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Title: Triceps surae fascicle stretch is poorly correlated with short latency stretch reflex size

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Triceps surae fascicle stretch is poorly correlated with short latency stretch reflex size

Abstract

Introduction: The short latency stretch reflex (SLR) is well described, but the stimulus that evokes the SLR remains elusive. One hypothesis states that reflex size is proportional to muscle fiber stretch, so this study examined the relationship between these 2 parameters in human triceps surae muscles.

Methods: Achilles tendon taps and dorsiflexion stretches with different amplitudes and preactivation torques were applied to 6 participants while electromyography and muscle fascicle length changes were recorded in soleus and medial gastrocnemius (MG).

Results: In response to tendon taps, neither fascicle length nor velocity changes were correlated with SLR size in either muscle, but accelerometer peaks were observed immediately after hammer-tendon contact. Similar results were obtained after dorsiflexion stretches.

Discussion: Muscle fascicle stretch is poorly correlated with SLR size, regardless of perturbation parameters. We attribute the SLR trigger to the transmission of vibration through the lower limb, rather than muscle fiber stretch.

Key words: dorsiflexion stretch, tendon tap, reflex EMG, ultrasound, muscle fascicle

Introduction

The stretch reflex is a physiological response to stimulation of muscle spindles. In the human triceps surae muscle group, the stretch reflex is often broadly divided into 2 or 3 components based on their onset latencies¹. The earliest response, the short latency reflex (SLR), has received the most scientific attention and is predominantly but not exclusively mediated by velocity-sensitive muscle spindle Ia afferents^{2,3}. In the gastrocnemius and soleus muscles, the SLR appears as a short-lasting burst of electromyographic activity at a consistent latency of ~40ms⁴.

In spite of several decades of SLR research, the stimulus that evokes the response remains surprisingly elusive. It is often assumed that because muscle spindles are distributed throughout a muscle, reflex size is directly proportional to muscle fiber stretch amplitude and/or velocity, and thus muscle fiber stretch is the stimulus for the SLR. However, numerous factors complicate the relation between muscle fiber length changes and muscle spindle afferent firing behavior. For example, the fusimotor system can induce internal spindle length changes independent of external muscle fiber length changes⁵, suggesting that a linear correlation between muscle fiber and muscle spindle stretch is unlikely. Furthermore, Achilles tendon taps and foot sole vibration are both sufficient to evoke SLRs in triceps surae muscles², often simultaneously in proximal and antagonist leg muscles where the muscle fibers cannot have undergone any length change^{6,7}. The SLR can even be elicited during muscle shortening^{2,7}. Of the few studies that have examined muscle fiber stretch in relation to SLR characteristics in humans, the muscle stretch either appeared to occur too late to be responsible for the SLR⁸ or was generally poorly related to SLR parameters⁹. These

findings collectively suggest that SLR size is not necessarily related to the amplitude and/or slope of muscle fiber stretch.

An alternative hypothesis has been proposed that the stimulus for the SLR is “propagation of vibration along a taut tendon and muscle fiber”¹⁰, as may occur in running due to foot-ground contact or when inducing mechanical perturbations, tendon taps, or foot vibration. The resulting vibratory waves then cause small, sinusoidal spindle oscillations, which may or may not be accompanied by length changes of extrafusal muscle fibers^{2, 7, 11, 12}. This hypothesis can account for the consistent triceps surae SLR latencies of ~40 ms observed in a range of studies with widely varying stretch parameters^{4, 6, 13-15}, as well as the aforementioned weak correlations between SLR characteristics and muscle fiber stretch parameters. The aim of this study was to examine directly the relationship between SLR size and muscle fascicle stretch in the human triceps surae in response to Achilles tendon taps and mechanical dorsiflexion stretches with varying stretch amplitudes and pre-stretch joint torques. It was hypothesized that muscle fascicle stretch amplitude and velocity would be related poorly to the size of evoked SLR responses, in accordance with the vibratory wave hypothesis outlined above.

