Journal of Theoretical Biology 365 (2015) 301–310

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

On high heels and short muscles: A multiscale model for sarcomere loss in the gastrocnemius muscle

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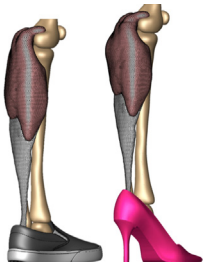
HIGHLIGHTS

- Skeletal muscle can change its length through the addition and removal of sarcomeres.
- Frequent high heel wear induces muscle shortening associated with a loss of sarcomeres.
- We create a multiscale model of the lower limb from magnetic resonance images.
- Wearing 13-cm-high heels shortens the gastrocnemius by 5% with local extrema of 22%.
- Our model indicates that this induces a sarcomere loss of 9% with local extrema of 39%.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 29 May 2014
Received in revised form
28 October 2014
Accepted 29 October 2014
Available online 7 November 2014

Keywords:
Skeletal muscle
Growth
Contracture
Finite element analysis

ABSTRACT

High heels are a major source of chronic lower limb pain. Yet, more than one third of all women compromise health for looks and wear high heels on a daily basis. Changing from flat footwear to high heels induces chronic muscle shortening associated with discomfort, fatigue, reduced shock absorption, and increased injury risk. However, the long-term effects of high-heeled footwear on the musculoskeletal kinematics of the lower extremities remain poorly understood. Here we create a multiscale computational model for chronic muscle adaptation to characterize the acute and chronic effects of global muscle shortening on local sarcomere lengths. We perform a case study of a healthy female subject and show that raising the heel by 13 cm shortens the gastrocnemius muscle by 5% while the Achilles tendon remains virtually unaffected. Our computational simulation indicates that muscle shortening displays significant regional variations with extreme values of 22% in the central gastrocnemius. Our model suggests that the muscle gradually adjusts to its new functional length by a chronic loss of sarcomeres in series. Sarcomere loss varies significantly across the muscle with an average loss of 9%, virtually no loss at the proximal and distal ends, and a maximum loss of 39% in the central region. These changes reposition the remaining sarcomeres back into their optimal operating regime. Computational modeling of chronic muscle shortening provides a valuable tool to shape our understanding of the underlying mechanisms of muscle adaptation. Our study could open new avenues in

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http://dx.doi.org/10.1016/j.jtbi.2014.10.036
0022-5193/

orthopedic surgery and enhance treatment for patients with muscle contracture caused by other conditions than high heel wear such as paralysis, muscular atrophy, and muscular dystrophy.

1. Motivation

More than two thirds of all American women frequently dress in high-heeled shoes (American Podiatric Medical Association, 2003), 40% wear their high heels on a daily basis, 10% even more than eight hours per day (Yoon et al., 2009). High heels are a major contributor to foot problems and lower limb pain, associated with chronic conditions such as hallux vagus, corns, callusses, metatarsalgia, Achilles tendon tightness, planar fasciitis, and Haglund's deformity (Cronin, 2014). In the United States alone, the annual health care cost attributed to high-fashion footwear is estimated to exceed $3 billion (Thompson and Coughlin, 1994). High-heeled footwear forces the foot into a plantarflexed position associated with shortening of the calf muscle–tendon unit (Cronin et al., 2012). Short-term, this position is energetically inefficient: it causes excessive actin–myosin overlap and forces muscle fibers into a non-optimal operating range (Ebbeling et al., 1994). Long-term, our calf muscles adapt to their new position: they shorten to reposition the actin–myosin overlap into back its optimal regime (Cronin, 2014). Fig. 1 summarizes the spatial scales involved in chronic muscle adaptation (Wisdom et al., 2014).

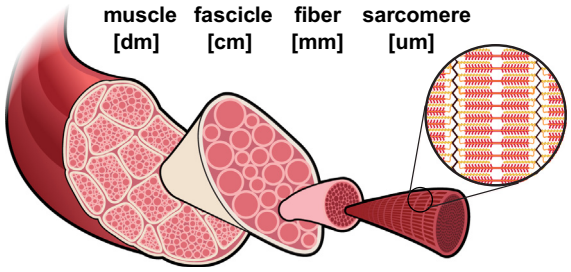

Fig. 1. Chronic muscle adaptation across the scales. Muscle shortening spans from the whole muscle level via the fascicle level and fiber level all the way down to the sarcomere level and bridges five orders of magnitude in length.

