

## THE BIOMECHANICS OF DYNAMICALLY CONTRACTING SKELETAL MUSCLE

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History-dependent properties of skeletal muscle contraction have been observed for half a century. The origin of these properties has been the focus of intense scientific debate. One of these properties, the force enhancement following muscle stretching, has been associated with the development of sarcomere length non-uniformities. Here, we show that this long-held belief is likely not correct. We show this by rejecting three specific hypotheses that arise directly from the sarcomere length non-uniformity theory. We further found novel evidence that force enhancement is likely associated with the development of extra tension in a passive, molecular spring, such as titin or nebulin. This finding has a profound impact on the theory of force enhancement following muscle stretching, and has direct implications for muscle injuries occurring during active muscle stretching.

**KEY WORDS:** history dependence of force production, force enhancement, sarcomere length non-uniformity, passive force, titin

**INTRODUCTION:** Much of our knowledge on skeletal muscle mechanics is based on static measurements of the force-length relationship (Gordon et al., 1966), or the steady-state, time-independent description of the force-velocity relationship (Hill, 1938). However, most natural movements occur dynamically, do not reach steady-state values, and produce history-dependent effects.

Here, I will focus on history-dependent effects, specifically force depression following muscle shortening and force enhancement following muscle stretching. These properties have been well known for half a century (e.g. Abbott and Aubert, 1952), however, the mechanisms underlying these phenomena are ill-understood and have been the centre of intense debate in recent years (Herzog, 1998).

Force enhancement following muscle stretching is of particular importance to athletic performance because (1) stretching of the muscle allows for force production in subsequent movements that exceeds the corresponding force production without prior stretch. (2) force enhancement following muscle stretching has been associated primarily with the development of sarcomere length non-uniformities (Morgan, 1990). Such non-uniformities are said to occur only on the descending limb of the force-length relationship, thereby predicting that force enhancement cannot take place at all muscle lengths (Morgan et al., 2000). Finally, (3) force enhancement on the descending limb of the force-length relationship has been associated with instability of force production (Zahalak, 1997) and injury (Morgan, 1994).

The purpose of this paper and associated talk is to test specific hypothesis about force enhancement following muscle stretching based on the sarcomere length non-uniformity theory, and to gain insight into the injury potential of muscles stretched on the descending limb of the force-length relationship.

**METHODS:** Standard muscle stretching procedures were used in a variety of preparations ranging from single frog fibres tested in vitro to voluntary, in vivo human muscle contractions. Stretches were performed at lengths covering the ascending and descending limb of the force-length relationship, at a variety of speeds and distances of stretch.

**RESULTS:** Muscle stretching results in a steady-state force enhancement beyond the corresponding isometric force on the ascending (Fig. 1) and descending limb of the force-length relationship (Fig. 2). On the descending limb, the steady-state force enhancement also exceeded the isometric force at the muscle length from which the stretch was initiated (Fig. 2). Force enhancement on the descending limb of the force-length relationship was typically greater than that on the ascending limb, and was accompanied by an increased passive force

following stretching that was particularly apparent at the greatest muscle lengths and the greatest stretch amplitudes (Fig. 3).

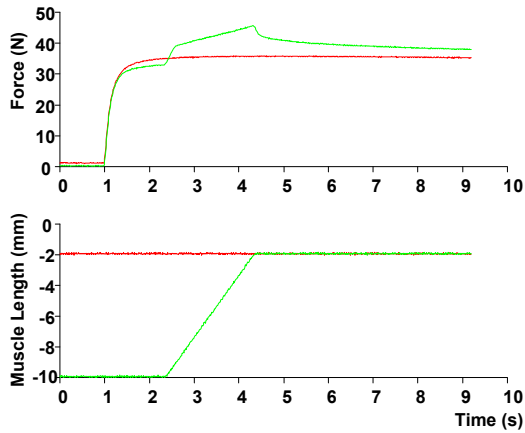


Figure 1: Example of force enhancement following muscle stretch on the ascending limb of the force-length relationship in cat soleus.