Materials and Methods

Participants

Six healthy participants (2 men, 4 women; age 31 ± 5 years; height 173 ± 9 cm; body mass 69 ± 13 kg) with no history of neurological, cognitive, metabolic, cardiovascular, pulmonary, or lower limb musculoskeletal impairment volunteered to participate in this study. Prior to

testing, participants were informed fully of the experimental procedures, and each participant provided written informed consent. The study was approved by the University of Jyväskylä ethics committee and was performed in accordance with the Declaration of Helsinki.

Protocol

Electromyography (EMG) electrodes were attached to the soleus, medial gastrocnemius (MG), and tibialis anterior (TA) muscles of the right leg, and an ultrasound probe was positioned over MG to enable simultaneous visualization of both MG and soleus muscle fascicles. Subjects lay prone, with the knee extended fully and the ankle at 90°. A series of 10-12 Achilles tendon taps were performed with a tendon hammer dropped manually from a height of 25 cm, with a minimum of 20s between repetitions. EMG and ultrasound data were recorded continuously. Subjects were then seated in an ankle dynamometer capable of inducing rapid dorsiflexion stretches (see ⁹), where they performed maximal voluntary contractions (MVCs) of the plantar- and dorsi-flexors. A minimum of 3 of each contraction type were performed with ~2 minutes between trials, and the highest torque value during a steady plateau was used as MVC. Dorsiflexion stretches were then applied at a range of amplitudes and velocities, and with different preactivation levels (Table 1). For trials with 10 or 50% torque levels, the target torque was displayed on a screen, and subjects were required to maintain this level for at least 1s prior to stretch onset. For each condition shown in Table 1, a minimum of 10 trials were obtained, with minimum rest periods of 20s between trials. The order of conditions was randomized, and before each condition, 4-5 submaximal plantar flexion contractions were performed to minimize the effects of thixotropy ¹⁶. Torque, ankle angle, dynamometer pedal position, EMG, and ultrasound data were sampled continuously.

MVC trials were repeated at the end of the protocol to ensure that the test protocol did not induce obvious signs of fatigue.

Data collection and analysis

Electromyography (EMG). Surface EMG activity was recorded at 2 kHz via an A/D board and Spike2 software (both by Cambridge Electronic Design, UK), and stored in a computer for subsequent processing. Bipolar surface electrodes (Ambu; 720, Ølstykke, Denmark) with an inter-electrode distance of 2 cm were used. Before electrode placement, the skin was shaved, abraded, and cleaned with alcohol to ensure an interelectrode resistance value below 1 k Ω . EMG signals were band-pass zero-lag filtered (5 Hz–450 Hz) with a digital 4th order Butterworth filter, and averaged to produce a representative EMG profile from 10-12 trials per condition. SLR onset was then measured manually from the representative EMG trace as the first major deflection in the EMG record following the stimulus, as determined by visual inspection. Trials with no obvious stretch reflex were excluded from further analysis on a muscle-by-muscle basis. SLR amplitude was defined as root mean square (RMS) EMG within a 20 ms window from the onset of the response, and values were normalized to RMS EMG from the MVC trial during a 1 s torque plateau.

Ultrasound. An ultrasound system (Aloka α -10; Aloka, Japan) and a linear probe (B-mode; 7 MHz; 60 mm field of view) were used to image the medial gastrocnemius and soleus muscle fascicles at a sampling frequency of 204 Hz. The probe was positioned over the medial gastrocnemius to allow simultaneous visualization of the soleus muscle and secured over the skin surface with a compressive bandage to minimize probe movement relative to the skin. A digital pulse was used to synchronize ultrasound data collection with other sources. Muscle

fascicle lengths were determined using an automated fascicle tracking algorithm validated previously^{17,18}, and fascicle velocities were obtained by differentiating length with respect to time. Fascicle velocity was determined over the entire stretch phase, as well as in the first 5ms from perturbation onset, since the latter should theoretically be more closely related to SLR size. Ultrasound data were analyzed from at least 10 trials per subject and condition.

Other measured parameters. For tendon tap trials, a custom-built tendon hammer with a built-in contact sensor was used to evoke reflex responses and to synchronize data sources. Hammer trajectory data were also sampled. For stretch trials, torque was determined using a force sensor built into the dynamometer pedal. In all trials, a custom-made 5 x 5mm accelerometer was mounted over the skin surface approximately 20 cm proximal to the calcaneus, to determine whether tendon taps and dorsiflexion stretches evoked measurable acceleration over the skin surface at the level of the triceps surae muscles. Temporal data and the ultrasound synchronization pulse were sampled at 1000 Hz using Spike2 software (CED, Cambridge, UK).

