

RESEARCH ARTICLE

Pre-landing wrist muscle activity in hopping toads

Laura J. Ekstrom^{1,*} and Gary B. Gillis²

ABSTRACT

Coordinated landing requires preparation. Muscles in the limbs important for decelerating the body should be activated prior to impact so that joints may be stiffened and limbs stabilized during landing. Moreover, because landings vary in impact force and timing, muscle recruitment patterns should be modulated accordingly. In toads, which land using their forelimbs, previous work has demonstrated such modulation in muscles acting at the elbow, but not at the shoulder. In this study, we used electromyography and high-speed video to test the hypothesis that antagonistic muscles acting at the wrists of toads are activated in advance of impact, and that these activation patterns are tuned to the timing and force of impact. We recorded from two wrist extensors: extensor carpi ulnaris (ECU) and extensor digitorum communis longus (EDCL), and two wrist flexors: flexor carpi ulnaris (FCU) and palmaris longus (PL). Each muscle was recorded in 4–5 animals (≥ 15 hops per animal). In all muscles, activation intensity was consistently greatest shortly before impact, suggesting the importance of these muscles during landing. Pre-landing recruitment intensity regularly increased with aerial phase duration (i.e. hop distance) in all muscles except PL. In addition, onset timing in both wrist flexors was also modulated with hop distance, with later onset times being associated with longer hops. Thus, activation patterns in major flexors and extensors of the wrist are tuned to hop distance with respect to recruitment intensity, onset timing or both.

KEY WORDS: Anuran, Landing, EMG

INTRODUCTION

Animals that jump must land, and the extent to which such landings are controlled, as well as the mechanisms underlying that control, have been the focus of a growing body of literature. At least two important themes have emerged from this work on the mechanics and neuromuscular control of landing. The first is that jumpers prepare for landing by activating limb muscles prior to impact, as demonstrated over 40 years ago in human subjects (Melvill Jones and Watt, 1971a,b). Often, such pre-activation is found in antagonistic muscles at a given joint, which, when simultaneously contracting, act to stiffen the joint (e.g. De Serres and Milner, 1991; McKinley and Smith, 1983; Santello, 2005). Such co-contractions and increased joint stiffening are important for preventing limb collapse in response to the forces encountered at impact and for allowing a controlled landing (Yeadon et al., 2010). A second theme to emerge is that of flexibility in the motor control strategy for landing. In humans and other mammalian model species, both the timing and intensity of preparatory, pre-landing muscle activity are

modulated with respect to the expected timing and force of impact (e.g. Prochazka et al., 1977; Santello and McDonagh, 1998).

More recently, Gillis et al. (2010) examined whether these themes were consistent with the landing behavior of a non-mammalian jumper, the cane toad *Bufo marinus* Linnaeus 1758, which decelerates its body after impact using its forelimbs exclusively. Studying antagonistic muscles acting at the elbow, they found preparatory electromyographic (EMG) activity as animals approached landing, and also demonstrated modulation in these patterns of muscle activity, with longer hops leading to more intense pre-landing EMG bursts occurring later with respect to take-off time (i.e. the onset of muscle activity is coupled more closely with landing time, rather than at a fixed interval after take-off). However, a subsequent study of various pectoral muscles acting across the shoulder joint revealed pre-landing activity that was not modulated consistently with hop distance (Akella and Gillis, 2011).

In this study, we explored motor patterns of antagonistic muscles that act at the wrist joint of hopping and landing toads. Co-contraction of antagonistic muscles is critical for increasing joint stiffness before impact (e.g. De Serres and Milner, 1991; McKinley and Smith, 1983; Santello, 2005), and in jumping humans, antagonists are used to stabilize the ankle joint and control its angle during landing (Santello and McDonagh, 1998). Because toads rely on their forelimbs for deceleration after impact, we predicted that they modulate wrist stiffness and stability in an analogous manner to the control of the ankle joint in jumping humans (Santello and McDonagh, 1998). Therefore, we tested the hypotheses that (i) the activity of antagonistic flexor and extensor muscles acting at the wrist is present and intense shortly before impact, and (ii) the intensity of this activity is modulated predictably with hop distance and thus the force of impact (Nauwelaerts and Aerts, 2006). Specifically, we quantified the onset timing and intensity of pre-landing activity in two extensors [extensor carpi ulnaris (ECU) and extensor digitorum communis longus (EDCL)] and two flexors [flexor carpi ulnaris (FCU) and palmaris longus (PL)] (Fig. 1), which together control major wrist movements. We predicted that longer hops lead to later and more intense pre-landing EMG activity in wrist flexors and extensors, as previously shown in human limb muscles (Santello, 2005) and in antagonistic muscles at the elbow in toads (Gillis et al., 2010).

