THE EFFECT OF TENDON VISCOELASTIC STIFFNESS ON THE DYNAMIC PERFORMANCE OF ISOMETRIC MUSCLE

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Abstract—The effect of tendons viscoelastic stiffness on the dynamic response of the cat's tibialis anterior muscle under isometric conditions was determined. It was shown that the dynamic response model of the muscle derived under sinusoidal contraction-relaxation in the range of 20–80% of its maximal isometric tension was not statistically different before and after the dissection of the whole distal tendon. It was suggested that under isometric conditions in the force range of 20–80% of the maximal, the tendon acts as a very stiff force transmission linkage without significantly modifying the muscle's performance.

INTRODUCTION

The dynamic performance of a muscle–tendon unit reflects the active and passive electromechanical properties of its constituent viscoelastic tissues (Hill, 1938; Fung, 1981). While much is known about the active and passive properties of the whole muscle–tendon, only relatively few data document the tendon properties under various dynamic conditions (Alexander, 1981). A recent informative review by Proske and Morgan (1987) points out several important observations on the tendon's properties and their relevance to the control of movement.

Firstly, the tendon consists of interwinding collagen fibrils, which demonstrate a wavy pattern under passive (no load) conditions. When loaded, the loosely woven pattern of the fibrils disappears as they straighten out. Further increase in load stretches the fibrils themselves and results in high stiffness. Such architectural constraints give rise to non-linear length–tension relationships in which the tendon is relatively compliant at low loads, but very stiff under moderate to high loads. This non-linear phenomena was confirmed in our previous work (Zhou et al., 1987) during increasing force contraction of isometric muscle. A brief non-linear 'toe-off' region was observed as muscle contraction was initiated, but always terminated by the time 20% of the maximal isometric tension was exceeded, giving way to a linear increase in tension as the tendon entered the high stiffness region. Furthermore, during such increasing contraction a saturation non-linearity was exhibited just before (>80%) the maximal isometric force was reached, suggesting the possible contribution of the tendon's viscoelastic properties. The mid-force range (20–80% of maximal isometric tension) was linear with respect to time, and independent of contraction rate.

Secondly, the muscle–tendon unit subjected to isometric condition displays drastic changes in the slope of its force–velocity relation upon increase in the load above the maximal isometric tension (Katz, 1939). It is conceivable therefore, that under isometric or shortening (concentric) contractions the tendon acts as a nearly rigid force transmission linkage, while under eccentric (lengthening) contractions, it stretches and protects the muscle from exhibiting inferior performance (by preventing cross-bridges binding) or exposure to damage. This is an important observation, as many daily functions require eccentric contraction (landing from a jump, going down a staircase, running, etc.). In fact, landing from a jump may require absorption of forces which are several times body weight. Direct evidence that the tendon acts as a very stiff force transmission linkage under isometric contraction is still lacking.

The third important observation made in the review of Proske and Morgan (1987) is the relationship of tendon length to its stiffness. Short tendons exhibit higher stiffness than long tendons. Long tendons, therefore, are relatively more compliant and may introduce significant changes in the dynamic performance of the muscle–tendon unit.

Proske and Morgan (1987) concluded their review by suggesting that the tendon plays a major role in lengthening (eccentric) contractions as opposed to isometric or shortening (concentric) contractions. They also indicated the inability of current techniques to study tendon properties over the mid-range of muscle generated forces.

The objective of this study is to determine the possible effect of tendon properties on the dynamic response of the muscle under isometric conditions and across the 20–80% of the maximal tension. In order to assess such possible effects of tendon viscoelastic properties, a muscle with relatively long tendon is selected and excited such that its dynamic performance could be quantified. Preferably, an increasing decreasing excitation of the muscle should be utilized at various rates in order to allow the
stretch–relaxation properties of the tendon to exhibit their effect. Sinusoidal excitation at various frequencies may serve as the optimal stimulus to elicit such behavior. Furthermore, the long tendon could be dissected out during the experiment, and the muscle's dynamic response to sinusoidal excitation determined again such that the tendon properties are excluded, allowing a comparative analysis.