Statistical analysis

Pearson product moment correlations were used to examine relationships between muscle length/velocity changes and reflex size. As multiple correlations were tested, an α of 0.02 was used to minimize type I errors. Pre-Post differences in MVC torque and differences in SLR latency between conditions were examined using dependent samples *t*-tests.

Results

Tendon taps

Mean SLR latencies in the tendon tap condition were 40 ± 4 ms in MG and 43 ± 4 ms in soleus. Corresponding mean SLR amplitudes were 0.0156 ± 0.0157 mV and 0.0301 ± 0.0179 mV, corresponding to $9 \pm 7\%$ and $20 \pm 11\%$ relative to MVC in MG and soleus, respectively. For both muscles, neither fascicle length nor velocity changes were correlated with SLR size (MG: $P = 0.043 - 0.338$; soleus: $P = 0.214-0.941$), but accelerometer peaks were observed immediately upon contact of the hammer with the tendon (see Figure 1). Peak fascicle lengthening in response to tendon taps ranged between 0.7 - 1.2 mm in MG, equating to a 2 - 4.3% length change relative to the resting length. In soleus, the corresponding values were 0.4 - 1.2 mm and 1.3 - 4.4%, respectively.

Dorsiflexion stretches

No differences were observed in MVC torque between the beginning and end of the protocol (mean difference: $1.8 \pm 0.7\%$; $P = 0.724$), confirming the absence of fatigue. For the 10% and 50% stretch conditions, the actual torque levels achieved prior to stretch onset were 10.2 ± 0.7 and $48.5 \pm 1.7\%$, respectively.

In both muscles, clear SLR responses could be observed in most trials ($92 \pm 4\%$) and occurred at mean latencies of 41 ± 3 ms in MG and 44 ± 3 ms in soleus across all conditions. Latency did not differ between conditions (MG: $P = 0.772$; soleus: $P = 0.603$). Peak fascicle lengthening in response to dorsiflexion stretches ranged between 0.2 - 2.8 mm in MG,

equating to a 0.6 - 6.7% length change relative to the resting length. In soleus, the corresponding values were 0.3 - 2.4 mm and 1 - 8.5%, respectively.

In general, the amplitude and velocity of MG and soleus fascicle stretch during mechanical dorsiflexion were poorly correlated with SLR size (Table 2). This was true when preactivation level was held constant and only perturbation amplitude altered, as well as when perturbation amplitude was held constant and preactivation level varied (Figures 2 and 3).

Discussion

The main finding of this study was that in response to Achilles tendon taps and mechanical dorsiflexion perturbations, both the amplitude and velocity of muscle fascicle stretch, as measured with ultrasound, were poorly correlated with SLR size. This was true regardless of perturbation amplitude and the level of joint torque prior to stretch. These findings, in combination with consistent, early accelerometer bursts measured over the skin surface and repeatable SLR latencies, all support the notion that the trigger for the SLR must occur in the first few milliseconds of a mechanical perturbation. Moreover, increasing preactivation torque was often associated with a larger SLR but smaller and/or slower fascicle stretch (Figure 3). Thus, the results suggest that the stimulation of muscle spindle Ia afferents that is a prerequisite to elicit an SLR occurs due to transmission of vibratory stimuli through the lower limb at the beginning of the perturbation, rather than by exceeding a certain threshold of muscle fiber stretch. Although functional movements in which the SLR is naturally elicited, such as running, were not examined, it is likely that the explanation of how SLRs are

evoked also extends to such movements, since SLR latencies are very consistent across tasks^{11, 13}.