RESULTS

We analyzed 239 hops from 10 individuals (Table 1), ranging from 4 to 254 ms in aerial phase duration. We collected data from 106 hops for the EDCL in five animals, 94 hops for the ECU in four animals, 113 hops for the FCU in four animals and 130 hops for the PL in five animals (Table 1). Simultaneous recordings from multiple muscles (maximum of four) were made from multiple individuals. Preparation for landings always involved forelimb protraction and wrist extension (Fig. 2C). The toad touches down initially with its first digit, followed by the rest of the manus (Fig. 2D,E). After impact, the elbow flexes and the wrist extends as the body and legs of the toad land. All muscles were active prior to

¹Biology Department, Wheaton College, Norton, MA 02038, USA. ²Department of Biological Sciences, Mount Holyoke College, South Hadley, MA 01075, USA.

*Author for correspondence (ekstrom_laura@wheatoncollege.edu)

Received 15 September 2014; Accepted 19 May 2015

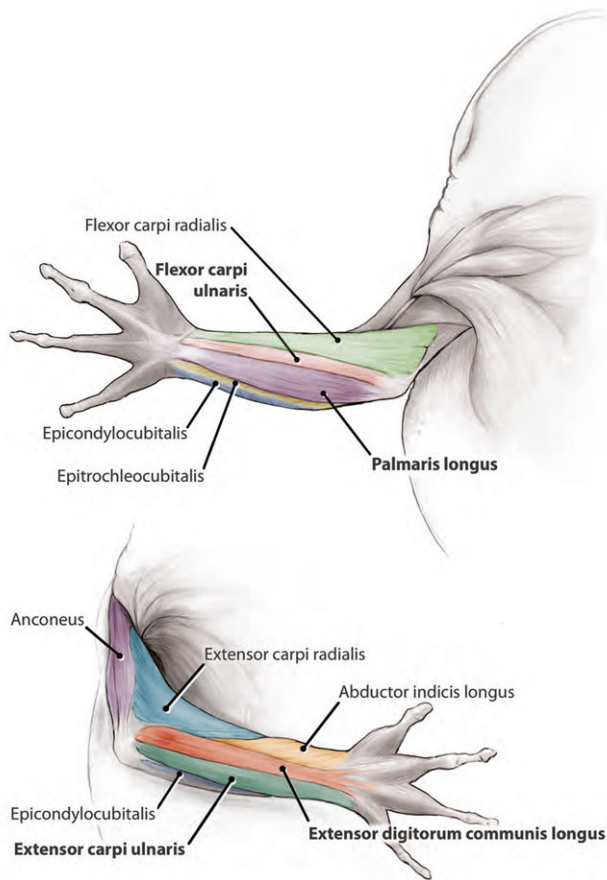


Fig. 1. Toad arm from the ventral perspective, positioned to show the flexor compartment (top) and the extensor compartment (bottom) of the forearm. Muscles studied are labeled in bold. Other forearm muscles are also shown.

and during landing (Fig. 3). Typically, the EDCL was activated first (97 ± 54 ms after hop onset, mean \pm s.d.), followed by the ECU (152 ± 42 ms after hop onset), the PL (167 ± 53 ms after hop onset) and the FCU (184 ± 39 ms after hop onset) (Fig. 3). All muscles demonstrated activity timing that began, on average, at least 50 ms

Table 1. Contribution of individual toads to overall hops per muscle examined

Muscle	Total hops	Toad ID	No. of hops
EDCL	106	A	24
		B	19
		C	15
		D	22
		E	26
ECU	94	B	19
		C	15
		F	22
		G	38
FCU	113	A	24
		G	38
		H	18
		I	33
PL	130	D	22
		E	22
		F	26
		G	38
		J	22

EDCL, extensor digitorum communis longus; ECU, extensor carpi ulnaris; FCU, flexor carpi ulnaris; PL, palmaris longus.

prior to landing (EDCL 62 ± 15 ms, ECU 77 ± 37 ms, PL 62 ± 15 ms, FCU 57 ± 18 ms).

