

RESEARCH ARTICLE

Reduce torques and stick the landing: limb posture during landing in toads

Emanuel Azizi*, Neil P. Larson, Emily M. Abbott and Nicole Danos

ABSTRACT

A controlled landing, where an animal does not crash or topple, requires enough stability to allow muscles to effectively dissipate mechanical energy. Toads (*Rhinella marina*) are exemplary models for understanding the mechanics and motor control of landing given their ability to land consistently during bouts of continuous hopping. Previous studies in anurans have shown that ground reaction forces (GRFs) during landing are significantly higher compared with takeoff and can potentially impart large torques about the center of mass (COM), destabilizing the body at impact. We predict that in order to minimize such torques, toads will align their COM with the GRF vector during the aerial phase in anticipation of impact. We combined high-speed videography and force-plate ergometry to quantify torques at the COM and relate the magnitude of torques to limb posture at impact. We show that modulation of hindlimb posture can shift the position of the COM by about 20% of snout–vent length. Rapid hindlimb flexion during the aerial phase of a hop moved the COM anteriorly and reduced torque by aligning the COM with the GRF vector. We found that the addition of extrinsic loads did not significantly alter landing behavior but did change the torques experienced at impact. We conclude that anticipatory hindlimb flexion during the aerial phase of a hop is a critical feature of a mechanically stable landing that allows toads to quickly string together multiple, continuous hops.

KEY WORDS: Landing, Ground reaction force, COM, Stability, Hopping, Pitching moment

INTRODUCTION

Landing after a hop or jump is a common locomotor task among terrestrial organisms. These locomotor events can pose a significant biomechanical challenge given the large ground reaction forces (GRFs) associated with such impacts (Nauwelaerts and Aerts, 2006; Ericksen et al., 2013). Large GRFs can pose a potential danger to the bones, ligaments or muscles of the limbs, which are tasked with rapidly dissipating mechanical energy and decelerating the body (Aerts et al., 2013). Strategies used to ensure a safe landing often involve anticipatory motor control strategies (Santello, 2005) and modulation of limb posture prior to impact (Wikstrom et al., 2008). Anticipatory muscle recruitment, which is associated with landings across a diverse array of taxa (Dyhre-Poulsen and Laursen, 1984; Santello and McDonagh, 1998; Prochazka et al., 1977; Gillis et al., 2010), is thought to increase joint stiffness and allow for more effective energy dissipation by muscles (Horita et al., 2002; Santello, 2005). Furthermore, proper alignment of the limb at impact can

minimize the stresses experienced by skeletal elements and ligaments during landing (Wikstrom et al., 2008; Norcross et al., 2013).

In addition to possible injury, large GRFs associated with impact have the potential to destabilize the body during landing. These large GRFs can produce significant torques if they act with even a modest moment arm relative to the center of mass (COM). The excessive torques experienced during landing can produce a pitching or rolling moment about the COM, which can cause an organism to stumble or crash. One strategy to improve stability during landing is to use movements of the torso and the forelimbs to better align the COM with the GRF vector (Bates et al., 2013). Such changes in posture can stabilize the body by either reducing or quickly counteracting torques experienced at the COM (Blackburn and Padua, 2008). Thus, a safe and stable landing often involves an intricate interplay of limb and body configuration.

Although most anurans are considered highly specialized jumpers or hoppers, toads (Family: Bufonidae) are particularly effective at landing. In most anurans, the movements associated with the takeoff phase of a hop or jump are largely conserved (Zug, 1985). In contrast, the mechanics of landing tend to vary significantly among different anuran radiations. For example, species from basal radiations tend to land rather inelegantly, performing what amounts to a ‘belly flop’ during each landing (Essner et al., 2010). This pattern has led to the hypothesis that a finely tuned landing behavior may be a derived characteristic among certain radiations (Essner et al., 2010). Landing is also rather inconsistent in semi-aquatic species (Family: Ranidae), where the chest, torso or legs frequently contact the substrate during landing (Nauwelaerts and Aerts, 2006; Essner et al., 2010). However, landing behavior in toads is characterized by a controlled deceleration accomplished solely with the forelimbs (Gillis et al., 2010; Akella and Gillis, 2011). During landings, toads appear balanced and stable, providing sufficient time for the muscle of the forelimbs to dissipate energy and slow the body before gently bringing the hindlimbs toward the ground (Azizi and Abbott, 2013; Azizi, 2014).

