



## SYMPOSIUM

### Biomechanics and Control of Landing in Toads

Gary Gillis,<sup>1,\*</sup> Laura Ekstrom<sup>†</sup> and Emanuel Azizi<sup>‡</sup>

<sup>\*</sup>Department of Biological Sciences, Mount Holyoke College, South Hadley, MA 01075, USA; <sup>†</sup>Department of Biology, Wheaton College, Norton, MA 02766, USA; <sup>‡</sup>Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697, USA

From the symposium “Terrestrial Locomotion: Where do we stand, where are we going?” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2014 at Austin, Texas.

<sup>1</sup>E-mail: ggillis@mtholyoke.edu

**Synopsis** Anything that jumps must land, but unlike during jumping when muscles produce energy to accelerate the body into the air, controlled landing requires muscles to dissipate energy and decelerate the body. Among anurans, toads (genus *Bufo*) exhibit highly coordinated landing behaviors, using their forelimbs to stabilize the body after touch-down as they lower their hindlimbs to the ground. Moreover, toads land frequently, as they cover distances by stringing together long series of relatively short hops. We have been using toads as a model to understand the biomechanics and motor control strategies of coordinated landing. Our results show that toads prepare for landing differently depending on how far they hop. For example, the forelimbs are extended farther prior to impact after long hops than after short ones. Such kinematic alterations are mirrored by predictable modulation of the recruitment intensity of forelimb muscles before impact, such that longer hops lead to higher levels of pre-landing recruitment of muscles. These differences in kinematics and muscular activity help to control the most flexed configuration of the elbow that is achieved after impact, which in turn constrains the extent to which muscles involved in dissipating energy are stretched. Indeed, a combination of *in vivo* and *in vitro* experiments has shown that the elbow-extending anconeus muscle, which is stretched during landing as the elbow flexes, rarely reaches lengths longer than those on the plateau of the muscle’s length–tension curve (where damage becomes more likely). We have also been studying how movements of the hindlimbs after take-off help to stabilize animals during landing. In particular, the immediate and rapid flexion of a toad’s knees after take-off leads to a repositioning of the animal’s center of mass (COM) that better aligns it with ground-reaction forces (GRFs) at impact and reduces torques that would destabilize the animal. Finally, recent work on sensory feedback involved in preparation for landing demonstrates that vision is not required for coordinated landing. Toads can effectively utilize proprioceptive and/or vestibular information during take-off to help inform themselves about landing conditions, but may also use other sensory modalities after take-off to modulate landing behavior.

#### Introduction

Terrestrial locomotion requires organisms to transition from periods of producing mechanical energy to periods of dissipating it. To increase velocity, jump into the air, or ascend an incline, an organism needs to increase the mechanical energy of its body. In contrast, decelerating, running downhill, or landing from a jump requires the organism to dissipate mechanical energy. Such transitions between the production and dissipation of energy can even be extended to specific phases of steady-speed, level running in which the impact or collision of the limb against the substrate acts to dissipate energy

and decelerate the center mass over the first half of stance, whereas the second half of stance is characterized by increases in kinetic and potential energy as the body re-accelerates. Nevertheless, despite the ubiquity of dissipating energy during terrestrial locomotion, studies of walking, running, and hopping largely have focused on the energy-producing phases of the gait.

Among the energy-dissipating tasks, landing provides a unique opportunity to relate a mechanically simple event both with sensory and motor aspects of energy dissipation. Much of our current understanding of landing comes from studies of humans

jumping and dropping down from varying elevations (reviewed by Santello [2005]). These studies have consistently revealed that the sensory system informs the behavior of the musculoskeletal system in anticipation of impact (Santello et al. 2001). In fact, most studies have shown that muscles involved in landing are well prepared for, and tuned to, the timing and magnitude of an impending impact (Santello and McDonagh 1998). This type of anticipatory preparation for impact has also been demonstrated in a variety of other animal species (e.g., Prochazka et al. 1979; Dyhre-Poulsen and Laursen 1984; Konow et al. 2012) and is thought to be an important mechanism that protects the musculoskeletal system from injury.

Tuning motor patterns in anticipation of landing from a jump may be particularly important for organisms that are specialized for using jumping or hopping as a primary means of locomotion. Anurans (frogs and toads) are the most specialized vertebrate jumpers and it is likely that sensorimotor integration for landing is particularly important for some of the members in this group. Among anurans, toads (genus *Bufo*) move by stringing together many consecutive hops in which coordinated landings are an essential component of smooth, efficient locomotion. Toads are outstanding at landing, using their forelimbs exclusively to decelerate and stabilize the body after impact as they lower their hindlimbs to the ground. This is in contrast to other anurans such as ranid frogs, in which landings can appear clumsy and often end with the torso crashing into the substrate (Nauwelaerts and Aerts 2006).

