in spike number during the dynamic response were found for additional successive stretch-release trials examined for a few spindle afferents. Thus the reduction in dynamic response associated with prior movement is nearly complete after trial 1, after which the dynamic response achieves steady state.

Dependence of RDR on stretch interval and velocity

A clear dependence of RDR on the interval between stretch-release sets was demonstrated for all six spindle afferents examined in detail. Whereas there was no tendency for RDR to increase for set intervals ranging from 120 to 180 s, RDR did decrease monotonically at shorter intervals. Figure 4 shows a representative case in which RDR observed after a resting

![FIG. 3. Dynamic response measured from successive stretch-release trials for the entire sample of spindle afferents \( (n = 69) \) from rat triceps surae muscles: soleus (SOL), medial (MG), or lateral (LG) gastrocnemius plus 20 MG spindle afferents sampled from rats with ventral roots (VR) acutely severed. A: reduced dynamic response (RDR) demonstrated by fewer spikes in stretch-release trial 3 than in trial 1 (excluding initial burst spikes), and a shift in data points to the right of the line of identity. B: RDR was not expressed between trials 2 and 3 as indicated by the close association of data points with the line of identity.](image1)

![FIG. 4. Reduced dynamic response depends on interval between stretch sets. Data taken from pairs of stretch sets separated by different rest intervals. A: at short interset intervals (0.2 s), the dynamic responses were similar for all 3 stretch-release trials in the 2nd set of a pair (0.2 s). B: at longer interset intervals (120 s), the dynamic response during trial 1 was greater than in trials 2 and 3 in the 2nd set of the pair. C: plot of number of spikes during dynamic response for 2nd stretch sets that follow a first set at 3 different intervals (0.2, 5, and 120 s). Symbols are mean values (offset on x axis for clarity), and bars represent full range of values obtained from 4 presentations of paired stretch-release sets.](image2)
interval of 120 s (Fig. 4B) was essentially lost when only 0.2-s rest was permitted between sets (Fig. 4A). Apparently the short rest interval prevented trial 1 from achieving the greater response that occurs after the longer interval. After 5-s rest, RDR was present but reduced by about half of the value recorded after 120-s rest (Fig. 4C). The time constant of recovery for RDR, obtained with a single-exponential fit, was estimated at 14.9 ± 5.5 s for the case in Fig. 4. Time constants measured for the remaining five afferents ranged from 2.9 ± 0.8 to 23.6 ± 13.5 s. These values for the recovery of the maximal trial 1 response and, by extension, RDR are all longer than the time constants of recovery either for the initial burst (<1 s) (Hunt and Ottoson 1976; Proske and Gregory 1977) or for the response sensitivity of spindle afferents after large and abrupt muscle stretch (ca. 1.5 s) (Baumann and Hulliger 1991). These differences in time constant suggest that different mechanisms underlie the initial burst and the dynamic response (see DISCUSSION).

RDR was observed over a wide range of stretch velocities as shown in Fig. 5. Firing responses were measured for 33 spindle afferents at each of three stretch velocities. For these considerations, the number of spikes is normalized by the different durations of stretch: 750, 187.5, and 93.75 ms for 4, 16, and 32 mm/s, respectively. In other words, data are presented for each of these velocities as the average firing rate in the dynamic response. At all velocities in Fig. 5, the average firing rate for trial 3 is significantly smaller (P < 0.01) than for trial 1 and by essentially the same amount (17, 17, and 18 pps, respectively, for the slowest to fastest stretches). Thus RDR was expressed over an eightfold range in stretch velocity (4–32 mm/s).

**RDR reflected in motoneuron synaptic potential**

Intracellular records of motoneuron membrane potential were examined to determine whether the RDR was sufficient to alter the synaptic response of motoneurons to triangular stretch-release. Sets of three triangular stretch-release trials identical to those used to study afferent responses were repeated every 20 s. This rest interval was long enough to express RDR in spindle afferents (see preceding text) but short enough to permit adequate data collection under conditions where intracellular recording time was limited. Figures 6, A and B, shows for one motoneuron that stretch-evoked depolarization was reduced after trial 1. Superposition of traces on an expanded time scale in Fig. 6B shows that depolarization was similar for trials 2 and 3 and reduced from that in trial 1. These findings suggest that the magnitude of RDR is sufficient to substantially reduce motoneuron depolarization in successive trials of muscle stretch-release.

To quantify the changes in synaptic potentials across trials, the area under the voltage trace was integrated over 25 to 75% of the rising phase of depolarization as plotted for trial 3 vs. trial 1 (C) and for trial 3 vs. trial 2 (D). All data fall to the right of the line of identity in C but closer to that line in D (cf. Fig. 3).
further decline from trial 2 to trial 3 in Fig. 6D, the rightward shift is appreciably smaller than in Fig. 6C. These changes are qualitatively similar to those observed for the spindle afferent responses (cf. Fig. 3).

If caused by RDR of spindle afferents, then the reduction in synaptic response of the motoneuron should be eliminated when the interval between stretch sets is brief (see Fig. 4). This expectation was met for each of two motoneurons tested. For both motoneurons, the decline in the 25–75% voltage-time integral from the first to the third trial was greater for the first set of triangular stretches (−28 and −17%) than it was for a set that followed 0.2 s later (−3 and +15%).

**DISCUSSION**

The dynamic response of muscle spindle afferents observed after a period in which the muscle was not actively contracting and held at constant length was reduced in successive trials of muscle stretch-release. This dependence on prior movement extended beyond the initial burst throughout most of the dynamic response and was expressed by our entire sample of spindle stretches. Spindle afferents fired 16 pps slower on average after the first of three successive triangular stretch-releases. The reduction in dynamic response corresponded with a decrease in motoneuron depolarization in successive stretches. In general, these findings expand characterization of the variable nature of sensory feedback, and in specific, they suggest an additional mechanism, discussed in the following text, for the dependence of the stretch reflex on the history of muscle length changes.