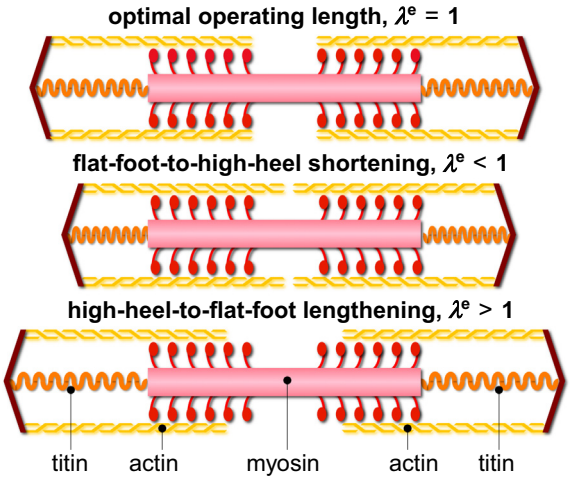

Fig. 2. Chronic muscle adaptation on the sarcomere scale. Sarcomeres are 3 μm long assemblies of thick filaments of myosin sliding along thin filaments of actin. An optimal overlap of actin and myosin is critical to maximum force generation. To maintain sarcomeres within their optimal operating range, skeletal muscle responds to chronic shortening by removing sarcomeres in series.

On the muscle level, frequent high heel wear affects primarily in the gastrocnemuius muscle, while the lengths of the soleus muscle and the Achilles tendon remain virtually unchanged (Kim et al., 2013). On the fascicle level, frequent high heel use shortens the average fascicle length of the medial gastrocnemius muscle by 12% (Csapo et al., 2010). Not surprisingly, these functional and structural changes affect the active range of motion of the ankle joint and cause a noticeable shift towards the supinated position (Cronin, 2014). This reduced range of motion decreases efficient shock absorption and increases the risk of ligament sprains (Kim et al., 2013). In addition, habitual high heel wearers compromise muscle efficiency, suffer from discomfort and muscle fatigue, and increase the risk of strain injuries (Cronin et al., 2012). Yet, switching back to flat footwear can be extremely painful (Knight, 2010); it overstretches the triceps surae and may trigger planar fasciitis (Opila et al., 1988), the most common cause of heel pain (Theodorou et al.).

The smallest functional unit involved in chronic muscle adaptation is a sarcomere. Sarcomeres are 3 μm long assemblies of thick filaments of myosin sliding along thin filaments of actin (Lieber, 2009). On the sarcomere level, an optimal overlap of actin and myosin filaments is critical to maximum force generation (Murtada et al., 2012). Not surprisingly, the sarcomere length is tightly regulated (Gordon et al., 1966). Fig. 2 illustrates a sarcomere unit at its optimal operating length, and in non-optimal shortened and lengthened positions. To always maintain each sarcomere within its optimal operating range, skeletal muscle responds to a chronic reduction in functional length through the active removal of sarcomeres in series (Tabary et al., 1972). Almost half a century ago, controlled immobilization experiments in mice (Williams and Goldspink, 1971) and cat (Tabary et al., 1972) have demonstrated the chronic loss of sarcomeres in series by fixing a muscle in a shortened position. Recent studies suggest that frequent high heel use has similar effects: It reduces the fascicle length, which may trigger the controlled removal of sarcomeres in an attempt to reposition the muscle in its optional operating regime (Csapo et al., 2010).

Taken together, the above studies provide valuable insight into chronic muscle shortening at the individual scales. Yet, the interaction of the underlying mechanisms across the scales remains poorly understood (Wisdom et al., 2014). Here we present a continuum model for chronic muscle adaptation, in which changes in whole muscle length are treated as emergent properties of local changes in sarcomere number, muscle fiber length, and fascicle length. Continuum modeling is a valuable tool to reveal the mechanisms behind skeletal muscle adaptation (Wisdom et al., 2014). Combined with the theory of finite growth (Ambrosi et al., 2011), the nonlinear field theories of mechanics provide high-resolution insight into local stretch concentrations in response to altered muscle kinematics (Böl and Reese, 2008). Multiscale models of finite growth correlate the global elastic stretch along the muscle fiber direction with the local sarcomere length (Böl et al., 2011). To maintain this length within its physiologically optimal regime, the local sarcomere number undergoes dynamic change, which translates globally into an inelastic stretch or growth (Göktepe et al., 2010). Previous models for cardiac muscle, the extensor digitorum, and the biceps brachii have successfully applied this concept to model positive growth associated with chronic muscle lengthening in dilated cardiomyopathy (Göktepe