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Biol. Lett. 2013 **9**, 20121045, published 19 December 2012

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Cite this article: Azizi E, Abbott EM. 2013 Anticipatory motor patterns limit muscle stretch during landing in toads. *Biol Lett* 9: 20121045.
<http://dx.doi.org/10.1098/rsbl.2012.1045>

Received: 6 November 2012

Accepted: 28 November 2012

Subject Areas:

biomechanics

Keywords:

force–length, landing, eccentric, hopping, motor control

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Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2012.1045> or via <http://rsbl.royalsocietypublishing.org>.

Physiology

Anticipatory motor patterns limit muscle stretch during landing in toads

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To safely land after a jump or hop, muscles must be actively stretched to dissipate mechanical energy. Muscles that dissipate energy can be damaged if stretched to long lengths. The likelihood of damage may be mitigated by the nervous system, if anticipatory activation of muscles prior to impact alters the muscle's operating length. Anticipatory motor recruitment is well established in landing studies and motor patterns have been shown to be modulated based on the perceived magnitude of the impact. In this study, we examine whether motor recruitment in anticipation of landing can serve a protective function by limiting maximum muscle length during a landing event. We use the anconeus muscle of toads, a landing muscle whose recruitment is modulated in anticipation of landing. We combine *in vivo* measurements of muscle length during landing with *in vitro* characterization of the force–length curve to determine the muscle's operating length. We show that muscle shortening prior to impact increases with increasing hop distance. This initial increase in muscle shortening functions to accommodate the larger stretches required when landing after long hops. These predictive motor strategies may function to reduce stretch-induced muscle damage by constraining maximum muscle length, despite variation in the magnitude of impact.

1. Introduction

The old adage 'what goes up, must come down' is not only an obvious reminder of the role gravity in shaping movement, but also highlights the fact that many muscle-powered movements often involve two distinct mechanical phases. To accelerate a body into the air, muscles function as motors by converting chemical energy into mechanical energy and allowing the body to move against the force of gravity. Muscles must then dissipate mechanical energy to decelerate the body during landing. Therefore, a simple hop requires muscles to act as both the motors and dampers of the body. This diversity in muscle function is a ubiquitous feature vertebrate movement, and one could argue that animals dissipate mechanical energy as often as they generate it. However, our understanding of how muscles operate during movement is largely shaped by their function as motors, whereas their function as dampers is less well understood.

One aspect of muscular energy dissipation that has received significant attention is the increased likelihood of muscle injury when muscles are actively stretched [1]. These lengthening (eccentric) contractions, which dissipate energy, can disrupt the cytoskeleton, causing soreness and a decrease in the muscle's capacity for force generation [2,3]. The likelihood of damage is thought to depend on the magnitude of stretch applied to muscles [4] or the amount of mechanical energy dissipated [5]. Although the exact mechanical factors that cause muscle damage are not broadly agreed upon, it is clear that the length at which muscles are actively stretched can significantly influence the severity of muscle damage [6–8]. Specifically, stretches applied at a relatively long