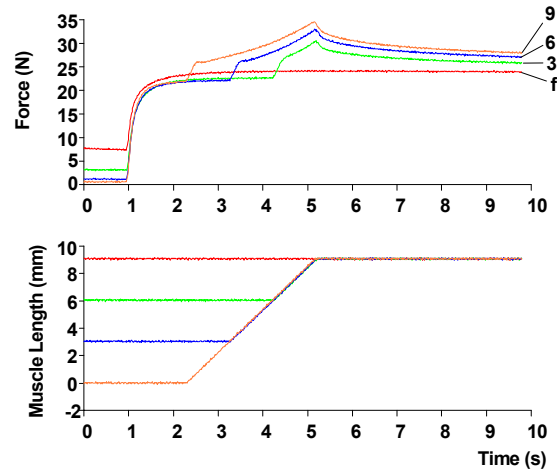


Figure 2: Example of force enhancement following muscle stretch on the descending limb of the force-length relationship for three stretch magnitudes in cat soleus. f=isometric force at final length; 3,6,9, steady-state forces following stretches of 3, 6, and 9 mm amplitude.

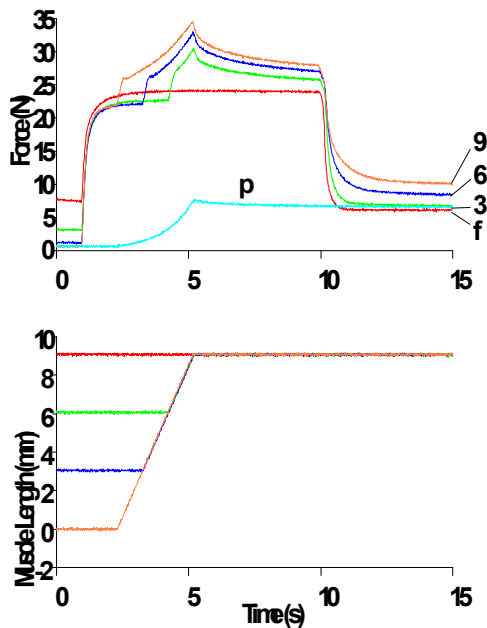
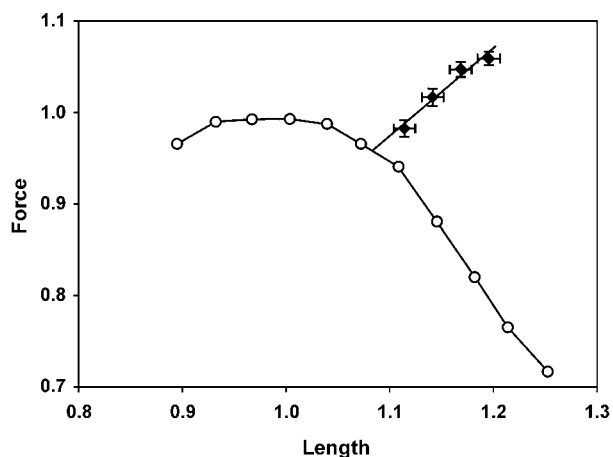


Figure 3: Example of force enhancement and passive force enhancement following muscle stretch on the descending limb of the force-length relationship for three stretch magnitudes. Also shown is a passive stretch of 9 mm amplitude. Note, the passive force enhancement following the deactivation of the muscle is related directly to the stretch magnitude.

**DISCUSSION AND CONCLUSIONS:**

The occurrence of force on the ascending limb of the force-length relationship indicates that force enhancement likely occurs without the development of sarcomere length non-uniformities, as such non-uniformities do not occur at those muscle lengths. The fact that force enhancement exceeded the isometric forces obtained at the muscle length from which the muscle was stretched, gives strong evidence that force production is stable on the descending limb of the force-length relationship (Allinger et al., 1996). In frog single fibres, we even found steady-state force enhancement that exceeded the maximal isometric force at optimal length (Fig. 4), a result that cannot be explained with the sarcomere length non-uniformity theory.



**Figure 4:** Mean ( $n=5$  fibres) steady-state force enhancement following stretches of 2.5, 5.0, 7.5, and 10.0% of optimal fibre length in frog single fibres, and the corresponding mean, normalized force-length relationship. Note that the steady-state force following the greatest stretch amplitudes were higher than the isometric force at optimal fibre length.

Finally, following active stretches at the greatest muscle lengths, we found that passive force was dramatically increased compared to the passive force at the same muscle length obtained following isometric contraction or passive muscle stretching. This result is the first direct indication that passive forces may be part of the mechanism causing force enhancement following stretch, and more importantly, such an increase in passive force during active muscle stretching at great lengths might contribute to the prevention of muscle injuries. At this point, we speculate that the giant protein titin produces this increased passive force during and following active stretch, as it has been demonstrated that the stiffness of this molecular spring can be changed by biochemical and by mechanical means (Trok and Barnett, 2001; Wu et al., 2001).

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