METHODS

Preparation

Four adult cats, anesthetized with intraperitoneal injection of chloralose (60 mg kg⁻¹) were used. The sciatic nerve was exposed, and all branches denervated except for the nerve of the tibialis anterior. The tibialis anterior has a relatively long distal tendon, about 2.0 cm long, which is approximately 34% of the muscle–tendon length and could be conveniently shortened by dissection (Baratta and Solomonow, 1990). Its proximal tendon is minimal, about 1–2 mm long at the muscle’s emergence from the bone, assuring minimal effect on the muscle’s dynamic response. A tripolar cuff stimulation electrode (Baratta et al., 1989) was placed on the exposed nerve for later connection to two stimulators as shown in Fig. 1. Interelectrode distance was 3 mm. The muscle–tendon was lifted at its distal insertion and firmly fixed in a metal holding device which was later connected to a force transducer. One pin was inserted through the distal femoral condyles and a second pin through the mid-tibia, and both clamped to a rigid platform in order to fix the preparation in isometric stability. The ankle joint was amputated to allow direct anatomical line of connection of the muscle–tendon unit to the force transducer. A skin flap was sutured over the tendon to prevent it from drying (if exposed to room air) and isotonic saline solution was injected into the skin flap to further insure that sufficient moisture was available to the tendon (Matthews and Ellis, 1968).

In the second part of the experiment, the tendon was shortened by 2 cm such that the metal clamp held the distal end of the aponeurosis (muscle–tendon junction).

Instrumentation

The details of the computer-controlled stimulation system were described (Zhou et al., 1987; Solomonow et al., 1987; Baratta and Solomonow, 1990; Baratta et al., 1989), and validated (Baratta et al., 1989, Solomonow et al., 1990) in previous reports. In short, a sinusoidal voltage wave of a given frequency and amplitude, generated by an IBM-XT computer, was delivered via two output channels to a linear voltage-controlled oscillator and a pulse modulator, respectively, as shown in Fig. 2(a). The voltage-controlled oscillator converted the input voltage to 100 ps pulses of supra-threshold amplitude and a rate that was proportional to the voltage input. Pulse rates from 0–100 pps (pulses per second) were available, and delivered to the nerve via the proximal and middle poles of the sleeve electrode to constitute the firing rate stimulus. The middle pole was used as the common for both stimuli.

The second sinusoidal voltage wave was first inverted and then multiplied by unit pulse train of 100 μs pulses at a rate of 600 pps. The amplitude of the pulses was governed by the sinusoidal voltage wave amplitude that could be varied via the computer keyboard as necessary. Normally, the pulse amplitude was calibrated experimentally to vary between the 'just-above-excitation' threshold of the smallest axon and the 'just-below-excitation' threshold of the largest motor axon (Blair and Erlanger, 1933; Zhou et al., 1987; Baratta et al., 1989). Because such high-frequency (600 pps) stimulus blocks muscular excitation (Wedensky, 1884; Tanner, 1962; Solomonow et al., 1983), as its pulse amplitude is decreased from the 'above threshold' of the smallest nerve axon, that unit escaped the stimulus inhibition and became active to induce contraction in the muscle fibers it innervated. Further reduction in the pulse amplitude allows progressively larger motor units to become active in an orderly fashion according to the 'size principle' recruitment (Henneman et al., 1965). This recruitment stimulus was applied to the distal pole of the sleeve electrode, while the middle pole served as the common, as mentioned above. Figure 2(b) provides a schematic of the stimulation system and its functional effect on the muscle.