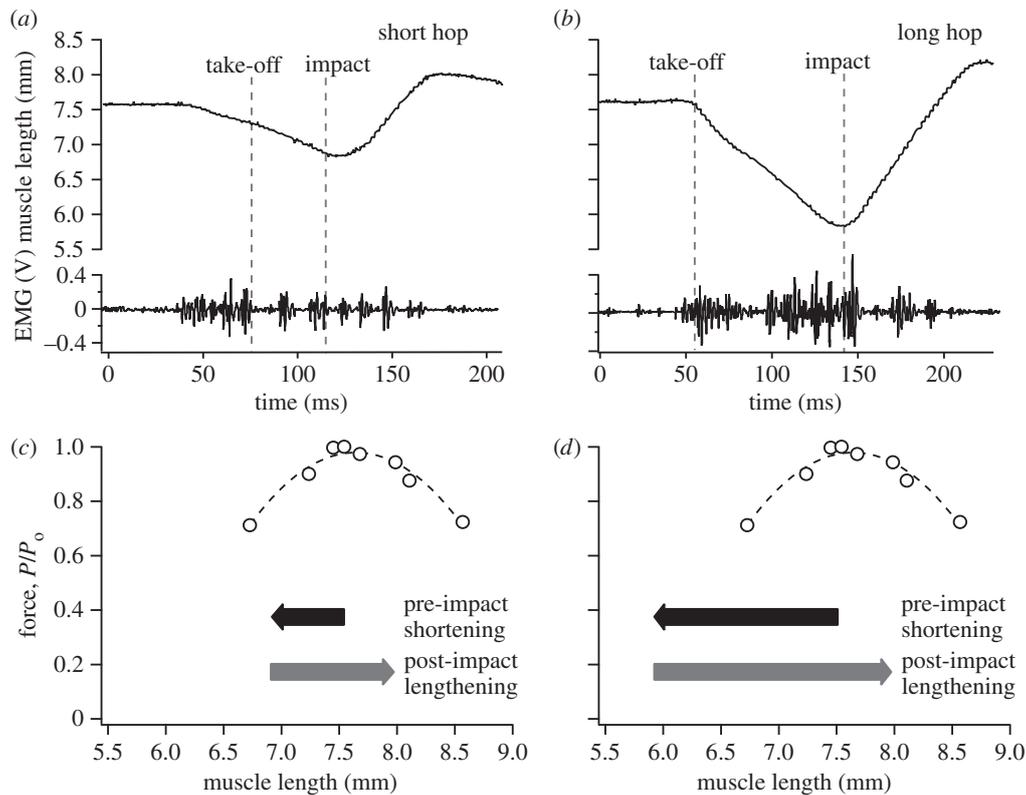


Figure 1. Muscle recordings and operating lengths during landing. Muscle length and EMG activity in the anconeus muscle during (a) short and (b) long hop. In both hops, EMG activity and muscle shortening precede impact. The time corresponding to the hindlimb leaving the ground (take-off) and forelimb touching down (impact) are also shown. (c,d) The operating lengths of the hops shown in (a,b) mapped onto the muscle's force–length curve. The force–length curve is normalized to maximum isometric force (P_0). Arrows only correspond to the length axis and show that despite the increased overall excursion associated with a long hop, the muscle reaches a similar maximum length during landing.

sarcomere length are significantly more damaging than the same stretch applied at a short sarcomere length.

Can anticipatory motor control strategies reduce the likelihood of eccentric muscle damage? Many studies of human landing behaviour have shown that muscles become active well in advance of impact with the ground (reviewed in Santello [9]). In addition, several studies have shown that the timing and intensity of motor patterns is modulated to match the height of the drop [10,11]. Such tuning of muscle activity in anticipation of impact is not limited to humans and has been documented in non-human primates [12], cats [13] and most recently in toads [14]. The anticipatory recruitment of landing muscles has thus far been considered a critical mechanism for stiffening joints and preventing the collapse of limbs at impact [15]. However, a complementary function of anticipatory muscle recruitment may be to alter the operating length of the muscle prior to an active stretch.

In this study, we test the hypothesis that modulation of motor activity prior to impact, functions to shorten muscle length, thereby accommodating the impending stretch and decreasing the likelihood of muscle damage. We use the anconeus muscle of toads (*Bufo marinus*), a primary elbow extensor, as an experimental model. This muscle has previously been shown to be recruited and modulated during hopping in this species [14]. We combine *in vivo* measurements of muscle length during landing with *in vitro* characterization of the muscle's force–length curve to quantify the operating length of the muscle. We use hop distance as a proxy for the amount of energy dissipated at landing, and predict that as hop distance increases, modulation of anticipatory motor patterns will serve a protective

function by limiting the maximum length of the muscle during active lengthening.

2. Material and methods

Five similarly sized (178–214 g) marine toads (*Bufo marinus*) were purchased from a herpetological vendor, fed vitamin enriched crickets ad libitum and housed in glass terraria.