Extensors

For the ECU, we found that only one of the four animals displayed a significant positive relationship between the timing of muscle onset and the duration of the aerial phase (Fig. 4A: $R^2=0.62$, $P<0.01$). In contrast, three animals displayed a significant relationship between pre-landing recruitment intensity and the duration of the aerial phase (Fig. 4B: $R^2=0.28$, $P<0.05$; $R^2=0.64$, $P<0.01$; $R^2=0.34$, $P<0.01$). Specifically, by measuring the integrated signal prior to forelimb touch-down (iEMG), muscles were shown to be activated more intensely prior to impact during hops with longer aerial phases. In the EDCL, none of the five animals displayed a significant relationship between either the timing of muscle onset (Fig. 4C) or the pre-landing recruitment intensity and the duration of the aerial phase (Fig. 4D).

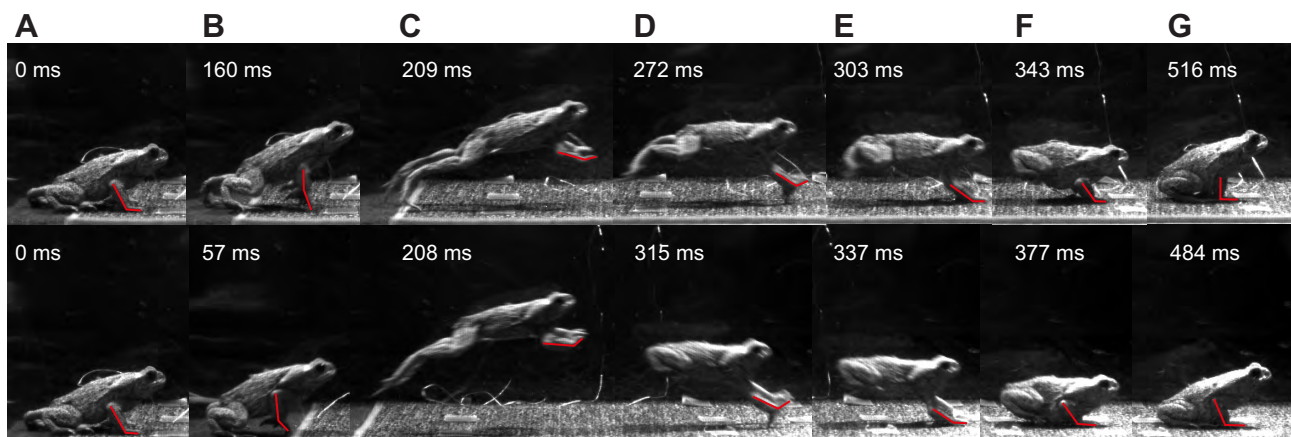


Fig. 2. Typical forearm movements during short (top row) and long (bottom row) hops. (A) Onset of movement, (B) flexion of wrist during take-off, (C) forelimb protraction and wrist extension in early preparation for landing, (D) initial impact with the first digit, (E) flexion of the wrist as the rest of the manus contacts the ground, (F) elbow flexion and wrist extension as the rest of the body lands, (G) recovery. Red lines trace the radioulna of the forearm and the manus to illustrate approximate 2D wrist angles.