Similar to landings in other organisms, stable and well-coordinated landings in toads are thought to be associated with anticipatory motor strategies prior to impact. The intensity of activation in the muscles of the forelimbs has been shown to be tuned to the perceived magnitude of the impending impact (Gillis et al., 2010). This tuning of forelimb activity can help to stiffen joints in anticipation of large impacts (Gillis et al., 2010) and also shift where landing muscles operate on the force–length curve (Azizi and Abbott, 2013). Anticipatory strategies may not be limited to the forelimbs but could also include changes in body angle or postural changes in the hindlimbs.

In this study, we used cane toads, *Rhinella marina* (Linnaeus 1758), as a model system to examine how hindlimb posture during landing affects the stability of the whole body. Previous studies have shown that the hindlimbs can make up more than 30% of body mass

Department of Ecology and Evolutionary Biology, University of California, Irvine, Irvine, CA 92697, USA.

*Author for correspondence (eazizi@uci.edu)

Received 22 May 2014; Accepted 16 August 2014

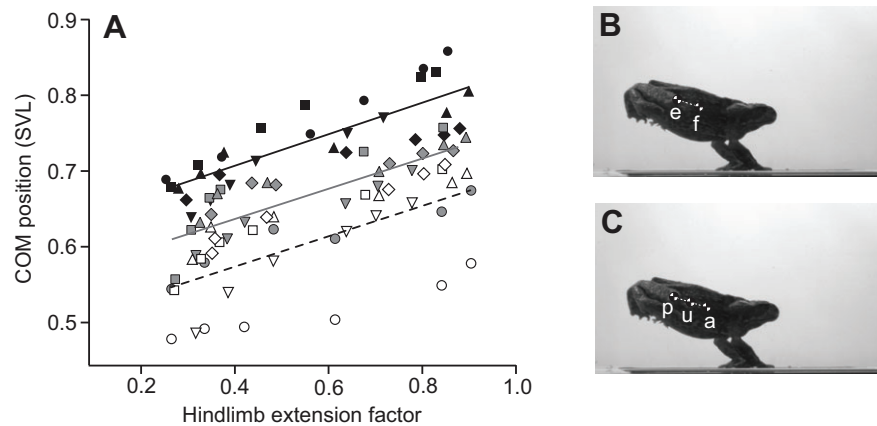


Fig. 1. The effect of hindlimb posture on the position of the center of mass. (A) Hindlimb extension factor is used as a metric of limb posture with a value near 1 representing a fully extended limb and a value of 0.2 representing a fully flexed limb (see Materials and methods for how the variable is calculated). The position of the center of mass (COM) moves more posteriorly (higher COM position values) as the limb is extended. The data shown are from five toads for unweighted (gray), anteriorly weighted (white) and posteriorly weighted (black) conditions. Extrinsic loading results in a constant shift in COM position. All three relationships are statistically significant ($P < 0.001$). Each individual is shown with a different symbol. (B) A schematic representation of the position of the COM when the limb is fully flexed (f) or fully extended (e). (C) A schematic representation of the effects of extrinsic loading on the position of the COM (P, posterior; u, unweighted; a, anterior) at a hindlimb extension factor of 0.5.

in anurans (James and Wilson, 2008). Therefore, we predicted that the posture of the hindlimb can have a significant effect on the position of the COM. We combined high-speed videography and force-plate ergometry to test the prediction that changes in hindlimb posture can function to align the COM with the GRF vector and reduce the torque experienced at the COM during landing. Finally, we used extrinsic loading to shift the position of the COM to test whether toads can modulate landing behavior to accommodate an artificial change in the position of the COM. Our study aims to reveal the relationship between posture and stability in organisms that consistently perform well-coordinated landings.

RESULTS

Changes in the posture of the hindlimbs had a significant effect on the position of the COM ($P < 0.001$; Fig. 1A). The position of the COM was located at ~55% of snout–vent length (SVL) when the hindlimb was fully flexed, and shifted posteriorly to ~75% of SVL when the hindlimb was fully extended (Fig. 1B). The application of

extrinsic loads (10% body mass) changed the relationship between hindlimb posture and COM position (Fig. 1A,C). The regression lines describing the relationship between hindlimb posture and COM position retained the same slope with the application of extrinsic loads as assessed through a non-significant interaction term ($P = 0.824$). The elevations of these lines, however, were significantly different ($P < 0.001$; ANCOVA), confirming that extrinsic loads resulted in a constant shift in COM position (Fig. 1A).