Toads were anaesthetized (MS222), and sonomicrometry and electromyography (EMG) transducers were surgically implanted in the anconeus muscle. Once transducers were implanted, toads were allowed 24 h to recover. Fascicle length (sonomicrometry) and muscle activity (EMG) were recorded during bouts of hopping. Sonomicrometry data were collected using a Sonometrics UDG (Sonometrics Inc., Ontario, CA, USA). EMG signals were amplified 1000 \times (A-M systems, WA, USA). All data were collected at 4000 Hz using a 16-bit A/D converter (National Instruments, TX, USA). Hopping bouts were imaged laterally at 250 FPS using a high-speed camera (Vision Research, NJ, USA). All data were synchronized using a common external trigger.

Once hopping data were collected, the force–length relationship of the same anconeus muscle was quantified using an *in vitro* preparation. The toads were euthanized with a double-pithing protocol. The anconeus muscle along with its nerve (SN 2) was then dissected out. The previously implanted sonomicrometry transducers were left in place and used to measure fascicle lengths *in vitro*. This protocol allowed us to directly relate *in vivo* muscle lengths during landing to the force–length curve characterized *in vitro* (figure 1). Therefore, in contrast to many previous studies, we did not need to define a resting length [16]. In addition, the use of sonomicrometry allows us to measure the length of the fascicle independent of any length

changes occurring in the series-elastic element during 'isometric' contractions [17]. The muscle was rigidly clamped in place and attached to a dual-mode servomotor (Aurora Scientific Inc., Ontario, CA, USA) to measure muscle force. The preparation was placed in an aerated amphibian ringer's solution at 22°C. We used the isolated nerve to stimulate the muscle maximally at varying lengths to characterize its force-length properties. All contractile properties are shown in the electronic supplementary material, table S1.

All sonomicrometry, EMG and force data were processed and analysed according to Azizi & Roberts [17]. Data from high-speed video were used to determine the timing of take-off and landing as well as hop distance (see the electronic supplementary material, video S1). The force-length data were fitted according to Otten [18], allowing us to determine the peak isometric force (P_0) and the fascicle length at peak force (L_0). To statistically assess the effect of hop distance on muscle length changes, we used a mixed model ANOVA with individual as a random effect.

3. Results

Our results show that shortening of the anconeus muscle prior to landing is tuned to hop distance and, therefore, functions to protect the muscle from being actively stretched to long lengths during the landing phase. Similar to a previous study [14], we find that the anconeus muscle is recruited well in advance of impact (figure 1). This early recruitment extends the elbow in preparation for landing and alters the operating length of the muscle during the energy dissipation phase after impact (figure 1). We find that as hop distance increases, the muscles shorten more before impact ($p < 0.0001$; figure 2*a*), moving the muscle further onto the ascending limb of the force-length curve (figure 1). The increased shortening in anticipation of impact functions to accommodate the increased lengthening required for the larger impacts associated with longer hops. Consistent with this interpretation, the lengthening of the anconeus after impact increases significantly with hop distance ($p < 0.0001$; figure 2*b*). The anconeus does not get stretched significantly beyond the muscle's optimal length ($p = 0.324$), and the maximum length at the end of the landing phase does not vary significantly with hop distance ($p = 0.6623$; figure 2*c*).

4. Discussion

Our results suggest that motor control strategies associated with energy dissipating tasks can constrain the maximum operating length of the muscle. Data spanning a $2.5\times$ range in hop distance show that the anconeus muscle is not stretched significantly beyond its optimal length (figure 2*c*). The muscle reaches the same maximum length, despite the significant increase in amount of lengthening needed to dissipate energy during long hops (figure 2*b*). The constant upper limit in length is largely accommodated by the variation in muscle shortening prior to impact (figure 2*a*).