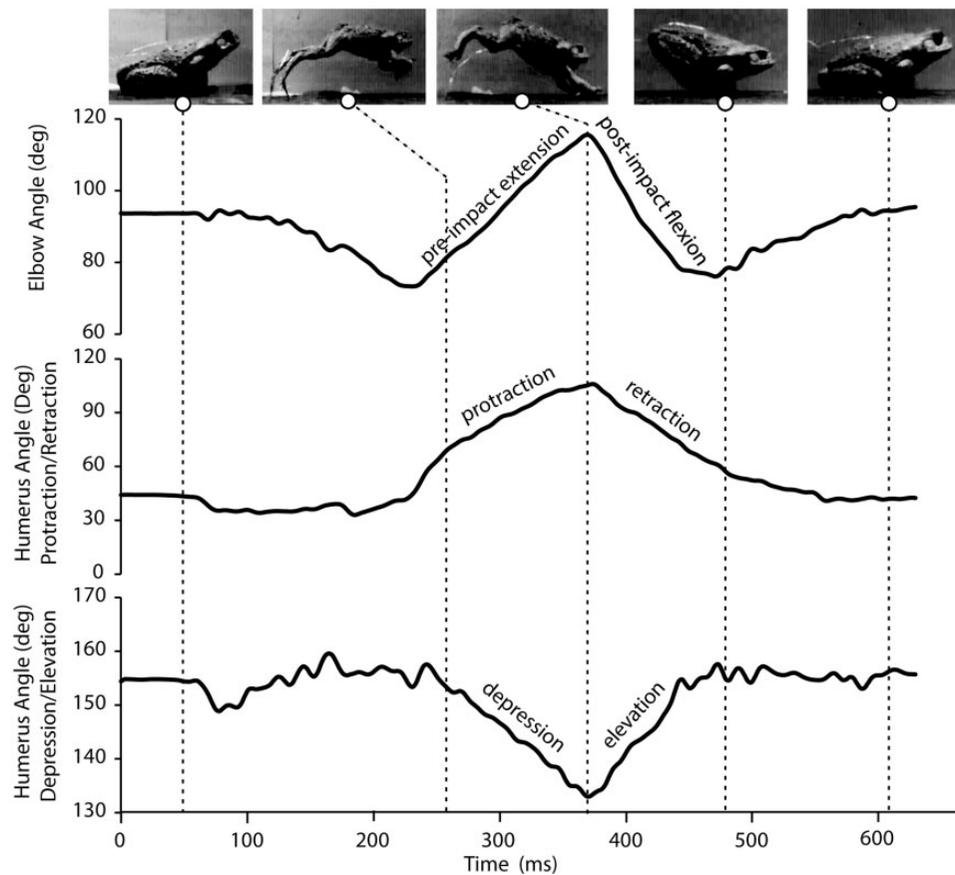
What makes toads so good at landing? Work by Emerson (1983) contrasted the pectoral girdle's functional anatomy between bufonids and ranids, and was followed up last year with a study by Griep et al. (2013) of the toad's pectoral girdle and shoulder dynamics during landing. We have been focusing distal to the pectoral girdle on what toads do with the rest of their forelimbs after take-off and during landing. We use this review as an opportunity to compile and share recent results that show how changes in strategies of motor control may alter the kinematics of toads' elbow joints and control the operating lengths of elbow extensor muscles after impact. We also examine how shifts in hindlimb posture in mid-air likely help to increase stability during landing. Finally, we assess the contributions of various sensory modalities in shaping the tuned, controlled landing behavior of toads. Using toads as a model system, we have been able to integrate biomechanics, muscle physiology, and sensory biology to better understand the fundamental principles governing controlled deceleration.

## Kinematics of limbs during hopping and landing

The take-off phase of anuran jumping has been well described for a variety of species with respect to the mechanics, muscular activity, and actions of the limbs used to drive the body into the air (reviewed by Marsh 1994). A typical jump begins with the animal resting on its hindlimbs, which are flexed and folded underneath it. Nearly simultaneous activation of hindlimb extensors leads to a rapid unfolding, or extension, of the hindlimbs until the animal is propelled into the air (e.g., Lutz and Rome 1994; Kamel et al. 1996; Olson and Marsh 1998; Gillis and Biewener 2000). In mid-air, the hindlimbs typically flex back toward the body, whereas the forelimbs are moved anteriorly in anticipation of landing (e.g., Emerson 1983; Peters et al. 1996; Nauwelaerts and Aerts 2006; Gillis et al. 2010). In this section, we outline the basic movement patterns of the hindlimbs and forelimbs of toads during hopping and landing.

### Kinematics of the hindlimbs

Given the role of hindlimb muscles as the primary producers of power for jumping, it is not surprising that hindlimb function during take-off has been studied extensively. However, what happens after take-off, even with the hindlimbs, is not yet very well understood. In one of the most primitive extant anurans, the tailed frog *Ascaphus montanus*, the hindlimbs remain extended throughout the entire flight-phase and are not recovered into a flexed configuration until well after landing (Essner et al. 2010). In other anuran species, the hindlimbs begin to flex roughly midway through the aerial phase in preparation for impact (Peters et al. 1996; Essner et al. 2010), thereby allowing animals to be ready to hop again shortly after landing. In toads, for whom coordinated landing is commonplace, the hindlimbs are immediately flexed after take-off (Gallardo et al. 2014). We have used angular excursions of the knee joint to characterize patterns of hindlimb flexion after take-off, and the amount of flexion at the knee during the recovery phase of the limb (as well as the amount and rate of knee-extension during take-off) increase with the distance hopped (hereafter "hop-distance") (Gallardo et al. 2014). The importance of this immediate and rapid flexion of the hindlimbs after take-off in toads, as well as its potential mechanism, is covered in more detail in a later section on stability and body mechanics.



**Fig. 1** Representative forelimb kinematic patterns taken from a single toad hop. As toads prepare for impact, a series of movements is undertaken that help to position the manus in front of and below the animal so it can brace for impact. These movements involve pre-landing elbow extension and nearly simultaneous humeral protraction and depression. Following impact, GRFs effectively reverse all these movements such that the elbow flexes whereas the humerus retracts and elevates.

### Kinematics of the forelimbs

In the past several years, growing attention has been paid to the role of the forelimbs and their underlying muscles in the execution of coordinated landing in toads (Gillis et al. 2010; Akella and Gillis 2011; Azizi and Abbott 2013; Griep et al. 2013). Toads are good models for studying the kinematics of joints in the forelimb during landing because they use their forelimbs almost exclusively to decelerate and control the body at impact.