Muscle force was measured by a Grass Ft-10 transducer attached firmly to the muscle–tendon by a clamp. The stiffness of this transducer is 100 N mm⁻¹. Since the maximal force generated from any muscle in this study did not exceed 30 N, and the maximal muscle length from insertion to insertion was 7 cm, the

![Fig. 1. Schematic of the tripolar electrode installed in the nerve-muscle preparation and showing the set-up of the two stimulators (FR—firing rate; R—recruitment; F—force transducer).](image-url)
Fig. 2. (a) Schematic of the experimental system used to elicit sinusoidal contraction-relaxation of the muscle. The functions inside the broken rectangle depict the computer control elements which generate a sinusoid of a given frequency. The arrows to $-K_1$ and $K_2$ represent the capabilities to calibrate the peak-to-peak voltage of each stimulus as necessary via the computer keyboard. $-K_1$ also represents $180^\circ$ phase shift of the recruitment stimulus. PM represents a pulse modulator in which sinusoid voltage modulates the amplitude of the 100 μs pulses at 600 pulses s$^{-1}$. VCO represents a linear voltage-controlled oscillator which constitutes the firing rate stimulus. The modifications of the stimuli waves by each component are also shown.

Fig. 2. (b) Simplified schematic illustrating the effect of the firing rate and recruitment stimuli on a sample population of motor units of increasing size with the corresponding increase in innervation ratios. The spikes represent 100 μs pulses and both stimuli have a common timebase (i.e. simultaneous). Note the sinusoidal decrease in the interpulse interval of the FR stimulus indicating increase in firing rate which is occurring concurrently with the release of progressively larger motor units from the high-frequency block as the recruitment stimulus amplitude decrease sinusoidally. The net effect is sinusoidal recruitment of motor units according to the size principles, with each larger motor unit activated at a slightly higher firing rate.

maximal error due to the transducer compliance was 0.43 %, a rather negligible value. The resonance frequency of the transducer is 700 Hz, well above the frequency response range of skeletal muscles (Stark, 1968; Baratta et al., 1989; Baratta and Solomonow, 1990). Muscle force and the sinusoidal input control voltage were sampled and stored on an IBM-AT computer via a data acquisition card with sampling rate of 64 Hz. The force and the two stimuli voltage envelopes were also displayed on a Gould 260 polygraph.

Protocol
Initially, the muscle’s optimum length was set by determining the maximal isometric force while modifying its length by turning a turn-buckle between the tendon and the force transducer. This resulted in about 1.5 N of pre-tension at the optimal resting length.

Initial calibration trials were conducted to identify the muscle’s maximal tetanic stimulation rate by applying a 3s duration pulse train at 40 pps and gradually increasing the rate by 2 pps in each trial until no further increase in force was observed. The second calibration test was made to identify the firing rate of fusion of the smallest motor unit by observing the force trace to yield twitches that consistently decayed to a force value slightly above zero baseline as the firing rate increased in each 3 s trial from 5 pps.

Additional calibration trials were conducted to define the recruitment stimulus voltage limits corresponding to the ‘just-above-threshold’ of the smallest diameter axon and the ‘just-below-threshold’ of the largest diameter axon. Further attempts were made to
R. BARATTA and M. SOLOMONOW

calibrate the stimulus upper and lower voltages such that the force response provided about 60% peak-to-peak swings about the mid-force value of the maximal isometric force available due to tetanic stimulation (e.g., force was varied from 20 to 80% of the maximal isometric force). This calibration was performed at an oscillation frequency of 0.4 Hz.

Data recordings were started once calibration trials were terminated. The sinusoidal input voltage [see Fig. 2(a)] was set at a frequency of 0.4 Hz for a period of 6 s; only the last 4 s of the force were used for analysis to fully eliminate the effect of the initial transient response which lasts about 1 s (Solomonow, 1984). Additional 6 s trials were also obtained for voltage input frequencies of 0.6, 0.8, 1.0, 1.2, 1.4, 1.6, 1.8, 2.5, 3, 5, and 6 Hz to provide sufficient data points for the analysis. Three minute intertrial intervals were strictly observed to prevent fatigue and possible post-tetanic potentiation (Bigland-Ritchie, 1981; Connolly et al., 1971; Granit et al., 1956) from influencing the data. A 3 min intertrial interval was chosen because it was nearly twice the time required of most muscles to fully recover their force after the previous 6 s trial, and to prevent any possible pre-conditioning of the preparation which is known to change its elasticity when subjected to continuous stretch-relaxation.