The profile of the GRFs in the vertical, horizontal and mediolateral directions are shown in Fig. 2. The magnitude of the mediolateral forces was generally very low, suggesting that most landings analyzed were symmetrical about the sagittal axis and that the impact resulted in relatively small rolling torques about the COM. The directional force components were used to calculate the magnitude and direction of the GRFs of a landing event. GRF magnitude ranged from about 2 to 4 body weights (Fig. 3A). The GRF vector was generally oriented posteriorly (negative horizontal forces), indicating that the arms were functioning as brakes during

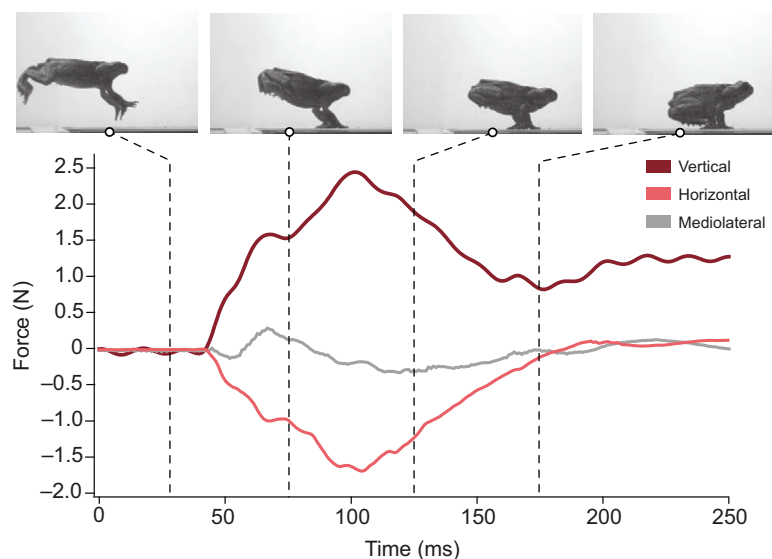


Fig. 2. The ground reaction forces during a representative landing sequence. High-speed video images are shown at the top and correspond to time points during force-plate recordings of a landing event. For all landing events, the magnitudes of the vertical and horizontal components of the ground reaction forces (GRFs) were significantly higher than the mediolateral forces. Negative horizontal forces refer to the posterior direction and indicate energy dissipation (braking). Raw force-plate data have been filtered using a quantile spline.

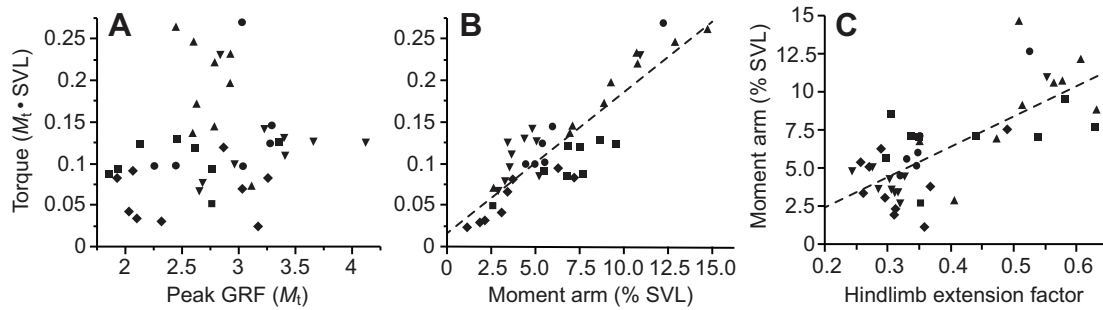


Fig. 3. Determinants of torque during landing. (A) There is no significant relationship between the torque experienced at the COM and the magnitude of the peak GRFs. Data are shown for five individuals and torques are normalized relative to toad body mass (M_t) and snout–vent length (SVL) while GRFs are normalized relative to M_t . (B) Torque acting at the COM increases significantly ($P < 0.001$) with increasing moment arm (orthogonal distance from the COM to the GRF vector). Taken together, these data suggest that the primary determinant of torque at the COM is variation in the moment arm. (C) Moment arm increases significantly with hindlimb extension factor ($P < 0.001$), suggesting that flexion of the hindlimb is an important strategy for aligning the COM with the GRF vector, thereby reducing torques. Each individual is represented by a different symbol.

landing (Fig. 2). The angle of the GRF vector did not vary significantly between loading conditions ($P = 0.13$).