We have focused on movements of the humerus and the elbow joint to characterize forelimb movements during hopping, and using a two-camera system have measured 3-D kinematics in five animals. Qualitatively, toads undergo a consistent and repeatable series of forelimb movements during hopping (Fig. 1). First, as the animal's hindlimbs start to extend in the take-off or propulsive phase, the elbow typically flexes as the humerus begins to protract (Fig. 1). Simultaneous extension of the hindlimbs and flexion of the elbow leads to the forelimb lifting

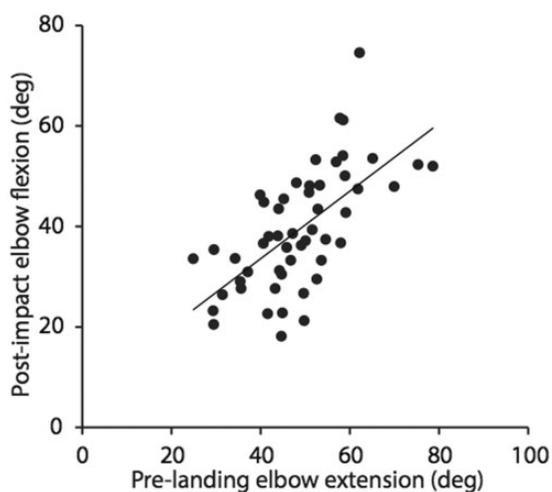
off the ground, and as the humerus protracts, the manus moves anteriorly. After this initial bout of elbow-flexion and humeral protraction, the elbow extends and the humerus is depressed, translating ventrally toward the ground as it continues to protract (Fig. 1) throughout the aerial phase. The combined effects of these movements lead to a continued re-positioning of the manus out in front of and below the animal as it apparently braces for impact (Fig. 1). After impact, the elbow flexes in response to GRFs, whereas the humerus is driven simultaneously dorsally and posteriorly as the animal decelerates (Fig. 1).

Quantitative characterization of excursions of the elbow during hopping indicates that the elbow initially flexes  $\sim 25\text{--}35^\circ$ , followed by an average of  $35\text{--}45^\circ$  of extension before landing. After landing, the elbow undergoes  $30\text{--}40^\circ$  of post-impact flexion on average. Using XROMM to study toads' forelimb (and pectoral girdle) movements after impact, Griep et al. (2013) found comparable amounts of post-impact

flexion of the elbow flexion ( $\sim 20^\circ$  in one animal and over  $40^\circ$  in another, thus highlighting the inter-individual variability present in this movement).

Although Griep et al. (2013) purposely studied only hops of comparable distance, we focused on addressing whether the hop-distance influences forelimb kinematic patterns prior to, and after, landing. Our results from the elbow illustrate how the kinematics of joints changes predictably with the hop-distance. First, the amount of extension of the elbow before landing increases considerably with hop-distance from  $\sim 25^\circ$  during the shortest hops to  $\sim 75^\circ$  during the longest hops. Second, as might be expected from the increasing GRFs associated with landing during longer hops (Nauwelaerts and Aerts 2006), post-impact flexion of the elbow also increases with hop-distance, from  $\sim 25^\circ$  during the shortest hops to  $>50^\circ$  during the longest hops. These two excursions of the elbow, post-impact flexion and pre-landing extension, change in nearly direct proportion to one another such that when one increases, the other increases in parallel (Fig. 2). The net result of these parallel relationships between the elbow's kinematics and hop-distance is that the most flexed position the elbow achieves after impact is largely independent of hop-distance, averaging  $80\text{--}100^\circ$ , depending on the animal.

Thus, although the general pattern of kinematics of toad's forelimbs is stereotyped during hopping, the magnitude of each movement changes predictably with hop-distance. In particular, animals appear to compensate for increasing degrees of elbow flexion



**Fig. 2** Plot of pre- and post-landing elbow excursions as a function of one another in five toads ( $R^2=0.41$ ;  $P<0.001$ ). This seemingly compensatory relationship leads to the control of the final, ultimate elbow angle achieved after impact, which remains similar across a range of hop-distances.

during landing after longer hops by extending the elbow further prior to impact. The result is that the ultimate angle the elbow reaches after impact is controlled, the implications of which are described in the next section.

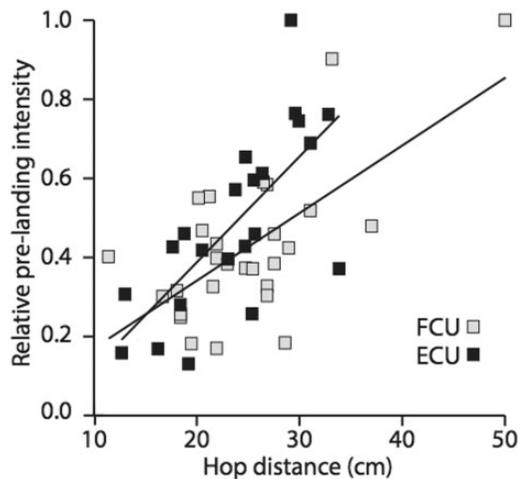
### Actions of muscles in preparation for, and after, impact

Early work by Liddell and Sherrington (1924) on stretch reflexes led researchers interested in the neuromuscular control of stepping and landing to initially assume that stretch receptors activated at touch-down were responsible for initiating muscular activity involved in resisting impact. However, surface electromyographic (EMG) experiments on humans in the 1970s demonstrated clearly that muscular activity involved in controlling landing began well before the impact itself (e.g., Jones and Watt 1971a; Greenwood and Hopkins 1976a). In addition to beginning prior to landing, this anticipatory muscular activity is also graded with respect to its intensity, and modulated with respect to the timing of its onset as well (Santello and McDonagh 1998). In other words, during human stepping and jumping, both the timing and the amplitude of anticipatory muscle recruitment in the legs are tuned to the expected timing and magnitude of impact. Moreover, similar results have been reported for other non-human mammals such as cats (Prochazka et al. 1979) and monkeys (Dyhr-Poulsen and Laursen 1984), and such anticipatory activity has been implicated as instrumental for coordinated landing (Watt 1976; Prochazka et al. 1979).

