Published in final edited form as:

J Biomech. 2010 March 3; 43(4): 606–611. doi:10.1016/j.jbiomech.2009.10.041.

The Effect of Shortening History on Isometric and Dynamic Muscle Function

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Abstract

Despite numerous reports on isometric force depression, few reports have quantified force depression during active muscle shortening (dynamic force depression). The purpose of this investigation was to determine the influence of shortening history on isometric force following active shortening, force during isokinetic shortening, and velocity during isotonic shortening. The soleus muscles of four cats were subjected to a series of isokinetic contractions at three shortening velocities and isotonic contractions under three loads. Muscle excursions initiated from three different muscle lengths but terminated at a constant length. Isometric force produced subsequent to active shortening, and force or shortening velocity produced at a specific muscle length during shortening, were compared across all three conditions. Results indicated that shortening history altered isometric force by up to 5%, force during isokinetic shortening up to 30% and shortening velocity during isotonic contractions by up to 63%. Furthermore, there was a load by excursion interaction during isotonic contractions such that excursion had the most influence on shortening velocity when the loads were the greatest. There was not a velocity by excursion interaction during isokinetic contractions. Isokinetic and isotonic power-velocity relationships displayed a downward shift in power as excursions increased. Thus, to discuss force depression based on differences in isometric force subsequent to active shortening may underestimate its importance during dynamic contractions. The presence of dynamic force depression should be realized in sport performance, motor control modeling and when controlling paralyzed limbs through artificial stimulation.

Introduction

Force depression, a history-dependent skeletal-muscle characteristic, is believed to result from either stress induced inhibition of cross bridge attachment (Marechal and Plaghki, 1979; Herzog, 1998; Rassier and Herzog, 2004) or sarcomere length non-uniformity (Julian and Morgan, 1979; Morgan and Proske, 1984; Edman et al., 1993). The most prevalent method used to investigate force depression is to compare isometric force following active shortening contractions to equal-length isometric force without prior shortening. Utilizing this method, previous investigators have revealed the magnitude of force depression increases with

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Conflict of Interest Statement: Funded by NIH: R01NS039677-05A1. Sponsor had no involvement in the study design, data collection, analysis or interpretation, writing of the manuscript or the decision to submit the manuscript.

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increased shortening distance (Abbott and Aubert, 1952; Sugi and Tsuchiya, 1988; Herzog et al., 1998; Josephson and Stokes, 1999; Lee et al., 2000; Meijer, 2002), increased force during shortening (De Ruiter et al., 1998) decreased shortening velocities (Sugi and Tsuchiya, 1988; Herzog and Leonard, 1997; Josephson and Stokes, 1999; Ettema and Meijer, 2000; Lee et al., 2000), and ultimately increased mechanical work (the integral of force over shortening length) (Josephson and Stokes, 1999; Herzog et al., 2000). In addition, investigators who have examined the transient aspects of force depression (force recovery following active shortening) reported that the rate of force re-development is also influenced by the amplitude and speed of shortening (De Ruiter et al., 1998; Corr and Herzog, 2005) and is inversely related to the magnitude of force depression (Ekelund and Edman, 1982; Corr and Herzog, 2005).

Surprisingly, few authors or investigators have described force depression during the actual shortening phase (dynamic force depression) (Bahler et al., 1968; Joyce and Rack, 1969; Lee and Herzog, 2003), as it may have more physiological relevance than isometric force depression following active shortening. Recently, Lee and Herzog (Lee and Herzog, 2003) reported that the minimum forces produced during isokinetic shortening were inversely related to shortening. The minimum forces produced during shortening, however, did not occur at the same muscle length for all conditions. Therefore, their measures of dynamic force depression may also have been influenced by muscle length. Thus, to date, the magnitude of dynamic force depression and how it compares to the more commonly reported isometric force depression remains unclear. Potential discrepancy between dynamic and isometric force depression is important to realize as it has implications for motor control modeling, motor behavior and sport performance. For example, if this discrepancy does exist one may question how intrinsic regulation of force during voluntary movement compensates for dynamic force depression. It would also be important to determine if replicating this compensation during functional electrical stimulation of paralyzed limbs would increase the accuracy of limb control.

The primary purpose of this investigation was to determine if shortening history equally affects dynamic muscle function and the more commonly reported isometric force depression utilizing muscle excursions that represent a physiological motion (sit-to-stand). We hypothesized that shortening history, both magnitude of active shortening and shortening velocity, would have a greater impact on dynamic force depression compared to isometric force depression. A secondary purpose was to determine if shortening history altered muscle function consistently across isotonic and isokinetic contractions. Due to the similar isometric forces that commonly precede isokinetic but not isotonic shortening, we hypothesized the effects of shortening history would be greater and more consistent during the isokinetic protocols compared to isotonic protocols.