**Conditioning the dynamic response**

Previous study identified some conditions under which the postburst dynamic response can be conditioned by preceding muscle length changes and contraction (Hunt 1990; Matthews 1972; Proske et al. 1993). Here we show that immediately successive trials of triangular stretch-release produce a systematic reduction in dynamic response common to all muscle spindles in rat triceps surae muscles. However, using a triangular stretch-release paradigm similar to ours, Houk et al. (1992) found no evidence of change in the dynamic response after the initial burst in cat muscles. The differing results between the latter two studies are probably not related to animal species because we find RDR in our preliminary studies of cat spindle afferents. A viable explanation is that the exposure of RDR in repeated stretch-release trials in our study depended on the reduction or elimination of gamma motoneuron drive of the muscle spindles resulting from, respectively, pentobarbital anesthesia or ventral root section. The gamma drive that was presumably present in the decerebrate cats used by Houk et al. has known effects on the dynamic response (Hunt 1990; Matthews 1972; Proske et al. 1993). These observations suggest yet another functional role of gamma motoneurons, whereby the intrinsic properties of passive muscle spindles, RDR in this case can be regulated by the CNS.

**Mechanism(s) underlying RDR**

Our consideration of the mechanism accounting for RDR begins with comparison of the initial burst and the remaining dynamic response. These two response properties of spindle afferent firing exhibit different behavior during successive trials of muscle stretch-release. First, the initial burst is expressed over a much shorter time and smaller magnitude of muscle stretch than the enhanced dynamic response in the first stretch trial: the initial burst is complete within tens of milliseconds and fractions of a millimeter of stretch and the dynamic response lasts hundreds of milliseconds over 3 mm of stretch. Second, the initial burst recovers by two-thirds its original firing rate after rest periods of ~0.5 s (Proske and Gregory 1977), whereas comparable recovery of RDR requires a rest period >10 times longer (see Fig. 4). In addition, the magnitude of the initial burst is much more sensitive to stretch velocity than is the dynamic response (cf. Fig. 5) (Houk et al. 1992; Hunt and Ottoson 1976). Finally, in the present study, the initial burst was variable in magnitude and occasionally absent in repeated sets of stretch-release trials, whereas the greater dynamic response in trial 1 compared with the subsequent two trials was present in all sets and less variable.

Because the differences between the initial burst and remaining dynamic response are found for de-efferented spindles, they must derive from movement dependence either of the transduction process or of the mechanical properties of intrafusal muscle fibers. Although we are unaware of demonstrations of the former, extensive consideration of the movement dependence of cross-bridge formation in intrafusal fibers suggests various explanations for the differences between response properties. One explanation is that the initial burst and dynamic response in de-efferented spindles reflect the operation of different populations of cross-bridges. It is commonly held that stretch of noncycling cross-bridges in intrafusal muscle fibers is responsible for the initial burst (see Proske and Morgan 1999). This leaves explanation of the dynamic response behavior to a different population of cross-bridges that are cycling (see following text). In the absence of neural drive, cross-bridge cycling may be driven by mechanical input (Poppele and Quick 1985; see Hunt 1990), although this possibility remains controversial (Dickson et al. 1989; see Proske et al. 1993). A more parsimonious explanation for differences between the initial burst and the dynamic response is that both reflect the behavior of the same population of intrafusal cross-bridges. The noncycling cross-bridges that resist stretch to produce the initial burst, once detached may re-attach during stretch as suggested, for example by Baumann and Hulliger (1991) to endow muscle spindles with properties observed for muscles with actively cycling cross-bridges. Chemically skinned muscle fibers with actively cycling cross-bridges (Campbell and Moss 2000) resist successive trials of triangular stretch-release with absolute tension that is greater throughout most of the stretch phase of the first trial, nearly identical in successive trials and similar in peak amplitude across all trials. The time course for full recovery of this tension profile for skinned muscle is much shorter (5 s) than that found here for spindle afferents (ca. 120 s), possibly the result of differences in experimental conditions or in extrafusal versus intrafusal cross-bridge cycling. Nonetheless, qualitative similarity in the profiles of tension for skinned muscle fibers and in spindle afferent firing during repeated stretch-release trials supports the possibility that RDR may be explained by the behavior of cycling cross-bridges.
Functional considerations

The stretch reflex compensates for a yield in force that can occur when a muscle is stretched. The reflex regulates stiffness in such a way that the muscle presents a largely elastic resistance to stretch (Lin and Rymer 1998). This elastic resistance presents an effective means of countering perturbations of a muscle that is previously at rest and not changing length; but if the elastic resistance remains high during ongoing or repetitive movements, it can produce force oscillations and limb instability (Lin and Rymer 2000, 2001). The latter problem is avoided, however, because with prior movement the muscle yields less (Axelson and Hagbarth 2001; Campbell and Moss 2000; Huyghes-Despointes 2003; Kirsch et al. 1994) and reflex strength decreases (see INTRODUCTION). Because the muscle’s intrinsic properties predominate during or soon after movement, its viscous-like properties act to stabilize the limb (Lin and Rymer 1993, 1998; see also De Serres et al. 2002). Results presented here suggest that the decrease in reflex strength is an automatic result of the reduction in dynamic response of spindle afferents and the associated decline in motoneuron depolarization. It appears, therefore, that some of the effects of prior movement on the stretch reflex can be localized to the peripheral nervous system and the process of sensory transduction.

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