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Journal of Biomechanics 40 (2007) 1518–1524

JOURNAL OF BIOMECHANICS

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History-dependence of isometric muscle force: Effect of prior stretch or shortening amplitude

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Accepted 28 June 2006

Abstract

It is well-recognised that steady-state isometric muscle force is decreased following active shortening (force depression, FD) and increased following active stretch (force enhancement, FE). It has also been demonstrated that passive muscle force is increased following active stretch (passive FE). Several studies have reported that FD increases with shortening amplitude and that FE and passive FE increase with stretch amplitude. Here, we investigate whether these trends continue with further increases in shortening or stretch amplitude. Experiments were performed using in situ cat soleus muscles ($n = 8$ for FD; $n = 7$ for FE and passive FE). FD, FE and passive FE were measured after shortening or stretch contractions that covered as wide a range of amplitudes as practically possible without damaging the muscles. FD increased approximately linearly with shortening amplitude, over the full range of amplitudes investigated. This is consistent with the hypothesis that FD arises from a stress-induced inhibition of crossbridges. FE increased with stretch amplitude only up to a point, and then levelled off. Passive FE, and the transient increase in force at the end of stretch, showed relationships to stretch amplitude that were qualitatively very similar to the relationship for FE, increasing only until the same critical stretch amplitude had been reached. We conclude that FE and passive FE do not increase with stretch amplitude under all circumstances. This finding has important consequences for determining the mechanisms underlying FE and passive FE because any mechanism that is proposed to explain them must be able to predict it.

Keywords: Force enhancement; Force depression; Magnitude; Cat soleus

1. Introduction

It is well-known that the isometric force that a muscle generates is influenced by its contractile history (Abbott and Aubert, 1952). The steady-state isometric force following active shortening is lower than the force developed during a purely isometric contraction at the same muscle length (force depression, FD), while the steady-state isometric force following active stretch is higher than during a purely isometric contraction (force enhancement, FE). Recently, it has been observed that passive force also exhibits a history-dependence, being higher after active stretch than following an isometric contraction or a passive stretch (passive FE, Herzog and Leonard, 2002).

The causes of these history-dependent effects are not well understood, although a number of mechanisms have been proposed (for a review see Rassier and Herzog, 2004). In order to be able to differentiate between these proposed mechanisms, it is necessary to have a detailed knowledge of the characteristics of FD and FE. Several studies have reported that FD increases with shortening amplitude (Granzier and Pollack, 1989; Herzog and Leonard, 1997; Herzog et al., 2000; Marechal and Plaghki, 1979; Sugi and Tsuchiya, 1988) and that FE and passive FE increase with stretch amplitude (Edman et al., 1978, 1982; Herzog and Leonard, 2002; Julian and Morgan, 1979; Schachar et al., 2004). However, it is not known whether the

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0021-9290/$ - see front matter
doi:10.1016/j.jbiomech.2006.06.014

amounts of FD, FE and passive FE would continue to increase over the full range of possible shortening or stretch amplitudes.

An in situ cat soleus preparation was used for all testing. This preparation was chosen because it is very robust, being able to withstand a large number of contractions of long duration, with large changes in length. This makes it ideal for the present investigation. The greatest ranges of shortening and stretch amplitudes that could be achieved without risk of damaging the muscle, or using a final muscle length at which active force was very low, were used. The primary objective was to test three hypotheses: (i) FD will continue to increase over the full range of shortening amplitudes, (ii) FE will continue to increase over the full range of stretch amplitudes, and (iii) passive FE will continue to increase over the full range of stretch amplitudes. A secondary objective was to characterise the relationships of FD, FE and passive FE to amplitude.

2. Methods

2.1. Surgical procedures

The experiments were performed using eight soleus muscles from four adult cats (3.9–6.5 kg), as previously described (Herzog and Leonard, 1997). Ethical approval for all procedures was given by the Animal Ethics Committee of the University of Calgary. The animals were anaesthetised using an Isoflurane/O_2/N_2O mixture, intubated and then maintained on 0.5–1% Isoflurane throughout testing. The tibial nerve was exposed and a silicone nerve cuff electrode was implanted for stimulation of the soleus muscle. The soleus was freed from the surrounding muscles and its insertion on the calcaneus was removed with a remnant piece of bone. The animal was secured in a prone position in a hammock and the experimental hind limb was attached to a stereotaxic frame with bilateral bone pins at the posterior iliac spines, femoral condyles and malleoli. The bone piece at the distal end of the soleus tendon was attached with sutures to a muscle puller (MTS, Eden Prairie, MN, USA) which controlled muscle length and measured force. Throughout the experiment, muscle temperature was maintained at 30–32 °C using heated saline and an infrared lamp.

2.2. Experimental protocol

For all contractions, the muscles were stimulated supramaximally (Grass S8800 stimulator, Grass-Telefactor, West Warwick, RI, USA) using a voltage of three times the α-motor unit threshold (2.5–3 V), applied at 30 Hz in 0.1 ms pulses (Herzog and Leonard, 1997). Throughout, muscle force and length data were recorded at 1000 Hz (Windaq, Dataq Instruments Inc., OH, USA). Between 45 and 60 s was allowed between contractions to prevent fatigue.

An isometric force–length relationship was obtained by performing 2–3 s isometric contractions at 3 mm length increments, beginning on the ascending limb of the force–length relationship and ending at approximately 12 mm longer than the length at which active force (total force−passive force) was maximal. The longest muscle length on the plateau of the active force–length relationship was taken as optimal length and was designated 0 mm. Muscle lengths shorter than 0 mm were considered negative and muscle lengths longer than 0 mm were considered positive.

A speed of 6 mm/s was used for all shortening contractions and a speed of 12 mm/s was used for all stretch contractions. The amount of FD is greater at slower speeds of shortening (Marechal and Plaghki, 1979), so the speed of 6 mm/s was chosen as a compromise between maximising the amount of FD and avoiding the risk of causing fatigue by maintaining the contraction for too long. FE is insensitive to stretch amplitude (Edman et al., 1978), so the speed of 12 mm/s was chosen as a compromise between the risk of damage from stretching too quickly and the risk of fatigue. The higher stretch speed allowed a greater range of stretch amplitudes than shortening amplitudes to be used.

In test 1, the effect of shortening amplitude on the amount of FD was determined using a final muscle length of −9 mm (i.e. 9 mm below optimal length). In the test contractions, the muscle was activated at a longer length and held isometric for between 1 and 3.5 s, before being allowed to shorten at 6 mm/s until it reached a length of −9 mm at 4 s after initial activation. It was then held isometric for a further 5 s. The amplitude of shortening was varied between 3 and 18 mm in 3 mm increments. Isometric reference contractions at −9 mm were conducted at the start of test 1 and after every two shortening trials. Force and length data for one muscle are shown in Fig. 1.

In test 2, the effect of stretch amplitude on the amount of FE was determined using a final muscle length of +9 mm (i.e. 9 mm above optimal length). In the test contractions, the muscle was activated at a shorter length and held isometric for between 1 and 2.75 s, before being stretched at 12 mm/s until it reached a length of +9 mm at 3 s after initial activation. It was then held isometric for a further 5 s. Stretch amplitude was varied between 3 and 24 mm in 3 mm increments. Isometric reference contractions at +9 mm were conducted at the start of the study and after every stretch contraction. Force and length data for one muscle are shown in Fig. 2.

2.3. Data analysis

The data were compressed in the data acquisition software by taking the median value of every 10 data