We initially addressed the question of whether toads too tuned limb muscular activity in relation to the expected force of impact; we recorded EMG activity in muscle antagonists acting at the elbow during hopping and landing. In both the long-head of the m. anconeus (extensor) and the m. coracoradialis (flexor), the intensity of pre-landing recruitment typically was tuned to hop-distance; in most animals, longer hops led to greater levels of EMG activation before impact (Gillis et al. 2010). Subsequent work on muscles that act antagonistically at the wrist, such as flexor carpi ulnaris and extensor carpi ulnaris, also demonstrate tuning in recruitment levels with respect to hop-distance (Fig. 3), although a number of muscles that act at the shoulder lack such tuning patterns (Akella and Gillis 2011).

In addition to recording EMG activity, we also used sonomicrometry in selected muscles to measure changes in the length of fascicles during hopping and landing. As shown in Fig. 4, strains in the long head

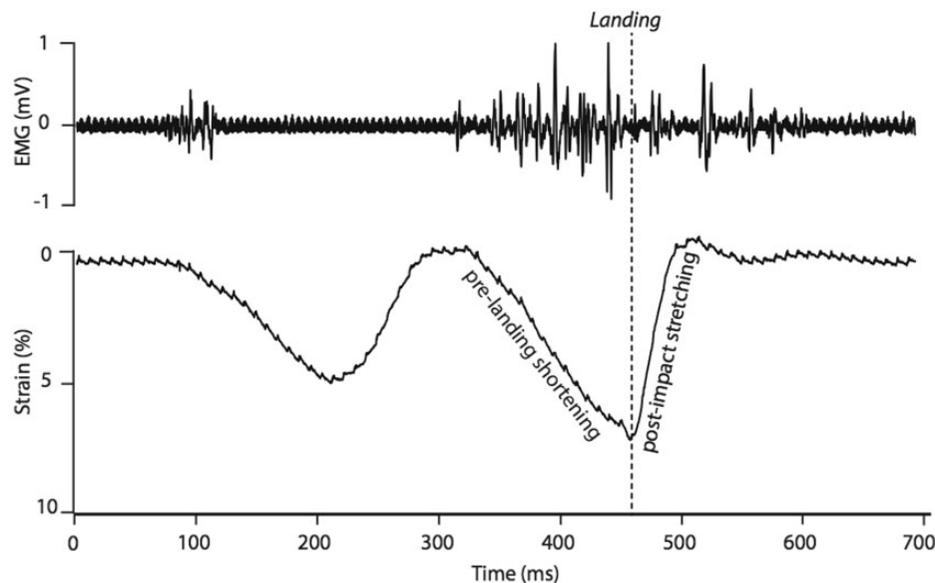
of the anconeus muscle reflect the elbow-joint excursions reported earlier. In particular, in mid-air substantial shortening of the m. anconeus parallels the pre-landing extension of the elbow consistently observed before impact, whereas after impact, as the elbow flexes in response to the GRFs, the anconeus muscle is rapidly stretched back to near its original length (Fig. 4).



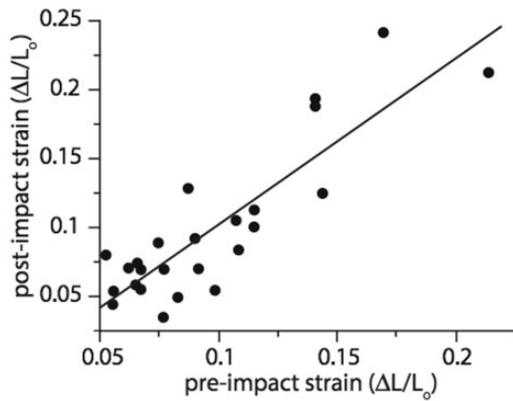
**Fig. 3** Pre-landing recruitment intensity is tuned to hop-distance in wrist antagonist muscles. Data are shown for the flexor carpi ulnaris (FCU; gray,  $R^2=0.42$ ,  $P<0.01$ ) in one toad, and from the extensor carpi ulnaris (ECU; black,  $R^2=0.50$ ,  $P<0.01$ ) in another.

After recording these pre-landing shortening strains and post-landing stretching strains in the anconeus muscle in a number of animals hopping over a range of distances, a result mirroring what we found for the kinematics of the elbow became evident. Specifically, as hop-distance increased, so too did pre-landing shortening strains and post-landing stretching strains. Indeed, they increased roughly in parallel with one another (Fig. 5), such that the increasing amount of anconeus muscle stretching associated with flexion of the elbow during landing after longer hops was compensated by an increasing degree of shortening in those fascicles prior to impact (Azizi and Abbot 2013). Thus, just as the angle of the elbow is controlled after impact (see previous section), so too is the maximum length to which the anconeus muscle is stretched (Azizi and Abbot 2013).