Our results show that variation in limb posture during landing explains much of the variation in the torque experienced at the COM (Fig. 3). The magnitude of the GRF does not vary significantly with COM torque ($P = 0.184$), explaining less than 5% of the variation in torque (Fig. 3A). Much of the variation in the torque experienced at the COM is explained by linear orthogonal distance between the COM and the GRF vector (moment arm). COM torque increased significantly with moment arm ($P < 0.001$) and moment arm explained more than 76% of the variation in torque (Fig. 3B). Our results show that the strategy used to reduce COM torque is to reduce the moment arm of the GRF about the COM by shifting the position of the COM through changes in hindlimb posture at landing (Fig. 3C). The moment arms of the GRF vector increased significantly as the hindlimbs were more extended during landing ($P < 0.001$).

These results suggest that rapid flexion of the hindlimbs helped to align the COM with the GRF vector and reduce torques at the COM. In all trials, the GRF vector was located anterior to the COM, suggesting that using limb posture to move the COM anteriorly reduced torques. This result is exemplified by comparing the measured torques with theoretical values based on where the COM

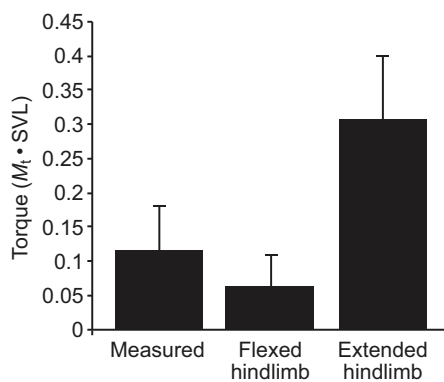


Fig. 4. Estimates of torques experienced at the COM with different hindlimb postures. The measured torques at the COM are compared with theoretical values of expected torques if the toads were to land with fully extended or fully flexed hindlimbs. There is no significant difference ($P = 0.341$) between the measured torques and calculated values with a flexed hindlimb. However, torques would increase significantly ($P < 0.001$) if the toads were to land with fully extended hindlimbs.

would be if the hindlimbs were either fully flexed or fully extended during landing. This comparison showed that torques at the COM would increase by more than a factor of two when comparing our measured results with theoretical estimates based on fully extended hindlimbs (Fig. 4).

The application of an extrinsic load anterior or posterior to the COM did not significantly alter landing behavior. Limb posture at landing did not differ significantly between three loading conditions (Fig. 5A; $P = 0.482$). As hindlimb posture did not vary between loading conditions, shifts in the COM position resulting from the extrinsic load did not significantly shift the moment arm and torque when the extrinsic load was applied. As the GRF vector was consistently located anterior to the COM, a posterior shift in the COM position significantly increased the moment arm and torque at the COM ($P < 0.001$; Fig. 5B,C).

DISCUSSION

Our results show that hindlimb flexion during the aerial phase of a hop allows for a more stable landing. Hindlimb flexion moves the position of the COM anteriorly, which allows for better alignment of the COM and the GRF vector when the forelimbs make contact with the substrate (Fig. 1). Aligning the COM with the GRF vector reduces pitching torques that tend to destabilize the body at impact. These results suggest that preparation for a safe and stable landing is not limited to preparing the limbs and muscles to dissipate mechanical energy but also involves changes in body configuration and COM position to reduce destabilizing torques.

The flexion of the hindlimbs was observed during nearly all hops recorded. This observation is consistent with recent findings, which suggest that the rapid flexion of the hindlimb may be associated with elastic recoil of the limb after the hindlimbs are fully extended during takeoff (Schnyer et al., 2014). This interpretation is based on the fact that the intensity of muscle activation in hindlimb flexors decreases with hop distance despite an increase in the magnitude and rate of hindlimb flexion (Schnyer et al., 2014). In fact, we have also observed that the only hops where hindlimbs are somewhat extended at impact are extremely short hops. This may be explained by the observation that hindlimbs are not fully extended during takeoff and, as a result, may not fully load elastic elements involved in recoil. An alternative interpretation may be that very short hops have a short aerial phase, which simply does not provide sufficient time to flex the hindlimbs. Despite landing with partially extended hindlimbs and a COM further from the GRF vector, short hops are not associated with significantly higher torques because the