Once the data for the whole muscle-tendon unit was collected, the tendon was shortened by dissecting 2 cm of its distal position. The metal clamp was reattached at just about the distal border of the aponeurosis, eliminating most of the tendon length from the preparation. The test procedure described above was then repeated.

In summary, 15 frequency data points were collected from four preparations to yield a set of pooled data for each of the two muscle-tendon length conditions. In order to assert that the tendon did not slowly slip in the clamp and cause the muscle to shorten and modify the data, we compared maximal isometric force before and after each set of data. If the maximal force was lowered at the end of the trials, the data was dismissed, the clamp tightened and data collected again.

Analysis

The force output (see Fig. 3) and stimulus input voltage at the oscillation frequency of each trial were multiplied by a Hamming window prior to taking their fast Fourier transform (FFT) by software programmed on the IBM-AT computer and manipulated by the following equation to yield the gain and phase

\[ \frac{F}{V} = \frac{|F|}{|V|} e^{j\phi} \]

where \( F \) is the FFT of the force at the trial's fundamental frequency, \( V \) is the FFT of the stimulus voltage, and \( \phi \) is the phase difference.

To allow direct comparison of the data traces from the four muscles, the gain of each trial (see above equation) was normalized with respect to the gain obtained in the trial with oscillation frequency of 0.4 Hz for each muscle tested and then represented in decibels (dB) according to the following equation:

\[ \text{dB} = 20 \log \left| \frac{F}{V} \right| @ 0.4 \text{ Hz} \]

The gain of each trial at a given oscillation frequency was then represented as a single data point and was plotted on the conventional gain vs frequency and on a companion degrees vs frequency Bode plots. The gain and phase data from all the preparations at each tendon length condition were pooled and plotted showing the mean of all the data points at each oscillation frequency and the standard deviation of the raw data.

The method of least squares \((p < 0.05)\) was used to test for the best fit transfer function characterizing the data. Models with one and up to four real and complex poles were attempted to obtain the best fit for the gain plots, while the addition of a pure time delay to the best fit gain plots was used to derive the fit to the phase plots. The a priori inclusion of a pure time delay was selected in order to properly represent well known physiological delays such as: action potentials' conduction time in the nerve, neuromuscular junction transmission time, action potentials' conduction time in the muscle fibers, and excitation-contraction coupling. Such an approach will yield a more accurate and biologically representative model from the many possible. Based on the above a priori requirements, candidate test models which resulted in a pure time lead were not considered.

In order to identify any possible changes in the model parameters obtained before and after shortening the tendon, model parameters were derived for the data of each preparation at each condition (short and
long tendon), and a paired $T$-test ($p<0.05$) was applied. To further assert variability in the data, the $T$-test ($p<0.05$) was also applied to the pooled poles of the model with the intact tendon and the model without the tendon.

In order to determine if minor, yet important non-linearities associated with the hysteresis (related to the sinusoidal stretch–relaxation) of the tendon were present (Ker, 1981), the harmonic distortions of the preparation with and without the tendon were calculated at oscillation frequencies of 1, 3 and 6 Hz.

RESULTS

Figure 3 represents several typical force traces at various oscillation frequencies recorded from one preparation of the tibialis anterior. Visual inspection of the traces confirms the expected decline in the peak-to-peak force as the oscillation frequencies increased. Similar traces were obtained from the four preparations.

Figures 4 and 5 represent the pooled data from the four preparations with and without the distal tendon, respectively. The continuous line through the data points of Figs 4 and 5 represents the best fit model for each test category with the pole values $P_1$, $P_2$, correlation coefficient $R$, and standard error of the estimate $\text{SE}$ in the inset of each plot. The phase plot's inset also contains the pure time delay $T_a$ and the associated $R$ and $\text{SE}$.

The best fit model describing the data consisted of a second order, linear equation with double poles and a pure time delay as shown below

$$M(jw) = \frac{Ke^{-jw}}{(1 + a/jw)^2}$$

where

- $a = 1/w = 1/2\pi f$
- $K =$ model gain
- $t =$ pure time delay
- $f =$ corner frequency at $-6$ dB.