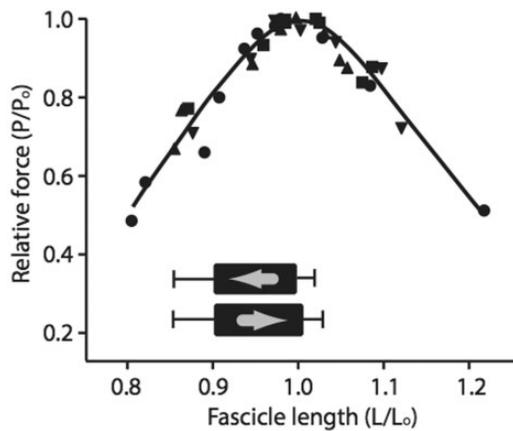
Further work was carried out to relate the *in situ* development of force in the m. anconeus of these same toads to muscle-length so that the muscles' operating lengths during hopping and landing could be mapped onto their respective force-length relationships (Azizi and Abbot 2013). Figure 6 indicates that the maximum lengths to which the anconeus muscle is stretched after impact, regardless of hop-distance, remained short of the descending limb of the muscle's force-length curve. Eccentric



**Fig. 4** Representative traces of anconeus EMG activity (top) and fascicle strain (bottom) highlighting how muscle length changes correspond to muscle activity patterns. In particular note the large degree of pre-landing anconeus shortening associated with the onset of the second, and larger, burst of anconeus EMG activity. This shortening strain is associated with pre-landing elbow extension that occurs as the animal braces for impact. Immediately after impact the elbow flexes, leading to the rapid post-impact stretching shown above. Note how the degree of pre-landing shortening corresponds well with the amount of subsequent post-impact stretching, leaving the muscle at a length close to where it started at the beginning of the hop.



**Fig. 5** The relationship between pre-impact strain (shortening) in the anconeus muscle during the aerial phase and the post-impact strain (stretching) after landing. Results from four individuals show that the shortening of the anconeus increases in anticipation of larger impacts, in which the stretch applied to the muscle is likely to be large. Data are normalized relative to each muscle's optimal length ( $L_0$ ).  $R^2=0.74$  and  $P<0.001$ .



**Fig. 6** Operating lengths of the long head of the anconeus muscle in relation to its length–tension curve. The active length–tension curve is characterized *in vitro* and averaged for four individuals. The length changes during the aerial and landing phase of the hop are normalized relative to the muscle's optimal length and mapped onto the curve (horizontal bars containing arrows). The top bar shows the pre-impact shortening during the aerial phase and the bottom bar shows the post-impact stretching that occurs after touchdown. Operating lengths are shown as means  $\pm$  SD.

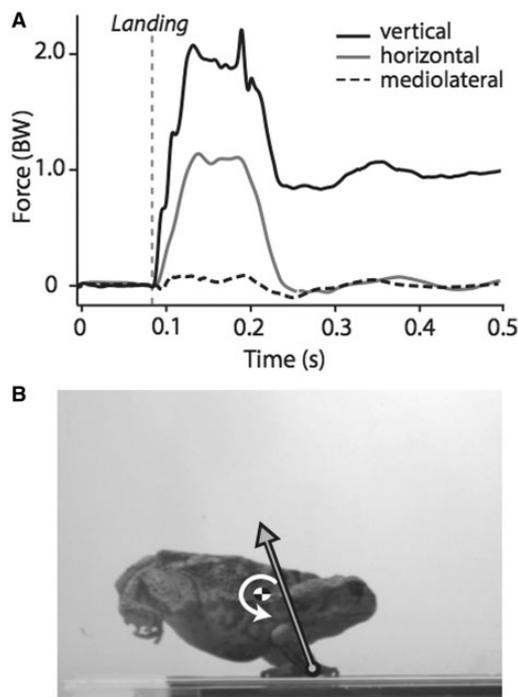
contractions that take place at relatively long muscle-lengths (i.e., on the descending limb) can lead to muscle damage (e.g., Talbott and Morgan 1998). Thus, our results suggest that toads vary recruitment of certain arm muscles with hop-distance in ways that ensure that major muscles that are contracting eccentrically after impact never reach the overly extended lengths at which damage becomes more likely (Azizi and Abbot 2013).

## Stability and whole-body mechanics

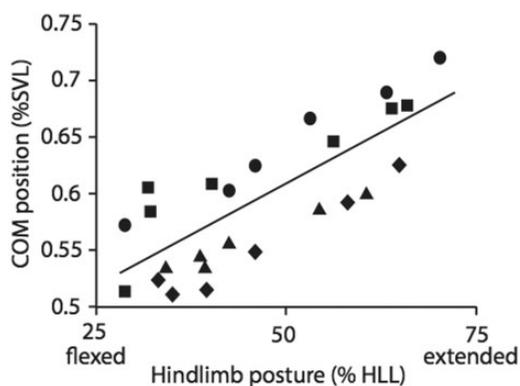
For many species of toads, hopping is the primary mode of locomotion used during dispersal from a breeding site or migration to new breeding sites (Forester et al. 2006), and cane toads are known to be capable of migrating long-distances (Phillips et al. 2007). To effectively traverse long-distances, toads must string together multiple, consecutive hops and smoothly transition from one hop to the next, which requires coordinated landing after each hop. A potential challenge of performing well-coordinated landings is to remain balanced during impact long enough to allow the muscles of the forelimb sufficient time to dissipate energy and effectively position the toad for the next hop. In this section, we describe how toads employ movements of the hindlimbs in mid-air to improve control and stability during landing.

One mechanism for increasing stability during landing is to minimize the torques acting on the COM. The impact of landing can produce relatively large GRFs, which can be two to three times greater than body weight (Fig. 7A) (Nauwelaerts and Aerts 2006). If the orientation of the GRF vector is in line with the animal's COM, the torque acting about the COM will be minimized, thereby resulting in a balanced, stable landing (Fig. 7B). Landings in which the GRF vector deviates significantly from this orientation can result in the animal either toppling forward until the head crashes into the substrate or toppling backward until the torso and legs crash into the substrate (Nauwelaerts and Aerts 2006). Such an uncoordinated landing can delay preparation for the subsequent hop and slow steady, cyclical hopping.