Methods

Protocols in this investigation were reviewed and approved by University of Utah Institutional Animal Care and Use Committee. Four fasted cats (3.0-5.2 kg) were initially anesthetized with Telezol: 10 mg/kg, intubated and subsequently anesthetized with isoflurane (1.5%-2.5%). The posterior aspect of the lower limb was opened and the gastrocnemius and plantaris tendon was freed from the calcaneus. A pin was inserted into the posterior aspect of the tibia and 9-0 suture was tied to the soleus tendon. Distances between the bone pin and tendon suture were measured through a range of joint angles, defined as the included angle between the shank and dorsal surface of the foot which allowed for identification of the soleus muscle lengths and excursions associated with the cat sit-to-stand motion (30°-110° ankle angle: ML₃₀ and ML₁₁₀). The calcaneus was then severed and the soleus tendon, along with a fragment of the calcaneus, was secured to a tendon hook. The experimental animal was positioned ventrally with the experimental limb extended horizontally and rigidly fixed to the table using bone pins

placed in the femur and tibia. The muscle was kept moist and warm (32 °C) during the experiment through the application of mineral oil and a heat lamp.

During isokinetic protocols, the tendon hook was connected in series to a load cell (Honeywell model 31, Morristown, NJ), servo-tube (Copley Controls STA25, Canton, MA) and linear encoder (Celesco, PT1E Chatworth, CA) (Figure 1A). Position was controlled by the servo-tube and force and position were simultaneously recorded (4000Hz) by the force transducer and linear encoder. During isotonic protocols, the load was attached to the tendon hook via a low-strain filament that passed through a micromanipulator which allowed for the adjustment of muscle length and served as a mechanical stop for the tendon hook, preventing the inactive muscle from being stretched by the load (Figure 1B). During these experiments the muscle shortened against a specified load and muscle displacement was recorded by a linear encoder (4000 Hz) that was attached in series with the muscle and in parallel with the load. In both protocols, the muscle was maximally stimulated (60 Hz bipolar 500µsec pulse width) using Grass SD9 stimulator via 10×10 Utah Slanted Electrode Array (USEA) (Branner et al., 2001) which was implanted (Rousche and Normann, 1992) on the sciatic nerve.

The soleus was subjected to a series of nine isokinetic contractions including three shortening velocities, and three initial muscle lengths. The three velocities were those required to shorten the muscle through its specific ML_{30} - ML_{110} range in two seconds (slow), one second (medium) and a half second (fast). With each velocity, the muscle shortened through three excursions that equaled 100%, 75% and 50% of the ML_{30} - ML_{110} range specific to each animal (Table 1). These excursions were met by varying the muscle length from which active shortening initiated and maintaining a constant final muscle length (ML_{110}) (Figure 2A). Stimulation was initiated 500-ms prior to shortening and continued for one second past shortening, allowing for the production a final isometric contraction. Three minutes prior to each set of three isokinetic contractions, the muscle was subjected to a four-second isometric contraction at the final muscle length (ML_{110}), which allowed for the comparison of isometric force with and without prior shortening. Nine isotonic contractions were also performed with three loads and three initial muscle lengths (Figure 2B). The smallest load was associated with the spring tension of the linear encoder (3.3 N). The medium and high loads were approximately 25% and 50% of maximum isometric force. Stimulation was maintained until the muscle shortened through ML_{110} . Three minutes separated each isometric, isokinetic and isotonic protocol to allow for complete muscle recovery. Furthermore, fatigue was monitored by subjecting the muscle to 1.5 second isometric contractions every 4th protocol. If force was reduced greater than 1%, additional recovery time was provided until isometric force recovered to initial values.

Isometric and dynamic force response to three levels of excursion and either shortening velocities or loads were analyzed. Force depression, the difference between isometric force with and without prior shortening, was determined for all excursions and shortening velocity combinations. The isokinetic force and isotonic velocity responses were determined as the muscle shortened through a specific portion of the sit to stance range (65-75% of full excursion) which avoided discontinuities at the onset of movement (Table 1 and Figure 2). Muscular power was calculated as the product of shortening velocity and muscular force. Muscular force was directly measured during isokinetic protocols, and was calculated during the isotonic protocols ($F = mg + ma + 3.30$, where m = mass, $g = 9.81\text{m/s}^2$, a = acceleration of the mass and 3.30 = spring tension of the linear encoder).

