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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.

1. 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 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 (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

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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.

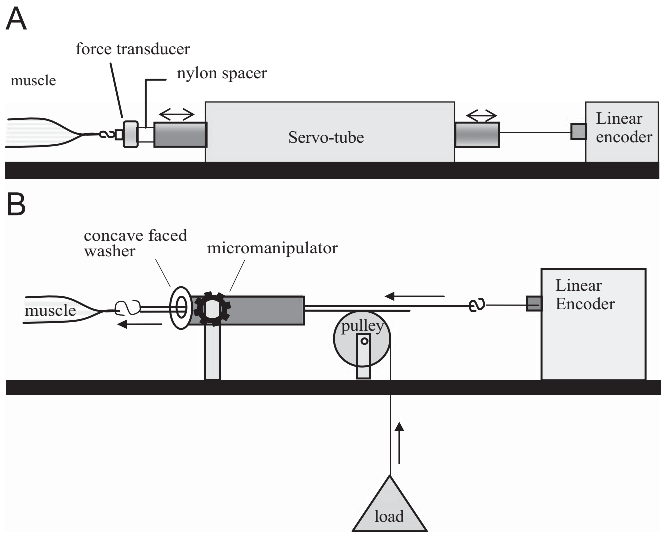

Fig. 1. (A) Force transducer, servo-tube and linear encoder connected in series to the muscle. Arrows indicated directional movement of servo-tube, which resulted in muscle lengthening and shortening. (B) Muscle attached in series to a load and linear encoder. The concave-faced washer prevented the tendon hook from moving beyond lengths set by the micromanipulator. The load and the linear encoder were attached in parallel to the muscle.

2. 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 gastrocneumius and plantaris tendon were freed from the calcaneous. 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: ML$_{30}$ and ML$_{110}$). The calcaneous was then severed and the soleus tendon, along with a fragment of the calcaneous, 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 Chatwsorth, CA) (Fig. 1A). Position was controlled by the servo-tube and force and position were simultaneously recorded (4000 Hz) 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 (Fig. 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 500 μs 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 2 s (slow), 1 s (medium) and a $\frac{1}{2}$s (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$_{110}$) (Fig. 2A). Stimulation was initiated 500 ms prior to shortening and continued for 1 s past shortening, allowing for the production of a final isometric contraction. Three minutes prior to each set of three isokinetic contractions, the muscle was subjected to a 4 s 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 (Fig. 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 s isometric contractions every 4th protocol. If force was reduced greater than 1%, additional recovery time was provided until isometric force recovered to initial values.

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 s^{-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).