The best model representing the dynamic response of the whole muscle–tendon preparation resulted in double poles at 2.7 Hz and a pure time delay of 14 ms. The correlation coefficients were above 0.97 indicating high quality fit. Similarly, the dynamic response model corresponding to the preparations after the tendon was removed yielded double poles at 2.6 Hz and a pure time delay of 9 ms. The correlation coefficient was over 0.98, indicating a high quality fit as well.

The paired $T$-test, as well as the $T$-test applied to the pooled data of the preparations with the intact tendon

![Fig. 4. The gain vs frequency (top) and phase vs frequency (bottom) Bode plots obtained from the preparation including the whole tendon.](image1)

![Fig. 5. The gain vs frequency (top) and phase vs frequency (bottom) Bode plots obtained after dissecting the whole distal tendon.](image2)
and the data from the preparations without tendon, resulted in no significant difference, indicating that the removal of the tendon had no significant impact on the muscle's performance.

Table 1 summarizes the percent total harmonic distortion for each preparation, with and without the tendon. The harmonic distortion figures of Table 1 further confirm that a consistent pattern of increased non-linearity in the preparations including the whole tendon was not present. Furthermore, the percent harmonic distortion was always below 2.5%, supporting the linearity of the muscle's dynamic response model in isometric conditions and in the force range of 20–80 % of the maximal. The absence of non-linearity as demonstrated by the low harmonic distortion further supports that the tendon did not undergo any significant stretch–relaxation.

**DISCUSSION**

The most important finding obtained in this study is that under isometric contraction and in the mid-force range of the maximal tension of the muscle, its dynamic response is independent of tendon’s viscoelastic properties. Under the above conditions, the tendon behaves as a very stiff linkage, allowing force transmission across the limbs joint in a precise and prompt manner. This conclusion confirms the suggestion of Proske and Morgan (1987), and Katz (1939), which assign the major significance of tendon viscoelastic stiffness to movements requiring eccentric contractions which impose high demands on the muscle–tendon unit in terms of loads much above the muscle’s maximal isometric tension, energy storage and recoil during the stretch–release cycle and minimization of the disturbance (prevention of shortening) to the contracting muscle fibers as well as exposing them to potential damage.

The fact that tendon viscoelastic properties are not exhibited under varying isometric contraction within the mid-force range of the muscle was also supported by the results of our previous study (Baratta and Solomonow, 1990). In that study, nine different muscles in the hindlimb of the cat were tested with sinusoidal excitation and under isometric conditions. The nine muscles had large variability in the tendon length and the muscle/tendon length ratio. Although the dynamic response of the different muscles resulted in the same general model as obtained here, the pole values ranged from 1.5 to 2.8 Hz. The statistical analysis employed to correlate various functional–architectural muscle properties (twitch time, fiber pennation, dominant fiber type, tendon length, etc.) to the poles of the dynamic response failed to identify tendon length or muscle/tendon length ratio as a factor that may directly influence the model poles.

The force variations utilized in this study covered the mid-range of the maximal isometric tension. This eliminated the short range (0–20 % of maximal force) stiffness of the tendon (Proske and Morgan, 1987; Zhou et al., 1987) from affecting the data. This should be kept in mind when comparing the results of this study to those of others, and when interpretation of the data is considered.

The length dependent stiffness of the tendon, however, had an obvious potential to affect the muscle dynamic performance if it was active in isometric contraction. The dynamic model of the preparation with the whole tendon was expected to represent more compliance. This should have resulted in the effective reduction in the dynamic model poles relative to the poles of the model obtained after the tendon was dissected out (since stiffer muscle–tendon units are expected to have higher resonance frequency). Never the less, the poles of the model with the full length of tendon were not statistically different from the poles of the model obtained after the tendon was dissected out, accounting only for the muscle dynamics.