It should be noted that in the majority of trials, it was possible to discern a stretch of the muscle fascicles in MG and soleus. The hypothesis that vibratory waves trigger the SLR, as summarized by Tfelt-Hansen¹⁹, states that ‘a vibration wave travelling through the muscle stimulates the muscle spindles by inducing a rapid sinusoidal oscillation of the spindle’. Thus, this hypothesis does not require that muscle fascicle length changes do not occur, but rather that these length changes are not necessarily related to the strength of the stimulus to the muscle spindles, and thus the size of the SLR (see Figure 3). In other words, the coupling between muscle fiber and muscle spindle length changes is not exactly 1:1⁹. Based on the consistent SLR latencies observed here across conditions, which are consistent with the shortest possible SLR latencies in these muscles (e.g.⁴), the stimulus for the SLR must occur within the first few milliseconds of the perturbation. This explains why SLR size is so closely related to initial perturbation acceleration¹⁴ but less related to stretch parameters at the level of the muscle fascicles.

It is also noteworthy that although acceleration was observed consistently in response to perturbations, the accelerometer signal cannot be used as an indicator of actual spindle firing. Various factors such as fusimotor activation and contraction-induced changes in muscle stiffness can modify spindle sensitivity (and thus vibration responses) independent of changes in skin stiffness. Thus, the relationship between skin-mounted accelerometer signals and SLR size would differ between test conditions but cannot be used to indicate differences in spindle firing behavior. Nonetheless, the presence of accelerometer bursts immediately after perturbation onset supports the hypothesis that SLRs are evoked by vibratory stimuli.

The hypothesis that the SLR is evoked by vibration is logical given that muscle spindles are sufficiently sensitive to respond to vibration amplitudes of less than $5 \mu\text{m}$ ²⁰, whereas length changes occurring in muscles *in vivo* can be in the order of several millimeters²¹. If an overt stretch of the muscle fascicles were required before an SLR could be evoked, the role of the muscle spindles in balance control and muscle stiffness regulation would likely be severely compromised. Moreover, due to the effects of tendon compliance, if muscle fiber stretch were the important parameter regarding SLR size, one would expect larger variation in SLR latencies across different test conditions than is typically observed ($SD < 2\text{ms}$; ¹⁴), particularly at low force levels where tendon slack may be present.

In cats, Eng & Hoffer²² reported correlations between local fiber stretch velocity and local SLR size, which disagrees with our data. This may be due to methodological differences, since we measured whole fascicle 2D length changes, which is a more global measure than local, directly measured fascicle strain (via sonomicrometry). Such local and invasive measures of fascicle behavior, combined with measures of EMG responses from the same region, would be extremely challenging in humans. In our setup, correlations observed between fascicle stretch parameters and SLR size may be slightly lower than would have been the case if recording EMG and ultrasound data from precisely the same region. The discrepancy between studies may also be due to differences in fiber-spindle coupling between cats and humans, or the distribution of spindles within the muscle. It should also be noted that ultrasound used in this way cannot provide as high time resolution as EMG measures, which may have a smoothing effect on the actual muscle length/velocity changes.

Due to the similarity between SLR latencies in response to mechanical perturbations and those recorded during running¹¹ and hopping³, it seems likely that the vibration hypothesis extends to those conditions and can explain the triggering of SLR responses. Although it makes intuitive sense to assume that muscle fascicle length changes would parallel changes in SLR size, as noted above, a 1:1 ratio between fascicle stretch and spindle stimulation is unlikely to occur during movement *in vivo*, because, among other reasons, the fusimotor system can modify spindle sensitivity independent of muscle fiber length changes⁵. Moreover, Achilles tendon taps and foot sole vibration can both evoke SLRs not just in triceps surae muscles², but also in proximal leg muscles where the muscle fibers do not undergo measurable length changes^{6,7}. The SLR can even be elicited during muscle shortening^{2,7}. The vibration hypothesis can account for all of these findings, and it explains why SLR latencies are so consistent across different test conditions. Nonetheless, it should be noted that this study only examined the coupling between fascicle behavior and SLR size, i.e. events within ~40 ms of a perturbation. During locomotion, spindle firing occurs throughout the stance phase, so the coupling between spindle firing and fascicle behavior may differ at different phases. For example, Grey et al.²³ hypothesised that the medium latency stretch reflex (MLR) is at least partly mediated by length-sensitive type II spindle afferents. Thus, it is possible that MLR size is related to fascicle length changes.