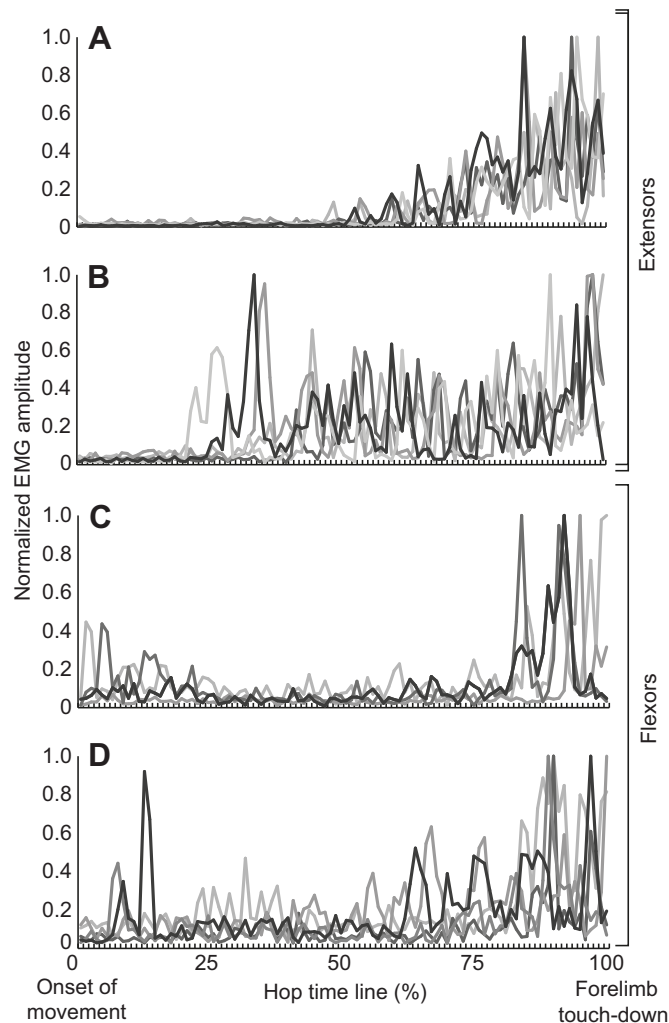


Fig. 3. Representative normalized, rectified EMG traces of five hops from each muscle to highlight the typical timing of activity. (A) Extensor carpi ulnaris (ECU), (B) extensor digitorum communis longus (EDCL), (C) flexor carpi ulnaris (FCU) and (D) palmaris longus (PL). Raw EMGs were downsampled to normalize to 100% of the hop duration. Note that all muscles are active prior to impact and intensity is typically greatest shortly before forelimb touch-down. The y-axis is scaled to the maximum EMG amplitude observed in each hop.

Flexors

Four of the five animals displayed significant positive relationships between the timing of PL onset and the duration of the aerial phase (Fig. 5A: $R^2=0.44$, $P<0.01$; $R^2=0.18$, $P<0.05$; $R^2=0.35$, $P<0.01$; $R^2=0.68$, $P<0.01$). Specifically, PL onset occurred later during longer hops. Four animals displayed significant relationships between pre-landing recruitment intensity in the PL and the duration of the aerial phase (Fig. 5B: $R^2=0.48$, $P<0.01$; $R^2=0.31$, $P<0.01$; $R^2=0.19$, $P<0.05$; $R^2=0.65$, $P<0.01$). All four animals examined for FCU activity displayed a significant relationship between onset timing and aerial phase duration (Fig. 5C: $R^2=0.25$, $P<0.05$; $R^2=0.28$, $P<0.05$; $R^2=0.47$, $P<0.01$; $R^2=0.39$, $P<0.01$). Two animals demonstrated tuned pre-landing recruitment intensity (Fig. 5D: $R^2=0.41$, $P<0.01$; $R^2=0.13$, $P<0.05$).

DISCUSSION

This study was designed to test whether antagonistic muscles acting at the wrists of cane toads exhibit predictable changes in pre-landing

activity patterns with hop distance. As found in muscles acting at the elbow joint (Gillis et al., 2010), our work demonstrates distance-dependent anticipatory activity in wrist flexors and extensors in preparation for landing. Most muscles tested exhibit tuned lengths, amplitude or both in response to hops of varying lengths. Comparable to the strategy employed by jumping humans (e.g. Santello, 2005) and other mammals studied to date (Dyhre-Poulsen and Laursen, 1984; Prochazka et al., 1977), toads modulate forelimb muscle recruitment to match the timing and/or force of impact experienced during hops of different length. The finding that both flexors and extensors are activated prior to landing and are tuned simultaneously suggests their importance in stabilizing the wrist joint at impact. Indeed, a lack of tuning of leg muscles in humans prior to impact can result in a lack of coordination or tissue damage (Fu and Hui-Chan, 2007; Nigg and Liu, 1999).

Both extensors (ECU and EDCL) and flexors (FCU and PL) are activated prior to impact, suggesting their potential for playing important functional roles in landing. Of these muscles, the PL, the FCU and its antagonist, the ECU, all regularly display tuned pre-landing activation patterns with respect to onset timing, intensity or both. Pre-landing activity in the EDCL begins earlier, on average, than in the other three muscles, and is not generally modulated with hop length. Perhaps instead of playing an important role in stabilization at impact, it is more critical for in-air positioning of the manus and digits before landing, a role also ascribed to several muscles acting at the elbow and shoulder of hopping cane toads (Akella and Gillis, 2011; Gillis et al., 2010). In both flexors, some activity is occasionally observed early in the hop (Fig. 3). These muscles may be employed to adjust the animal's posture or augment propulsive forces during take-off as has been demonstrated in several ranid species (Essner et al., 2005a,b; Wang et al., 2014). Though the propulsive component of anuran jumping is powered almost exclusively by the hindlimbs (e.g. Marsh, 1994; Nauwelaerts and Aerts, 2006; Peters et al., 1996), forelimbs can be used to lift the center of mass during the take-off phase (Wang et al., 2014).