The time dependent properties of the tendon were expected to impact the dynamic performance of the muscle as the sinusoidal contraction frequency was increasing. The expected manifestation of the tendon's time dependent properties were in a significant change in the phase angle (time delay), as well as in the effective change in value of the poles and harmonic distortion of the model corresponding to the whole muscle–tendon compared to the model with the shortened tendon. Statistically significant changes in the harmonic distortion, time delay or poles of the two models were lacking, however, pointing out again that the tendon stiffness was very high, and not affected by the tension levels generated by the muscle in the range of 20–80 % of its maximal isometric force.

Furthermore, the stretch–relaxation cycles applied to the tendon by the sinusoidal force variations were expected to demonstrate the hysteresis associated under such conditions with non-linearity of the force in the model corresponding to the preparation with

**Table 1. Percent total harmonic distortion in each preparation at 1, 3 and 6 Hz before and after dissecting the whole distal tendon**

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<td>1 Hz</td>
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<td>3 Hz</td>
<td>0.3</td>
<td>0.14</td>
<td>0.46</td>
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<td>6 Hz</td>
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<td>0.02</td>
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<td>0.36</td>
<td>0.14</td>
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the intact tendon. The harmonic distortion figures of the two models, however, did not demonstrate any significant variability, further confirming that the tendon faithfully transmitted the muscle forces.

If considering that the tendon did not stretch significantly during isometric contraction, yet the force increased and decreased upon the application of the stimulus, one can safely assume that the muscle fibers managed to shorten, allowing the cross-bridges to function. The question arises, therefore, what structure within the muscle–tendon stretched to allow the sarcomeres to shorten? The answer to this is provided in the recent work of Ettema and Huijing (1989) and Huijing and Ettema (1988/89). They pointed out, using photographic technique, that during an abrupt isometric contraction from 0–100% of maximal force, the majority of the stretch in the muscle–tendon unit was measured in the aponeurosis, while only minimal stretch was measured in the tendon (due to its compliance in the 0–20% force). During slow relaxation from a contraction, large changes (10%) in aponeurosis length were present, indicating that the aponeurosis is the structure which allows muscle fiber shortening.

The above findings, with those of Proske and Morgan (1984) from partially excited cat tendon, fully support the findings of this study and explain the relationships between the contractile mechanism of the muscle fibers, the compliance of the aponeurosis and the relative stiffness of the tendon in isometric contraction.

The emerging fact that the tendon does not play a significant role during isometric contraction in the mid-force range of the maximal force is further confirmed by the work of Katz (1939). He noticed that the slope of the force–velocity relation changed abruptly, becoming steeper, as the muscle load exceeded its maximal isometric tension. The abrupt changes in the slope suggest that once the external load exceeds the muscle's maximal tension, the tendon is stretched and imparts its viscoelastic properties. The stretching tendon prevents the detachment of the cross-bridges in the sarcomeres, allowing the muscle to continue its function and prevents potential damage to its various tissues. The cost of tendon stretching, however, was the reduction of the contraction velocity.

It is, therefore, apparent that as long as the overall tension in the muscle–tendon varies within the mid-range of the maximal isometric force and the contraction is isometric or concentric (shortening), the tendon acts as a very stiff linkage. In eccentric contractions and at loads exceeding the muscle's maximal isometric self-generated tension, the tendon does stretch and its viscoelastic properties are evident in the movements' dynamic performance.

It should be pointed out, therefore, that the dynamic performance of a muscle in the range of 20–80% of the maximal isometric tension is dominated primarily by the properties of the muscle fibers and the aponeurosis while the tendons properties are not influential in any noticeable manner, representing high stiffness. While the advantages of high tendon stiffness during concentric or isometric contractions is manifested in fast, accurate force transmission and therefore in precise, brisk movement, such contractions are limited by inability to negotiate with loads exceeding the muscle's maximal self-generated force. Eccentric contractions, however, would include the tendon viscoelastic properties and provide the ability to negotiate with loads exceeding the muscle's self generation force, store contractile energy and release it by recoil during the relaxation (shortening) cycle and protect the muscle's contractile mechanism.

It seems, therefore, that the tendon properties are optimally designed to allow wide range of movement type, allowing man and animal to negotiate with fine, accurate movements as well as flexibility and safety in dealing with extremes of load and high impact in locomotion.

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REFERENCES