Conclusions

In response to tendon taps and mechanical dorsiflexion perturbations, muscle fascicle stretch amplitude and velocity measured with ultrasound are poor indicators of SLR size, and thus cannot be accurately used to estimate the strength of muscle spindle excitation. The results support the hypothesis that the SLR is triggered by vibration that accompanies the onset of

the perturbation. Specifically, the consistent presence of acceleration signals measured over the skin surface, and beginning at perturbation onset, offers direct evidence that such a vibratory stimulus is present in the lower limb in response to both tendon taps and mechanical perturbations. As hypothesized many years ago by Lance and De Gail ⁷, “percussion of a bone or other firm part of a limb or the trunk in man initiates a vibration wave...stimulating the receptors of any sensitive muscle spindle lying in its path to produce reflex contraction of that muscle”.

Tables

Table 1. Experimental conditions. The order of the stretch trials was randomized. Torque refers to the proportion of maximal voluntary torque (MVC) produced immediately prior to stretch onset.

Condition	Stretch amplitude (°)	Stretch velocity (°/s)	Torque (% of MVC)
Tendon tap	-	-	0
Plantar flexion MVC	-	-	-
Dorsi-flexion MVC	-	-	-
Dorsi-flexion stretch	1.5	120	0
	1.5	120	10
	1.5	120	50
	3	120	0
	3	120	10
	3	120	50
	6	120	0
	6	120	10
	6	120	50

Table 2. Correlations between muscle stretch parameters and SLR size. Values denote Pearson r value followed by *P*-value. * $P < 0.02$. All correlation and *P*-values denote the

correlation between the listed parameter and SLR size for that muscle. 0, 10, and 50% refer to the joint torque produced prior to perturbation as a proportion of MVC torque.

Constant joint torque		MG	0%	10%	50%	Soleus	0%	10%	50%
Fascicle lengthening amplitude			0.252, 0.328	0.179, 0.506	0.082, 0.762		0.165, 0.591	0.115, 0.709	0.551, 0.051
Fascicle lengthening velocity			0.470, 0.073	0.238, 0.375	0.491, 0.054		-0.280, 0.354	0.250, 0.411	0.663, 0.013*
Fascicle velocity in first 5ms			-0.179, 0.478	0.467, 0.068	0.270, 0.715		0.415, 0.158	0.592, 0.033	0.503, 0.039
Constant perturbation amplitude		MG	1.5°	3°	6°	Soleus	1.5°	3°	6°
Fascicle lengthening amplitude			0.108, 0.701	-0.340, 0.182	0.303, 0.237		0.137, 0.672	0.287, 0.319	0.379, 0.202
Fascicle lengthening velocity			0.595, 0.019*	0.235, 0.364	0.305, 0.234		0.360, 0.251	-0.034, 0.908	0.329, 0.272
Fascicle velocity in first 5ms			0.182, 0.516	-0.080, 0.753	-0.101, 0.691		0.371, 0.235	0.371, 0.191	0.346, 0.247

Figure legends

Figure 1. Left: Example data from a single subject in the tendon tap condition. Data from 10 trials are shown. The accelerometer signal shows vibration (measured over the triceps surae skin surface) coinciding with hammer-skin contact. Right: Data from the same subject in the dorsiflexion stretch conditions. Each trace represents the mean of 10-12 trials, and data are from the 10% condition with varying perturbation amplitudes.

Figure 2. Correlations between SLR amplitude and muscle fascicle stretch velocity within 5ms of perturbation onset. Left: Constant perturbation amplitude, varying preactivation. Right: Constant preactivation, varying perturbation amplitude. Correlation r values are shown. Note that none of these values reached the $\alpha < 0.02$ significance level.

Figure 3. Group mean (+ 1 SD) data for all dorsiflexion perturbation conditions. All parameters are plotted on the same y-axis, and units are shown in the legend. Note that in general, increasing preactivation results in a larger SLR but smaller and/or slower fascicle lengthening.

Abbreviations

EMG, Electromyography

MG, Medial gastrocnemius muscle

MLR, Medium latency stretch reflex

MVC, Maximal voluntary contraction

RMS, Root mean square

SLR, Short latency stretch reflex

TA, Tibialis anterior muscle

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