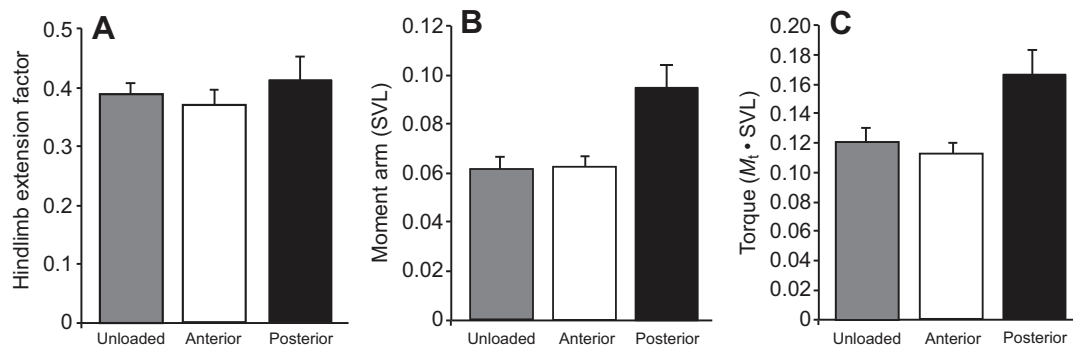


Fig. 5. The effects of extrinsic loading on landing mechanics. (A) There is no significant difference in the degree of hindlimb extension with extrinsic loads added to the anterior or posterior regions of the body ($P=0.482$). (B,C) Posterior loading does, however, significantly increase the GRF moment arms (B) and hence torques (C) around the COM ($P<0.001$). These results suggest that toads are attempting to move their COM as anteriorly as possible. A posteriorly located extrinsic load simply shifts the COM away from the GRF vector.

magnitude of the GRFs is also lower. Therefore, proper alignment of the COM seems to be a strategy that is most important during longer hops and larger impacts.

The addition of extrinsic loads successfully shifted the position of the COM but had little effect on the landing behavior of toads. The lack of behavioral modulation in response to our extrinsic loads may be due to the fact that loads corresponding to 10% of body weight were simply not heavy enough to be sensed by toads or affected a sensory modality that did not inform landing behavior. Previous work has implicated proprioception, the vestibular system and vision as potentially important in modulating landing behavior (Gillis et al., 2014). Of these modalities, vision would be totally unaffected by our perturbation. However, a more likely explanation may be that hindlimb flexion is primarily due to the elastic recoil of the limb during the aerial phase (Schnyer et al., 2014). If the hindlimb passively recoils when extended during take-off, then the behavior is not going to be modulated by altered sensory information or changes in motor control strategies (Schnyer et al., 2014). Finally, as our analysis only included stable landings, we cannot rule out the possibility that the addition of extrinsic loads increased the likelihood of unstable landings or crashes, which were not recorded or included in our analysis.

Toads are not the only animals that change their body posture in anticipation of impact. Several flightless animals have been shown to modulate their body posture during aerial behaviors in order to land from a fall or jump (Jusufi et al., 2011). This behavior is most familiar in the righting reflex of mammals, where the visual and vestibular systems trigger the production of rolling moments that reorient the body to a prone position so that the limbs can safely dissipate mechanical energy at impact. Such postural changes include movements of the torso, appendages or tail, which modulate the instantaneous moment of inertia (Jusufi et al., 2011). Specifically, the mammalian righting reflex is largely driven by a combination of axial flexion, extension and torsion (Laouris et al., 1990). In contrast, lizards primarily rely on the movement of the tail to generate a corrective rolling (Jusufi et al., 2011) or pitching moment while airborne (Libby et al., 2012). Similarly, the hindlimb flexion observed during the aerial phase of a toad hop has the potential to alter body orientation at impact. Hindlimb flexion (accelerating the mass of the hindlimbs toward the hip) during the aerial phase will generate a force posterior to the COM, thereby producing a torque about the COM that will cause the body to pitch down. Changes in body orientation can alter arm angle at impact, thereby allowing for more effective energy dissipation (Nauwelaerts and Aerts, 2006; Griep et al., 2013). The movement of the hindlimbs

during the aerial phase is analogous to aerial corrective maneuvers using the torso or tail and likely plays an important role in determining body angle impact.