Given that both flexors, but only one extensor, demonstrate tuning prior to landing, there is likely an imbalance between the flexor and extensor contributions to stabilizing impact. At impact, forces act to extend the wrist, and thus perhaps it is not surprising that the activation patterns in the wrist flexors studied are modulated with distance to counteract variable landing forces and dissipate the animal's potential and kinetic energy via eccentric, or lengthening, contractions (see Azizi and Abbott, 2013). In contrast, actions of extensors before and after impact probably involve important roles in limb positioning and joint stabilization, respectively. Such functional distinctions between extensors and flexors have also been attributed to distal limb muscles of mammals, where those on one side of a joint are responsible for energy absorption and stiffness control, whereas their antagonists are involved mainly in joint stabilization and limb positioning (Burkhart and Andrews, 2013; Hobara et al., 2007; Iida et al., 2011; Minetti et al., 1998; Santello, 2005; Yeadon et al., 2010). Our future investigation of the relative physiological cross-sectional area (PCSA) as well as the moment arms of these muscles will provide us with clearer, more definitive answers with respect to this potential imbalance of joint torques generated by flexors and extensors during landing.

Our research demonstrates that flexors and extensors of the wrist are co-activated prior to impact in cane toads, suggesting their importance in controlling landing in these highly mobile, terrestrial anurans. This work has focused exclusively on hops in which movement is completed upon landing. However, these animals often cover longer distances by performing multiple hops in

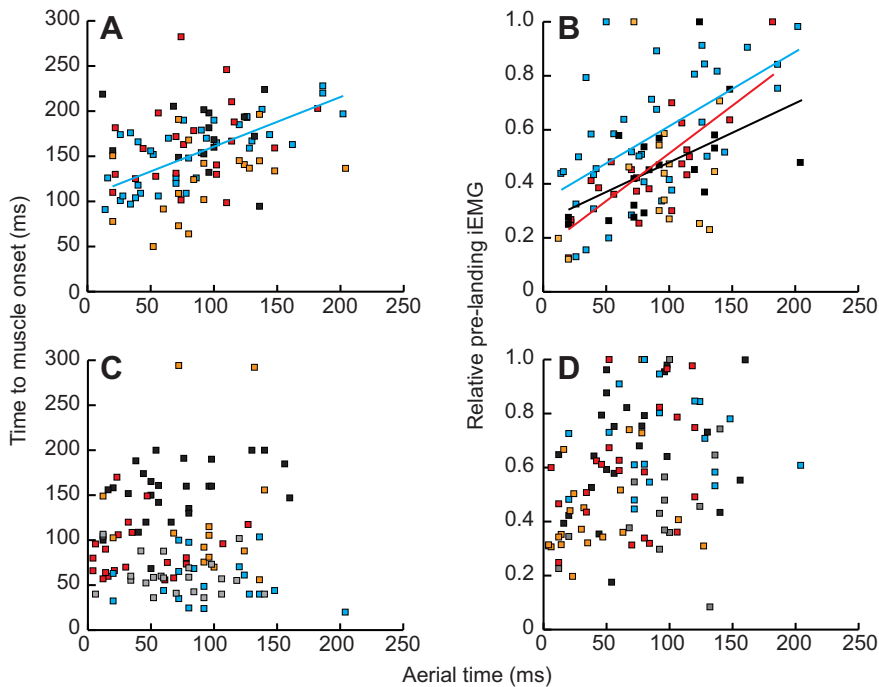


Fig. 4. Plots of pre-landing EMG timing and intensity (iEMG) in the wrist extensors in relation to hop aerial time. (A,B) ECU; (C,D) EDCL. Different colors represent different animals. Lines indicate significant relationships ($P < 0.05$) for individual animals.

succession. Their cyclic bounding locomotion has recently been described as energetically economical when compared with single hops (Reilly et al., 2015). This reduction in energy expenditure may be as a result of elastic energy cycling (Reilly et al., 2015). Other research has shown that energy absorption within muscle and tendon – especially at the most distal joint of a landing limb, can change depending on the follow-up movement or lack thereof (Ambegaonkar et al., 2011; Biewener et al., 1998). Both pre-landing and post-landing muscle activation can differ when a planned subsequent activity is performed immediately after impact (Ambegaonkar et al., 2011). Moreover, tendon and aponeurosis, both of which are seen at the wrist and elbow (Fig. 1), also exhibit a range of actions depending on the animal's

activity, such that a full deceleration can result in power attenuation in order to protect the muscle during lengthening contractions, whereas continuous hopping can result in power amplification to conserve energy (Azizi and Roberts, 2009; Konow et al., 2012; Roberts and Azizi, 2010, 2011; Tilp et al., 2012). The recent finding that the forelimbs, and not just the hindlimbs, are involved in force production during hopping (Wang et al., 2014) suggests that both of these scenarios may be present depending on the animal's activity. Therefore, to further explore how muscle and connective tissue at the wrist contribute to energy absorption and/or generation, we plan to investigate their actions under both continuous hopping and full deceleration conditions.