The independent variables in this investigation were excursion and either shortening velocity during isokinetic contractions or load during isotonic contractions. Since all cats were subjected to all combinations of the independent variables, repeated measures ANOVAs were used to determine if interaction existed among the independent variables. Planned multiple comparisons using Tukey-Ciminera-Heyse procedure (Tukey et al., 1985; Sankoh et al.,

1997) were performed to identify differences within the dependent variables: force depression, isometric force following active shortening, force produced during isokinetic shortening, and shortening velocity produced during isotonic shortening. Similar planned multiple comparisons were also performed on power produced at a shortening velocity of 42 mm·sec⁻¹ (42 mm·sec⁻¹ was selected as it was closest to the shortening velocity that produced max power and within the three shortening velocities utilized in the study). All comparisons were performed with alpha equal to 0.05.

Results

Neither excursion nor shortening velocity significantly influenced isometric forces following active shortening. However, dynamic force depression was significant for eight of the nine conditions (Figure 3A), and was influenced by both excursion and shortening velocity (Figure 3B).

Excursion significantly influenced force during isokinetic contractions and shortening velocity during isotonic contractions. Specifically, force during active shortening decreased as excursion increased for six of the nine conditions (Figure 4). Shortening velocity also decreased as excursion increased during isotonic contractions: all planned comparisons achieved statistical significance (Figure 5). Furthermore, repeated measures ANOVA revealed a significant interaction between load and excursion such that excursion had the most influence on shortening velocity when the loads were the greatest.

For each experimental animal, isometric force, isokinetic force and isotonic velocity during 50% and 75% excursion were expressed relative to values for full excursions (Figure 6). Excursion significantly influenced relative isometric forces produced after isokinetic shortening ($\leq 4\%$), as well as relative forces produced during isokinetic shortening ($\leq 30\%$). During the isotonic contractions, load, excursion, and load by excursion interaction significantly influenced relative shortening velocity ($\leq 63\%$). Excursion accounted for a greater portion of the variability in force produced during isokinetic contractions ($\eta^2 = 0.76$) and velocity during isotonic protocols ($\eta^2 = 0.56$) compared to isometric forces subsequent to active shortening ($\eta^2 = 0.36$).

Power-velocity relationships indicated a downward shift with increased excursion (Figure 7). This is supported by pairwise comparisons that indicate power produced at 42 mm·sec⁻¹ (the maximal velocity achieved in all conditions) was significantly reduced as excursion increased for two of the three isokinetic comparisons and all three isotonic comparisons. The only simple comparison that did not achieve statistical significance ($p = 0.07$) was between 75% and 100% excursion for isokinetic protocols.

Discussion

We are the first to quantitatively compare history dependent functional deficits across three common indices of muscle function. Our main finding was shortening history impacts muscle force, muscle shortening velocity, and ultimately muscular power, during dynamic contractions greater than isometric forces following active shortening (Figure 6). Thus, to discuss force depression based on differences in isometric force subsequent to active shortening may underestimate its importance during dynamic contractions. Furthermore, results from isokinetic and isotonic protocols varied in that force depression during isokinetic shortening was consistent across the range of shortening velocities used in this investigation. Depression in velocity during the isotonic protocols, however, was dependent upon both excursion as well as the load applied to the muscle. Recognizing that dynamic muscle function (i.e. shortening velocity, force during shortening and ultimately power) is history dependent may increase the

accuracy of motor control models and limb control during artificial stimulation in spinal cord injured patients. For example, functional electrical stimulation is often used to enable spinal cord injured patients to stand. Failure of this simple task may occur when attempting this movement from lower seat heights, which requires greater muscle excursion, if dynamic force depression is not accounted for by adjusting the stimulation frequency or intensity.

Our results support those of previous investigators who reported force depression to be positively related to shortening distance (Abbott and Aubert, 1952; Herzog et al., 1998; Josephson and Stokes, 1999; Meijer, 2002; Schachar et al., 2004) and inversely related to shortening velocity (Herzog and Leonard, 1997; Josephson and Stokes, 1999; Ettema and Meijer, 2000). Our data, however, is in partial disagreement with previous reports that force depression is minimal or absent on the ascending limb of the force-length curve (Edman, 1975; Edman et al., 1993; Josephson and Stokes, 1999; Morgan et al., 2000). The cat sit-to-stand motion initiates on the descending limb, near the plateau of the soleus force-length relationship. This may explain the presence of force depression during the full excursion, but does not explain the force depression observed during the 75% and 50% excursions which occurred exclusively on the ascending limb.