The use of hindlimb flexion during the aerial and landing phase of a hop may be a feature that distinguishes anurans capable of stable, controlled landings from species that routinely crash into the substrate. The importance of hindlimb flexion is best exemplified by the relatively extreme landing behavior of the basal tailed frog (*Ascaphus montanus*). This species does not exhibit any hindlimb flexion during the aerial phase and, as result, consistently crashes into the substrate with its head or torso (Essner et al., 2010). Authors attribute such inelegant landings to the delayed flexion of the hindlimb in these species (Essner et al., 2010). In contrast, the toads used in our study flex their hindlimbs rapidly and achieve a relatively flexed posture before impact with the substrate (Fig. 2). The results of our study, which link hindlimb posture, the position of the COM and the torque experienced at the COM, provide a mechanistic explanation for why landing with extended hindlimbs results in unstable landings. In addition, the lack of hindlimb flexion in *Ascaphus* is implicated in the fact that they appear to have no way of modulating the pitch of the body while in air (Essner et al., 2010). It is worth noting that the impressive landing abilities of the toads used in our study appear unique among anurans studied to date. In fact, other derived species from the family Ranidae only dissipate a small proportion of the mechanical energy with their forelimbs during landing from a jump. GRF traces for these species show a clear second peak associated with the head, chest or torso crashing into the substrate (Nauwelaerts and Aerts, 2006). Therefore, despite being outstanding jumpers (Astley et al., 2013), Ranid frogs appear to lack the ability to consistently stick their landings. It is likely that landings are most important for continuous-hopping species like toads that string together consecutive hops during long locomotor bouts and are far less important for species performing single, less frequent jumps to avoid predators.

We conclude that a critical aspect of performing a safe and stable landing is to align the COM with the GRF vector in order to minimize torques acting on the body. We show that in the cane toad, the rapid flexion of the hindlimbs during the aerial phase functions to align the COM with the GRF vector at impact. In addition, hindlimb flexion likely changes the body angle at impact by imparting a pitching torque during the aerial phase. It is likely that the anticipatory changes in body configuration are a critical aspect of the controlled landing behavior, allowing toads to quickly transition from one hop to the next during long periods of continuous hopping.

MATERIALS AND METHODS

Five cane toads (*R. marina*) were purchased from a herpetological vendor, housed in glass terraria, and fed vitamin-enriched crickets *ad libitum*. Toads ranged in size from 10.2 to 10.7 cm in SVL and from 121 to 167 g in body mass (M_t). All husbandry and experimental procedures were approved by the Institutional Animal Care and Use Committee at The University of California, Irvine.

COM position

The position of each toad's COM was measured using a balance board approach (Lammers and Zurcher, 2011). M_t and the mass of the board (M_b) were first measured. The board was then placed so that one end was supported by a solid block and the other end was supported by a force plate (ATI Instruments, Apex, NC, USA), which was used to measure the mass of the partially supported board (W_b ; Fig. 6). The toads were then anesthetized using tricaine methanesulfonate (0.2 g l^{-1}) and placed on the board to measure the mass of the board plus the toad (W_{tot}). The position of the COM of the board and of the toad was then calculated using:

$$B_{\text{COM}} = W_b \times L / M_b, \quad (1)$$

$$T_{\text{COM}} = [(W_{\text{tot}} \times L) - (B_{\text{COM}} \times M_b)] / M_t, \quad (2)$$

where B_{COM} is the position of the COM of the board, T_{COM} is the position of the COM of the toad and L is the length of the board (Fig. 6).

Using the balance board approach, we quantified the position of each toad's COM across a full range of hindlimb postures. The COM was calculated as the hindlimbs were moved incrementally from fully flexed to fully extended while the toad was photographed from above. To quantify the degree of hindlimb extension, each photograph was digitized using ImageJ software (National Institutes of Health) and the ratio of the straight-line distance between the hip and the metatarsal pad to hindlimb length was measured. We defined this ratio as the hindlimb extension factor, with numbers approaching 1 representing a fully extended limb and numbers near 0.2 representing a fully flexed limb.

Extrinsic loading

Extrinsic loads corresponding to 10% ($\pm 0.2\%$) of body weight were added to each toad in order to artificially shift the position of the COM. Low profile metal weights were constructed and attached to the body using Velcro and cyanoacrylate adhesive. The weights were placed either anterior or posterior to the COM and generally shifted the position of the COM by