Avoiding the descending limb of the force-length curve can greatly reduce the likelihood of muscle damage [6,8]. Stretch-induced muscle damage is often associated with a decrease in the capacity for force production, which can be twice as severe when the muscle is stretched beyond its optimal length [8]. In fact, an active stretch of only 10 per cent initiated from a muscle's optimal length (L_0) can cause significant damage [8], suggesting that in the absence of anticipatory shortening even relatively short hops could

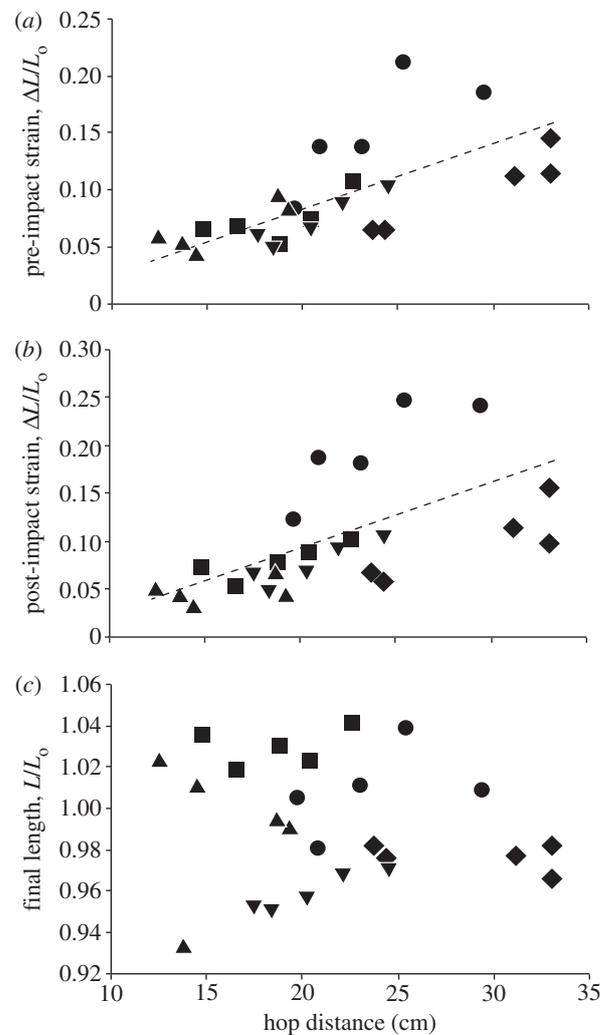


Figure 2. The effect of hop distance on the length changes and operating lengths of the anconeus. (a) The amount of muscle shortening before impact increases significantly with increasing hop distance ($R^2 = 0.44$). (b) The amount of muscle lengthening after impact increases significantly with increasing hop distance ($R^2 = 0.31$). (c) The maximum length of the muscle at the end of the landing event does not vary significantly with hop distance ($p = 0.662$).

result in muscle damage (figure 2*b*). However, the modulation of muscle shortening with hop distance suggests that shortening a muscle maximally prior to impact may bear a cost. The potential trade-off in this system is likely to be muscle force. Because operating on the ascending limb can result in lower forces, it is likely that muscle lengths are modulated to balance the safety of operating at short lengths with the cost of reduced force capacity.

The modulation of predictive motor patterns in advance of a motor task has been well established in studies of jump landing in humans [9]. Studies have shown that muscles become active prior to impact and that the nature of this pre-activation changes based on the height of the drop [10,11]. The pre-activation of muscles, specifically the co-contraction of antagonists, prior to impact is thought to function to stiffen the joints and may prevent limb collapse at impact [15]. The pre-activation of muscles may also function to increase the sensitivity of stretch receptors and prime the sensory feedback response of the limb after impact [9]. The results of this study highlight an additional

benefit of pre-activation prior to a landing impact. We show that anticipatory motor recruitment can also function to shift the operating length of the muscle, thereby allowing muscle stretches associated with landing to occur at relatively shorter and, therefore, safer lengths.

All husbandry and experimental procedures were approved by the IACUC at UC Irvine.

We thank Tom Roberts, Gary Gillis, Pooja Rana, Cally Harper and Nicole Danos. This study was supported by NSF grant no. 1051691.

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