To distinguish the effect of shortening history on isometric and dynamic muscle function, we compared the differences in isometric forces following active shortening to the differences in shortening forces and velocities produced during isokinetic and isotonic contractions, respectively. The difference in force within the shortening contraction was much greater than the difference in isometric force subsequent to active shortening. Specifically, when isometric forces for 50% and 75% excursions were expressed relative to full excursion, the maximum difference was only 4%. Shortening force, however, varied by 13% between those same conditions, and varied by up to 30% across other conditions (Figure 6). Furthermore, η^2 values related to excursion are greater for isokinetic forces (0.76) than isometric forces (0.36). This supports the conclusion that excursion had a greater influence on force during active shortening than isometric force following active shortening. These data support Lee and Herzog's (2003) report that indicate the minimum forces produced during shortening, their surrogate measure for dynamic force depression, decreased with increasing magnitudes of shortening. Furthermore the slope of the regression line between their indices of isometric and dynamic force depression (0.72) indicated dynamic force depression to be greater than isometric force depression.

Shortening history also influenced shortening velocity during isotonic contractions to a greater extent than isometric force following active shortening. During the isotonic protocols, the extent to which prior shortening influenced velocity was largely dependent on the load resisting the muscle: smaller loads resulted in smaller relative differences in shortening velocity (6.8%) and larger loads resulted in larger relative differences in shortening velocity (63%) (Figure 6). The sum of η^2 for excursion and the excursion by load interaction associated with isotonic shortening (0.72) is greater than the excursion η^2 associated with isometric force (0.36). Again, this provides further evidence that shortening history has a greater influence on dynamic muscle function compared to isometric force. These data also agree with previous reports that reports that indicate during isotonic contractions, muscle shortening velocities (at a specific muscle length) differ based on the length from which shortening was initiated (Bahler et al., 1968; Joyce and Rack, 1969).

Power-velocity relationships constructed from these data shifted down as excursion increased (Figure 7). This downward shift is supported, in part, by five of six planned comparisons (three for the isotonic protocols and two for the isokinetic protocols) that indicated decreased power at with increased excursion. The range in velocities selected for the isokinetic protocols, however, was narrower, and on average slower, than the range in velocities recorded during

the isotonic protocols. As a result, power calculated from the isokinetic protocols remained on the ascending limb of the power-velocity curve whereas power calculated from the isotonic protocols spans the ascending and descending limb of the power-velocity relationship. Furthermore, the fact that power produced at any specific velocity for the isotonic protocols was less than the power associated with the same velocity for the isokinetic protocols may be due to incomplete muscle activation during the isotonic protocols as these protocols did not have an initial 500-ms isometric phase to allow for complete activation. Although these data demonstrate the influence of shortening history on the power-velocity relationship, to fully understand the interaction between these two muscle characteristics, a follow-up investigation that includes a broader and more populated set of shortening velocities is warranted.

The results from this investigation are in accord with the major two proposed mechanisms of force depression: stress induced inhibition of cross bridge attachment (Marechal and Plaghki, 1979; Rassier and Herzog, 2004) and sarcomere non-uniformity (Julian and Morgan, 1979; Morgan and Proske, 1984; Edman et al., 1993). The stress induced inhibition of cross bridge attachment implies that greater stress applied to the sarcomeres will result in greater distortion (strain) of the actin filament. As the sarcomeres shorten, this distortion will reduce cross bridge attachments in the newly formed myofilament overlap zone. Thus, greater loads would result in greater inhibition of any myosin head attaching to the actin filament, and larger excursions would lead to a greater number of cross bridge attachments that are affected by this inhibition (Corr and Herzog, 2005). This would result in the observed reduced muscular force or shortening velocity during the active isokinetic and isotonic shortening phases, respectively. The sarcomere non-uniformity theory suggests that there exists heterogeneity in the ability of sarcomeres within a fiber to produce force. As a result, during active muscle shortening the stronger sarcomeres may be responsible for the initial shortening, while the weaker sarcomeres either remain isometric or are stretched (Morgan and Proske, 1984; Edman et al., 1985; Granzier and Pollack, 1989). As a result, the stronger sarcomeres will shorten until they reach the ascending limb of the force-length relationship, at which point forces between sarcomeres equilibrate. Further shortening by the stronger sarcomeres is then attenuated, and the remaining shortening is taken up by the weaker sarcomeres. As described by Morgan and Proske (1984), the absence of simultaneous shortening across all sarcomeres, especially when the stronger sarcomeres reach a point on the ascending limb in which they are unable to shorten further, would require greater shortening velocities for those sarcomeres that are shortening. The greater shortening velocities would result in lower force production as defined by the force-velocity relationship. Hence, greater excursions and forces would lead to a greater percentage of the sarcomeres reaching a length at which they are unable to shorten further. The remaining sarcomeres are then obligated to shorten at higher velocities, and therefore produce less force. However, several groups reported that sarcomeres remain stable on the ascending limb of the force-length relationship (Allinger et al., 1996; Zahalak, 1997; Morgan et al., 2000). This contradicts the dynamic and isometric force depression observed during the 50% and 75% excursions which were located exclusively on the ascending limb.