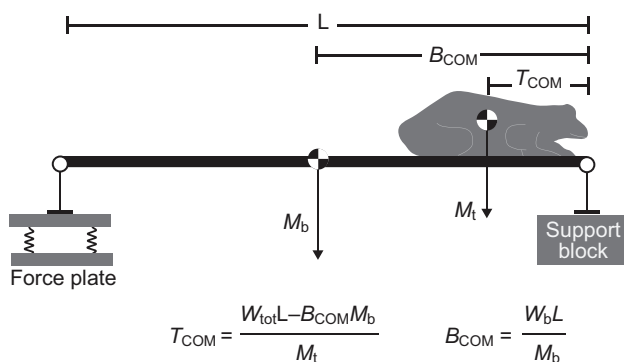


Fig. 6. Methods used to calculate the position of the COM. Toads were anesthetized and placed on a balance board with one end on a solid support block and the other end placed on the force plate. The hindlimbs were moved in regular increments from fully flexed to fully extended while the force (weight) was measured on the force plate. A digital camera was placed in dorsal view to characterize hindlimb posture as the limb was extended. The mass of the board (M_b) and the mass of the toad (M_t) were measured independently. W_b is the partially supported mass of the board and W_{tot} is the partially supported mass of the toad and the board. L is the length of the board, B_{COM} is the COM position of the board and T_{COM} is the COM position of the toad. Methods were modified from Lammers and Zurcher (Lammers and Zurcher, 2011).

about 10% of SVL (Fig. 1). The extrinsic loads were placed on the animals during quantification of the COM as well as during landing trials.

Kinetics and kinematics of landing

GRFs were measured during all landing trials using a six-axis, small animal force plate (MINI40, ATI Instruments). All hops were performed on the level, and animals jumped from a platform onto the working area (15 cm^2) of the force plate. The force plate was mounted on a damped vibration-resistant table (ThorLabs, Newton, NJ, USA) that reduced the ringing noise common to GRF measurements during rapid impacts. Data from the force plate were acquired using a 16-bit National Instruments DAQ (National Instruments, Austin, TX, USA) and Igor Pro (Wavemetrics Corp., Lake Oswego, OR, USA) data acquisition software.

Landing trials were filmed at $400 \text{ frames s}^{-1}$ using two high-speed cameras (Miro 120, Vision Research Corp., Wayne, NJ, USA). The filming arena was calibrated with a custom-made three-dimensional cube with 32 non-planar points (Hedrick, 2008). Video sequences were analyzed in MATLAB (The MathWorks Inc., Natick, MA, USA) using direct linear transformation and 3D digitizing scripts (Hedrick, 2008). Toads were externally marked to allow for automated tracking during video analysis. Markers were placed at the hip, along the femur, at the knee, along the tibiafibula, at the ankle and along the foot. These markers allowed us to quantify hindlimb posture during landing. In addition, the videos were used to determine the timing of takeoff and landing for each trial. Video recordings were synchronized with force-plate data using an external trigger source.

Data analysis

For each toad, 20 landing events were analyzed. Ten landing events were analyzed for unweighted conditions and 10 trials were analyzed when the animal was extrinsically loaded (five anterior and five posterior). The main criterion used to select the trials was that we aimed to reduce variation in the data due to variation in hop distance. As a result, we selected trials where hop distance was between 15 and 25 cm.

Force plate data were used to quantify the center of pressure, and the magnitude and orientation of the GRF vector. We largely focused our analysis at the time when peak GRFs were produced. Based on analysis of a subset of the data, the time of peak GRF was also the time when the body experienced the greatest torque at the COM. The video frame corresponding to the peak GRF was analyzed for hindlimb posture, which then allowed us to locate the position of the COM, based on our results from the balance board approach. Given the body coordinates at landing and the magnitude and orientation of the GRF, we then calculated the orthogonal distance (moment arm) between the GRF and the position of the COM. The product of the moment arm and the magnitude of the GRF allowed us to calculate the torque acting at the COM for each of the landing trials. To facilitate comparisons across individuals, lengths were normalized relative to SVL and forces were normalized relative to body mass.

To statistically examine the effect of extrinsic loading on the relationship between hindlimb posture and COM position, we used an ANCOVA with loading condition as the main effect, COM position as the dependent variable, and hindlimb extension factor as the covariate. If the interaction terms were non-significant, they were removed from the analysis (Fig. 1). Least-squares linear regressions were used to determine which parameters explained variation in the observed torques during landing (Fig. 3). A mixed model ANOVA was used to compare the measured with the theoretical values expected if the hindlimbs were fully flexed or fully extended, with individual included as a random effect (Fig. 4). Similarly, a mixed model ANOVA was used to compare the torques, moment arms and hindlimb postures between different loading conditions with individual included as a random effect (Fig. 5). All statistical analyses were performed in JMP (SAS Inc., Cary, NC, USA).