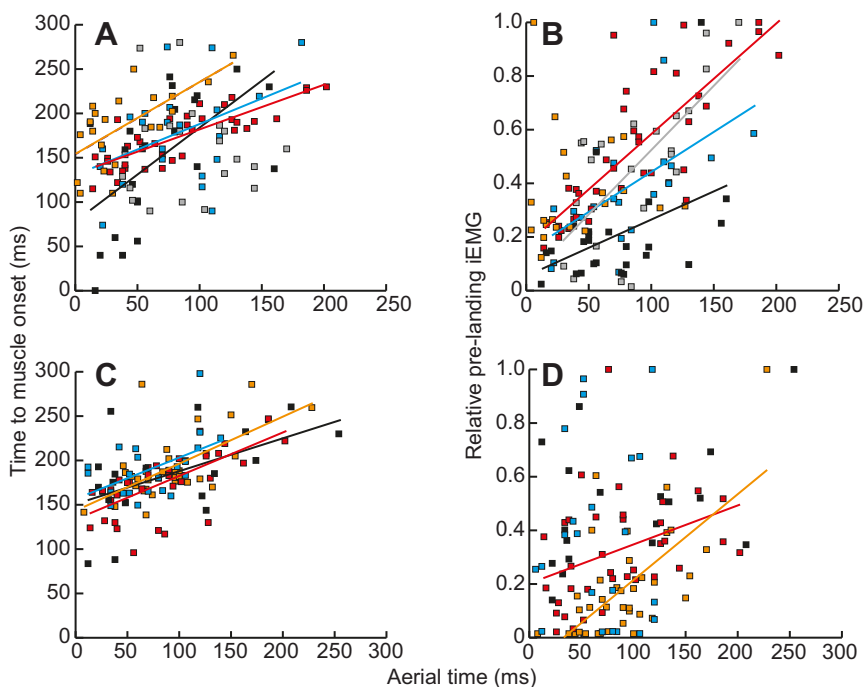


Fig. 5. Plots of pre-landing EMG timing and intensity (iEMG) in the wrist flexors in relation to hop aerial time. (A,B) PL; (C,D) FCU. Different colors represent different animals. Lines indicate significant relationships ($P < 0.05$) for individual animals.

MATERIALS AND METHODS

Animals

Ten cane toads, *B. marinus* (137.3±19.3 g), were obtained from a commercial supplier and housed in 80 l plastic containers (three toads per container) at approximately 24°C with 12 h light:12 h dark light cycles. The toads were fed crickets and mealworms and were provided with fresh water daily. All experimental work was approved by the IACUC at Mount Holyoke College.

Electromyography experiments

To investigate antagonistic muscle activity at the wrist, we studied two wrist extensors (ECU, EDCL) and two wrist flexors (FCU, PL) (Fig. 1).

Animals were anesthetized in a 1 l tricaine methanesulfonate (MS-222, 1.4 g l⁻¹) and sodium bicarbonate solution (1.4 g l⁻¹) until they were unresponsive (15–25 min). Once toads were anesthetized, we made skin incisions by scalpel along the forearm to reveal the muscles of interest. We then implanted fine-wire bipolar electrodes into the muscles (maximum of four per animal) using a 23-gauge needle, and sutured (6.0 silk) the electrodes to the surface of the muscle near the site of entry. The electrodes were made by twisting together two silver wires (0.1 mm diameter), stripping the insulation from the tips and offsetting them by 0.5 mm. We sutured the skin incisions shut using 4.0 silk, bonded the electrodes together with model cement, and sutured the electrode bundle onto the animal's back.

The free ends of the electrodes were soldered into connectors, whose wires carried signals to Grass P511 pre-amplifiers. The signals (amplified 1000×, high pass filter 3000 Hz, low pass filter 100 Hz) were filtered to eliminate 60 Hz noise and were digitized at 5000 Hz using a Digidata 1322A 16-bit A/D converter (Axon Instruments), and saved to a computer.