The force patterns produced during the initial phase of the protocols is likely the reason for the significant interaction seen in the isotonic but not isokinetic protocols. During the isokinetic protocol, the active shortening phase was preceded by a 500-ms isometric contraction resulting in equal force regardless of the subsequent shortening velocity. However, during isotonic contractions, the muscle would only shorten after it produced force greater than the resisting force (load). Thus, the initial stress on the actin filament, or sarcomere non-uniformity, was greater with higher loads. Noting this difference between these two protocols, the isotonic protocols used in the current study may be a more valid model of voluntary physiological movements. Most voluntary movements require muscles to become excited, produce forces, and shorten once the muscular forces exceed the resisting forces, similar to the isotonic protocols. In contrast, the isokinetic protocols, which began with an isometric phase allowing

the muscle to become fully activated prior to shortening, represents a paradigm which does not typically occur during voluntary movement.

In conclusion, shortening history imposed greater absolute and relative influences on dynamic muscle function compared to isometric force following active shortening. However, the extent to which shortening history influenced dynamic muscle function partially depends on the methods employed to produce the dynamic contractions (isokinetic or isotonic). The magnitude of force depression during isotonic shortening was largely influenced by the load applied to the muscle, whereas during isokinetic shortening force depression was constant across the range of velocities utilized. Thus it is important to consider the constraints imposed on muscle when evaluating the effects of shortening history.

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Figure 1.

A) Force transducer, servo-tube and linear encoder connected in series to the muscle. Arrows indicated directional movement of servo-tube which resulted in muscle lengthening and shortening. B) Muscle attached in series to a load and linear encoder. The concave faced washer prevented the tendon hook from moving beyond lengths set by the micromanipulator. The load and the linear encoder were attached in parallel to the muscle.

Figure 2.

Example data from constant velocity protocols (A) and isotonic protocols (B). The horizontal arrow indicates the full (100%) sit to stand muscle excursion. The shaded area represents the muscle lengths used for analysis (ML₆₅₋₇₅).

Figure 3.

Isometric force depression following active shortening. A) Isometric force with (vertical bars) and without (flat rectangles) prior shortening. # indicates significant differences between isometric force with and without prior shortening. B) Force depression expressed as the relative difference between isometric force with and without prior shortening. * with brackets indicate excursions within the same shortening velocity that resulted in significantly different isometric force depression. Likewise, #, \$ and & signify the shortening velocities within the same excursion that resulted in significantly different isometric force depression (e.g. columns marked with # are significantly different from each other).

Figure 4. Average force during shortening for all constant velocity conditions. * indicate values within each shortening velocity that were significantly different.

Figure 5.

Average shortening velocity for all isotonic conditions. * indicate values within each load that were significantly different.

Figure 6.

The relative increase in isometric force, average shortening force and average shortening velocity. Values for 50% and 75% excursions are relative to 100% excursions.

Figure 7.

Power-velocity relationships for both isotonic (CL) and constant velocity (CV) contractions. Dotted vertical line represents 42 mm·sec⁻¹, the shortening velocity at which power values were analyzed. To maintain clarity of the figure, statistical significance symbols were omitted. However, within the isovelocity protocols, power produced at 42 mm·sec⁻¹ for the 50% excursion was significantly greater than power produced for the 75% and full excursions. Within the isotonic protocols power produced at 42 mm·sec⁻¹ for all three excursions were significantly different from each other.

Table 1

Ranges of isometric force, excursion and shortening velocity.

Max isometric force at optimal length (N)	26.5 - 41.1		
	Levels of excursion		
	100%	75%	50%
Excursions (mm)	18.8 - 22.8	14.1 - 17.1	9.4 - 11.4
Shortening distance prior to analysis range (mm)	12.5 - 14.5	7.6 - 8.9	2.8 - 3.4
	Levels of shortening velocity		
	Slow	Medium	Fast
Shortening velocity (mm-sec ⁻¹)	9.1 - 11.6	18.2 - 23.3	36.7 - 44.6

Excursions and shortening velocity were based on muscle lengths associated with the cat sit to stand motion, and therefore were different between animals due to variation in animal size (3.0-5.2 kg).