How do toads minimize torques acting at the COM? In some anurans, the hindlimbs can make up approximately one-third of the total body weight (James and Wilson 2008). Although this fraction remains unknown in toads, and is surely considerably smaller, the posture of toads' hindlimbs at landing nevertheless can affect the position of the COM and therefore the torques acting on the body (Fig. 8). When the hindlimbs move from an extended to a fully flexed position, as happens after take-off when toads hop (see image sequence in Fig. 1), the animal's COM moves anteriorly  $\sim 20\%$  of snout-to-vent length. To test whether this shift in COM position reduces torques acting on the body, we measured the magnitude and orientation of the GRF vector during landing in 10 hops from each of six toads. In nearly all landings, the vector's position was slightly anterior to the animal's COM (Fig. 7B)



**Fig. 7** (A) GRF data for a representative landing. A six-axis force plate is used to characterize the vertical, horizontal, and mediolateral GRFs. The data are used to characterize the direction and magnitude of the GRF vector. (B) The torque acting at the COM is defined by the position and magnitude of the GRF vector (gray arrow) relative to the position of the COM.



**Fig. 8** The relationship between hindlimb posture and the position of the COM. A force-balance was used to characterize the position of the COM as the hindlimb was moved from a fully flexed to fully extended posture. Limb extension moves the COM posteriorly whereas limb flexion moves the COM anteriorly. Data from four individuals show a positive relationship between the position of COM and hindlimb posture ( $P < 0.001$ ).

(Rana et al. 2013). Thus, the flexion of the hindlimbs after take-off can help stabilize the animal at impact by moving the COM anteriorly and closer to the GRF vector. In fact, a theoretical analysis indicates that torques at the COM would be  $\sim 35\%$  higher if

the animal landed with fully extended, rather than fully flexed, hindlimbs (Rana et al. 2013).

Variation in hop-distance can have important implications for stability during landing. Long hops, which have a longer aerial phase, provide toads sufficient time to flex their hindlimbs fully before impact (Gillis and Biewener 2000). In contrast, the relatively short aerial phase (or its absence) does not provide sufficient time to flex the hindlimbs fully before landing, leaving the COM farther from the GRF vector during short hops. However, because the magnitude of the GRF vector is smaller in short hops, torques about the COM are still relatively small despite this increased distance between the COM and vector. Nevertheless, the ability of hindlimb flexion to help reduce destabilizing torques likely depends on hop-distance.

What drives the hindlimb flexion observed immediately after take-off? Recent experiments measuring levels of muscular activity of a knee-flexor (iliofibularis) during toads' hopping reveal that its activity just precedes the onset flexion of the knee after take-off (Gallardo et al. 2014). This would seem to suggest that flexion of the hindlimbs is driven by active muscular force. However, a comparison of short and long hops reveals that the intensity of muscular activity in the iliofibularis decreases with increasing hop-distance despite the fact that the rate and magnitude of knee flexion are greater during long hops (Gallardo et al. 2014). This pattern suggests that elastic recoil of tissues, like hindlimb flexor muscles themselves, which are stretched as the limbs extend during take-off, may play a relatively important role in helping flex the limbs after take-off during long hops and decrease reliance on active generation of force by the muscles (Gallardo et al. 2014).

Based on our results, we can draw three important conclusions about how toads achieve stable landings during hopping. First, changes in the configuration of toads' hindlimbs after take-off can be used to move the COM during the aerial phase of a hop. Second, the rapid flexion of the hindlimbs after take-off does indeed better align the COM with the GRF vector, thereby reducing the torques acting on the body. Third, the significance of hindlimb flexion and its underlying mechanisms depends strongly on hop-distance.

### The importance of sensory feedback for landing

Coordinated landing is dependent on an organism's ability to predict the expected time and force of

impact (reviewed by Santello 2005). How an animal is informed by external and internal cues about its speed, acceleration, and position in relation to the ground has become increasingly well understood over the past 50 years. In this section, we review work aimed at elucidating the importance of sensory feedback for controlling impacts during terrestrial locomotion and describe recent, unpublished results highlighting the roles of different sensory systems during hopping and landing in toads.

Early work demonstrating anticipatory activity of limb muscles in human landings suggested that vision and the vestibular system both are critical for executing coordinated landing (Jones and Watt 1971b; Greenwood and Hopkins 1976a, 1976b; Dietz and Noth 1978). Further work on monkeys, cats, and diving and landing birds also emphasized the importance of visual and vestibular cues for anticipatory activation of muscles (Watt 1976; Lee and Reddish 1981; McKinley and Smith 1983; Dyhre-Poulsen and Larsen 1984; Lee et al. 1993). Specifically, visual input was deemed critical for establishing the timing of pre-landing muscular activity, whereas vestibular input was important for tuning its amplitude (McKinley and Smith 1983).

More recent work with human subjects has shown that humans can adapt to a loss of visual input (Santello et al. 2001; Liebermann and Goodman 2007; Magalhães and Goroso 2009, 2011; Castellote et al. 2012). For example, humans can perform coordinated drop-landings immediately after removal of continuous visual feedback and experience only slight changes to EMG and kinematic patterns (Santello et al. 2001; Liebermann and Goodman 2007). However, if all prior cues of the distance fell are removed, they initially exhibit un-tuned landings, but then can use vestibular and proprioceptive feedback from those initial drops to better control landing after subsequent drops from the same height (Magalhães and Goroso 2009). This suggests that a “landing program” may be learned as a result of feedback from multiple sensory systems, and work on subjects with long-term blindness emphasizes the potential importance of non-visual sensory systems in the development of such programs (Magalhães and Goroso 2011).