Once the toads recovered from anesthesia, we placed them in a glass terrarium (89×43×43 cm) with a plywood base covered in felt for traction. The terrarium was lit using 500 W lights to enable filming of a lateral view of the toads using a Photron Fast-Cam (500 frames s⁻¹, 1280×512 pixel resolution). We placed a toad at one end of the terrarium and encouraged it to jump using light taps, claps or voices. We recorded jumps of varying distance and synchronized video data with EMG signals using a 5 V trigger that stopped video recording and marked the event on the EMG recordings. After recording at least 15 hops of a variety of distances, we killed the toads by overnight submersion in MS-222 (1.4 g l⁻¹). We dissected the toads 24 h post mortem to confirm electrode placement.

Data analysis

Video of the hops was analyzed in ImageJ (Schneider et al., 2012) to determine the time of hop movement onset, take-off (when hindlimbs leave the ground) and touch-down (when forelimbs make contact). Aerial time was calculated as the difference between take-off and touch-down, and was used as a surrogate for hop length (in toads, aerial phase duration and hop length are tightly correlated; Gillis and Biewener, 2000). From rectified EMG traces, we obtained (i) pre-landing intensity and (ii) onset timing. Pre-landing intensity was calculated as the area under the curve (integrated EMG, iEMG) from the onset of muscle activity to forelimb touch-down using a custom-written MATLAB script (MATLAB R2012b, Mathworks, Natick, MA, USA). To compare trends among individuals, pre-landing intensities within an individual were normalized by scaling each value to that individual's maximum value. Onset timing of muscle activity was identified visually as the beginning of a burst of activity that occurred after take-off and prior to touch-down. This variable is reported as the time in ms after hop movement onset. For each muscle in each animal, we regressed pre-landing intensity and onset timing against aerial phase duration (SPSS Statistics 20, Chicago, IL, USA). Relationships were considered significant if $P < 0.05$.

Acknowledgements

The authors thank Rebecca Hicks and Hilary Katz for help with experimental procedures. Anneliese Lilienthal provided the illustration for Fig. 1.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Both authors contributed to the conception, design and execution of the experiments, as well as the interpretation of the findings and drafting the manuscript. L.J.E. performed data analysis and prepared the figures.

Funding

This work was supported by the National Science Foundation [grant number 1051603 to G.B.G.]. L.J.E. was supported by the Howard Hughes Medical Institute (HHMI) [grant number 52006307 to Mount Holyoke College].