Recently, we have begun using toads to test the importance of vision, proprioception, and the vestibular system for coordinated landing. Anurans have long been described as being highly dependent on vision for recognizing prey and for feeding and escape responses (Maturana et al. 1960; Ingle 1971; Sternthal 1974; Roster et al. 1995; Anderson and Nishikawa 1996). However, multiple sensory systems

can be involved in a single motor behavior. For example, feeding in frogs is initiated by visual stimuli, but the subsequent motor control is also influenced by proprioception (Anderson and Nishikawa 1996; Valdez and Nishikawa 1997; Corbacho et al. 2005). Integrating sensory information from multiple sources to achieve successful motor control is likely a common strategy, and thus likely to be important during hopping and landing by toads.

Multiple sources of sensory input are available to toads before and during hopping. In addition to visual information about landing sites obtained before a hop, toads can also receive proprioceptive feedback during take-off from changes in the lengths and velocities of muscle fascicles in the limbs and from vestibular feedback from changes in acceleration of the body. To begin to tease apart the roles of vision, proprioception and the vestibular system in facilitating the control of landing by toads, we initiated a series of studies in which we manipulate or perturb one or more sensory systems while trying to maintain the other(s) as normal.

In one set of experiments, for example, we compared the hopping of animals on a level surface before and after bilateral ablation of the optic nerves. Our results suggest that toads are capable of controlled landing with no visual input and can even tune the pre-landing intensity of muscular activity of the forelimb in the absence of visual information (Fig. 9B).

In a second set of experiments, we compared hopping on the level with hopping from a 15-cm elevated platform to test whether toads relied exclusively on proprioceptive and/or vestibular input obtained during take-off. If this were the case, animals should not vary motor output to their anconeus muscles during elevated hops. However, if visual and/or vestibular information after take-off can be integrated into the motor response, then presumably animals would modulate pre-landing patterns of muscular activity to account for the greater impending impact forces associated with landings from elevated hops. Our results demonstrated that pre-landing recruitment of the anconeus muscle is more intense during elevated hops (Fig. 9A), indicating that animals can take advantage of feedback from the vestibular and/or visual systems after take-off, and are not solely reliant on sensory information received during the take-off itself.

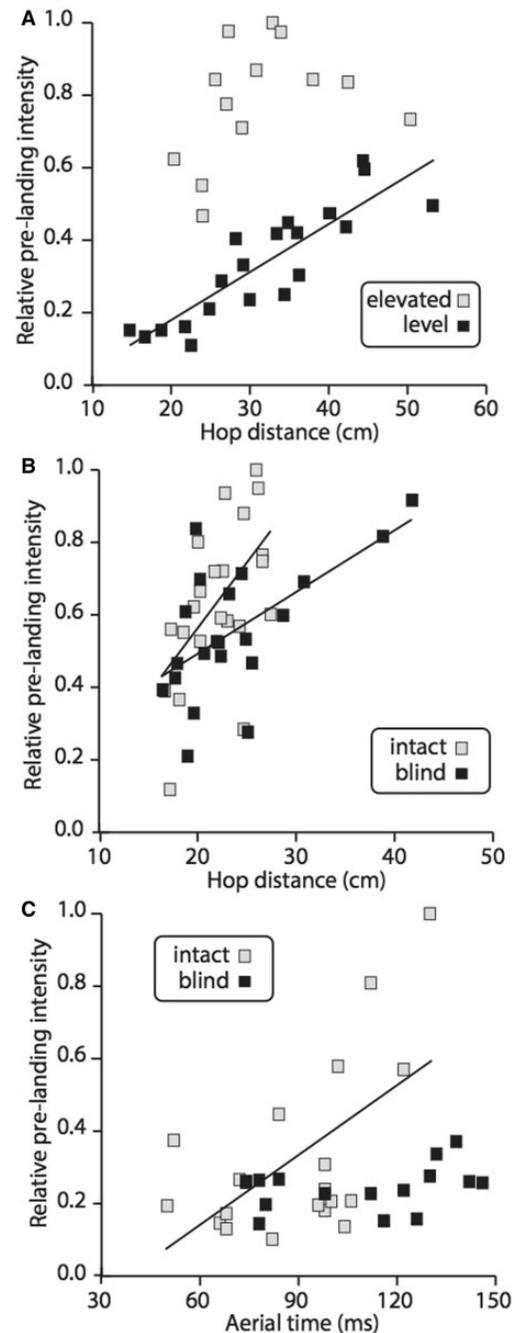
Finally, to isolate the role of the vestibular system in landing, we compared how animals prepared for impact when dropped from different heights before and after ablation of the optic nerves. When toads with intact visual systems were dropped from

different heights, increasing degrees of pre-landing intensity of recruitment were correlated with increasing height of the drop (Fig. 9C). However, when vision was removed, pre-landing intensity of recruitment did not change with height of drop (Fig. 9C), suggesting that the vestibular system alone may not be sufficient for coordinating landing. However, in these experiments, we dropped animals straight down, so that only changes in linear acceleration were detectable by the toads' vestibular systems. In reality, changes in angular acceleration are prominent during hopping and may play an important role in coordinating the landing response.

Taken together our results have three implications for the roles of sensory feedback in controlled landing in toads. First, vision is not necessary, which is also the case in humans and other mammals (McKinley and Smith 1983; Santello 2005). This is not entirely surprising given that important parameters such as when, and how hard, an animal will land are a function of an animal's velocity and angle at take-off (Marsh 1994), which are largely determined before the animal is airborne. Proprioceptors in muscles and tendons along with the vestibular system have all the sensory information available during take-off to permit appropriate, advanced preparation for impact. The second implication of these experiments is that sensory information obtained solely during take-off can be modified after the animal leaves the ground. Our results indicating increased pre-landing intensity of recruitment during elevated hops demonstrates that sensory feedback not associated with the take-off itself, likely from the vestibular and/or the visual system, can be employed to account for conditions gleaned after the animal has left the ground. Finally, our experiments with dropping the animals indicate that vestibular feedback on linear acceleration is not enough to help prepare an animal for landing from drops of different heights. Accounting for angular accelerations will be the next step in our assessment of the importance of the vestibular system in helping animals prepare for impact, control their deceleration, and execute coordinated landings.