References

- Akella, T. and Gillis, G. B. (2011). Hopping isn't always about the legs: forelimb muscle activity patterns during toad locomotion. *J. Exp. Zool. A Ecol. Genet. Physiol.* **315A**, 1–11.
- Ambegaonkar, J. P., Shultz, S. J. and Perrin, D. H. (2011). A subsequent movement alters lower extremity muscle activity and kinetics in drop jumps vs. drop landings. *J. Strength Cond. Res.* **25**, 2781–2788.
- Azizi, E. and Abbott, E. M. (2013). Anticipatory motor patterns limit muscle stretch during landing in toads. *Biol. Lett.* **9**, 20121045.
- Azizi, E. and Roberts, T. J. (2009). Biaxial strain and variable stiffness in aponeuroses. *J. Physiol.* **587**, 4309–4318.
- Biewener, A., Konieczynski, D. and Baudinette, R. (1998). In vivo muscle force-length behavior during steady-speed hopping in tammar wallabies. *J. Exp. Biol.* **201**, 1681–1694.
- Burkhardt, T. A. and Andrews, D. M. (2013). Kinematics, kinetics and muscle activation patterns of the upper extremity during simulated forward falls. *J. Electromyogr. Kinesiol.* **23**, 688–695.
- De Serres, S. J. and Milner, T. E. (1991). Wrist muscle activation patterns and stiffness associated with stable and unstable mechanical loads. *Exp. Brain Res.* **86**, 451–458.
- Dyhre-Poulsen, P. and Laursen, A. M. (1984). Programmed electromyographic activity and negative incremental muscle stiffness in monkeys jumping downward. *J. Physiol.* **350**, 121–136.
- Essner, R. L., Nauwelaerts, S. and Rome, L. C. (2005a). Forelimb function during takeoff in *Rana pipiens*. *Comp. Biochem. Physiol. A* **141**, S152.
- Essner, R. L., Nauwelaerts, S. and Rome, L. C. (2005b). Forelimb and caudopelvic function during take-off in *Rana pipiens*. *Integr. Comp. Biol.* **45**, 993.
- Fu, S. N. and Hui-Chan, C. W. Y. (2007). Are there any relationships among ankle proprioception acuity, pre-landing ankle muscle responses, and landing impact in man? *Neurosci. Lett.* **417**, 123–127.
- Gillis, G. B., Akella, T. and Gunaratne, R. (2010). Do toads have a jump on how far they hop? Pre-landing activity timing and intensity in forelimb muscles of hopping *Bufo marinus*. *Biol. Lett.* **6**, 486–489.
- Gillis, G. B. and Biewener, A. A. (2000). Hindlimb extensor muscle function during jumping and swimming in the toad (*Bufo marinus*). *J. Exp. Biol.* **203**, 3547–3563.
- Hobara, H., Kanosue, K. and Suzuki, S. (2007). Changes in muscle activity with increase in leg stiffness during hopping. *Neurosci. Lett.* **418**, 55–59.
- Iida, Y., Kanehisa, H., Inaba, Y. and Nakazawa, K. (2011). Activity modulations of trunk and lower limb muscles during impact-absorbing landing. *J. Electromyogr. Kinesiol.* **21**, 602–609.
- Konow, N., Azizi, E. and Roberts, T. J. (2012). Muscle power attenuation by tendon during energy dissipation. *Proc. R. Soc. B Biol. Sci.* **279**, 1108–1113.
- Marsh, R. L. (1994). Jumping ability of anuran amphibians. *Adv. Vet. Sci. Comp. Med.* **38**, 51–111.
- McKinley, P. A. and Smith, J. L. (1983). Visual and vestibular contributions to prelanding EMG during jump-downs in cats. *Exp. Brain Res.* **52**, 439–448.
- Melville Jones, G. and Watt, D. G. D. (1971a). Observations on the control of stepping and hopping movements in man. *J. Physiol.* **219**, 709–727.
- Melville Jones, G. and Watt, D. G. D. (1971b). Muscular control of landing from unexpected falls in man. *J. Physiol.* **219**, 729–737.
- Minetti, A. E., Ardigo, L. P., Susta, D. and Cotelli, F. (1998). Using leg muscles as shock absorbers: theoretical predictions and experimental results of drop landing performance. *Ergonomics* **41**, 1771–1791.
- Nauwelaerts, S. and Aerts, P. (2006). Take-off and landing forces in jumping frogs. *J. Exp. Biol.* **209**, 66–77.
- Nigg, B. M. and Liu, W. (1999). The effect of muscle stiffness and damping on simulated impact force peaks during running. *J. Biomech.* **32**, 849–856.
- Peters, S. E., Kamel, L. T. and Bashor, D. P. (1996). Hopping and swimming in the leopard frog, *Rana pipiens*: I. Step cycles and kinematics. *J. Morphol.* **230**, 1–16.
- Prochazka, A., Schofield, P., Westerman, R. A. and Ziccone, S. P. (1977). Reflexes in cat ankle muscles after landing from falls. *J. Physiol.* **272**, 705–719.
- Reilly, S. M., Montuelle, S. J., Schmidt, A. Naylor, E., Jorgensen, M. E., Halsey, L. G. and Essne, R. L., Jr. (2015). Conquering the world in leaps and bounds: hopping locomotion in toads is actually bounding. *Funct. Ecol.* doi:10.1111/1365-2435.12414
- Roberts, T. J. and Azizi, E. (2010). The series-elastic shock absorber: tendons attenuate muscle power during eccentric actions. *J. Appl. Physiol.* **109**, 396–404.

- Roberts, T. J. and Azizi, E.** (2011). Flexible mechanisms: the diverse roles of biological springs in vertebrate movement. *J. Exp. Biol.* **214**, 353-361.
- Santello, M.** (2005). Review of motor control mechanisms underlying impact absorption from falls. *Gait Posture* **21**, 85-94.
- Santello, M. and McDonagh, M. J.** (1998). The control of timing and amplitude of EMG activity in landing movements in humans. *Exp. Physiol.* **83**, 857-874.
- Schneider, C. A., Rasband, W. S. and Eliceiri, K. W.** (2012). NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* **9**, 671-675.
- Tilp, M., Steib, S. and Herzog, W.** (2012). Length changes of human tibialis anterior central aponeurosis during passive movements and isometric, concentric, and eccentric contractions. *Eur. J. Appl. Physiol.* **112**, 1485-1494.
- Wang, Z., Ji, A., Endlein, T., Samuel, D., Yao, N., Wang, Z. and Dai, Z.** (2014). The role of fore- and hindlimbs during jumping in the Dybowski's frog (*Rana dybowskii*). *J. Exp. Zool. A. Ecol. Genet. Physiol.* **321**, 324-333.
- Yeadon, M. R., King, M. A., Forrester, S. E., Caldwell, G. E. and Pain, M. T. G.** (2010). The need for muscle co-contraction prior to a landing. *J. Biomech.* **43**, 364-369.