## Conclusion

In this review, we have highlighted that a key motor-control strategy employed by humans and other mammals, namely the tuning of pre-landing patterns of muscular activity to the expected impact, is also present in toads. Moreover, our integrative approach has allowed us to link tuned activity of forelimb muscles to predictable kinematics of the forelimbs,



**Fig. 9** Various sensory modalities were tested to determine their contribution to generating tuned pre-landing intensity during hops (A and B) and drops (C). (A) Toads were able to prepare for greater impact by generating higher pre-landing intensities in the anconeus muscle when jumping off an elevated platform (gray) versus level hops (black,  $R^2=0.77$ ,  $P<0.01$ ) of the same horizontal distances (analysis of covariance,  $P<0.01$ ). Similarly, in (B), like the hopping toads with intact optic nerves (gray,  $R^2=0.31$ ,  $P<0.01$ ), blinded toads (black,  $R^2=0.37$ ,  $P<0.01$ ) could also tune muscle recruitment intensity with hop-distance. When dropping toads (C), those with intact optic nerves exhibited tuning of anconeus muscle recruitment with drop distance ( $R^2=0.33$ ,  $P<0.01$ ), however, vertical acceleration alone was not sufficient to generate such tuning during drop tests in blind animals.

revealing that the angle of the elbow after impact is controlled, as is the length to which a major elbow extensor is stretched as it dissipates energy during landing. This, in turn, results in landings that are both safe and stable, thereby allowing the toads to string together many hops during long-distance movements. We also demonstrated that coordinating a stable landing is not only reliant on the actions of the forelimbs, but also involves controlling the posture of the hindlimbs after take-off. Flexion of the hindlimbs begins immediately after the animal leaves the ground, which improves alignment of the animal's COM with GRFs after impact, thereby providing better balance and more stability during landing. Finally, sensory feedback is critical for controlled landing, but vision is not. Our results suggest that vestibular and/or proprioceptive input gained during take-off provides enough information to the animal to control landing. However, animals need not rely only on sensory information gathered during take-off, and appear also to be able to take advantage of sensory input from the vestibular and/or visual systems while in mid-air. We are continuing to perform experiments that will help unravel how the complex interactions between various sensory modalities inform and modulate landing behavior in toads.

### Future directions

Coordinated landing is not common to all anuran jumpers. For example, the most basal extant anurans do not use their forelimbs at all to brace for landing and instead hit the ground nose-first and perform “belly-flops” in which the torso routinely crashes into the substrate (Essner *et al.* 2010). This observation leaves open the question of when the signature features of coordinated landing in toads, such as rapid aerial retraction of the hindlimbs and modulated extension of the forelimbs in anticipation of impact, arose. By characterizing the actions and motor-control patterns of the forelimbs and hindlimbs across a phylogenetically diverse selection of anurans, we can begin to reveal whether coordinated landings and the control characteristics that permit them are limited to true toads, or are more broadly correlated with the presence of a terrestrial lifestyle and/or continuous hopping gait (or are distributed across the anuran phylogeny in some as yet unpredictable pattern).

We are also interested in learning how the coordination of landing develops, and toads once again provide an ideal model for addressing this question. To examine whether controlled landing and its associated preparatory movements and motor-patterns

are learned or innate, we will be performing kinematic and electromyographic analyses on toads taking their first hops after metamorphosing from tadpoles. If coordinated landing is innate, we expect to see comparable forelimb movements and patterns of muscular activity between an animal's first hops, and those found in adults. If not, we can address when and under what conditions coordinated landing behavior develops. Regardless, the study of anuran landing provides ample opportunity to integrate ecological, evolutionary, developmental, biomechanical, and neurobiological approaches into an understanding of an understudied but important locomotor action, controlled deceleration.

### Acknowledgments

We want to thank Rick Blob and Tim Higham for organizing this symposium and inviting us to take part in it. Support for our participation was provided by the Company of Biologists, and the Society for Integrative and Comparative Biology (Divisions of Vertebrate Morphology, Comparative Biomechanics, Neurobiology, and Animal Behavior). We also owe thanks to many excited and hard-working undergraduates, graduate students, and post-doctoral fellows who have been involved along the way, including Emily Abbot, Trupti Akella, Georgina Coleman, Suzanne Cox, Nicole Danos, Rashmi Gunaratne, Rebecca Hicks, Eleni Karagiannis, Hilary Katz, Janine Kopeski, Gina LaBeaud, Neil Larson, Karley LeMire, Erica Levin, Nell Maynard, Ali McCarthy, Kate Pelletier, Chris Panzini, Ameer Phan, Catherine Tierney, and Maxana Weiss. Jake Krans provided useful input into our approach to thinking about sensory systems and Thomas Liliatimen and Len McEachern can design, build, and wire just about anything and have helped in countless ways on many of these projects.

### Funding

This work was by the National Science Foundation [grant numbers 1051603 to G.G. and 1051691 to E.A.]. All experimental work described in this review was approved by IACUC committees at Mount Holyoke College, Wheaton College or the University of California, Irvine. Support for participation in this symposium was provided by the Company of Biologists, and the Society for Integrative and Comparative Biology (Divisions of Vertebrate Morphology, Comparative Biomechanics, Neurobiology, and Animal Behavior).

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