Acknowledgements

We are grateful to Amber Deslauriers, Pooja Rana, Marla Goodfellow and Pryanka Satish for help with data collection and analysis. Gary Gillis served as a valuable sounding board during the early stages of the project.

Competing interests

The authors declare no competing financial interests.

Author contributions

E.A. conceived and designed experiments and prepared the manuscript. E.M.A. conducted and executed experiments. N.P.L. conducted and executed experiments and analyzed data. N.D. analyzed and interpreted the data. All authors edited and revised the manuscript.

Funding

Funding for this work was provided by grant no. 1051691 from the National Science Foundation.

References

- Aerts, I., Cumps, E., Verhagen, E., Verschuere, J. and Meeusen, R. (2013). A systematic review of different jump-landing variables in relation to injuries. *J. Sports Med. Phys. Fitness* **53**, 509-519.
- 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* **315**, 1-11.
- Astley, H. C., Abbott, E. M., Azizi, E., Marsh, R. L. and Roberts, T. J. (2013). Chasing maximal performance: a cautionary tale from the celebrated jumping frogs of Calaveras County. *J. Exp. Biol.* **216**, 3947-3953.
- Azizi, E. (2014). Locomotor function shapes the passive mechanical properties and operating lengths of muscle. *Proc. R. Soc. B* **281**, 20132914.
- Azizi, E. and Abbott, E. M. (2013). Anticipatory motor patterns limit muscle stretch during landing in toads. *Biol. Lett.* **9**, 20121045.
- Bates, N. A., Ford, K. R., Myer, G. D. and Hewett, T. E. (2013). Impact differences in ground reaction force and center of mass between the first and second landing phases of a drop vertical jump and their implications for injury risk assessment. *J. Biomech.* **46**, 1237-1241.
- Blackburn, J. T. and Padua, D. A. (2008). Influence of trunk flexion on hip and knee joint kinematics during a controlled drop landing. *Clin. Biomech. (Bristol, Avon)* **23**, 313-319.
- Dyhre-Poulsen, P. and Laursen, A. M. (1984). Programmed electromyographic activity and negative incremental muscle stiffness in monkeys jumping downward. *J. Physiol. (Lond.)* **350**, 121-136.
- Erickson, H. M., Gribble, P. A., Pflieger, K. R. and Pietrosimone, B. G. (2013). Different modes of feedback and peak vertical ground reaction force during jump landing: a systematic review. *J. Athl. Train.* **48**, 685-695.
- Essner, R. L., Jr, Suffian, D. J., Bishop, P. J. and Reilly, S. M. (2010). Landing in basal frogs: evidence of saltational patterns in the evolution of anuran locomotion. *Naturwissenschaften* **97**, 935-939.
- 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., Ekstrom, L. and Azizi, E. (2014). Using toad landing as model for studying controlled deceleration. *Integr. Comp. Biol.* doi:10.1093/icb/ucu053.
- Griep, S., Schilling, N., Marshall, P., Amling, M., Hahne, L. and Haas, A. (2013). Pectoral girdle movements and the role of the glenohumeral joint during landing in the toad, *Rhinella marina* (Linnaeus, 1758). *Zoomorphology* **132**, 325-338.
- Hedrick, T. L. (2008). Software techniques for two- and three-dimensional kinematic measurements of biological and biomimetic systems. *Bioinspir. Biomim.* **3**, 034001.
- Horita, T., Komi, P. V., Nicol, C. and Kyröläinen, H. (2002). Interaction between pre-landing activities and stiffness regulation of the knee joint musculoskeletal system in the drop jump: implications to performance. *Eur. J. Appl. Physiol.* **88**, 76-84.
- James, R. S. and Wilson, R. S. (2008). Explosive jumping: extreme morphological and physiological specializations of Australian rocket frogs (*Litoria nasuta*). *Physiol. Biochem. Zool.* **81**, 176-185.
- Jusufi, A., Zeng, Y., Full, R. J. and Dudley, R. (2011). Aerial righting reflexes in flightless animals. *Integr. Comp. Biol.* **51**, 937-943.
- Lammers, A. R. and Zurcher, U. (2011). Torque around the center of mass: dynamic stability during quadrupedal arboreal locomotion in the Siberian chipmunk (*Tamias sibiricus*). *Zoology* **114**, 95-103.
- Laouris, Y., Kalli-Laouri, J. and Schwartze, P. (1990). The influence of altered head, thorax and pelvis mass on the postnatal development of the air-righting reaction in albino rats. *Behav. Brain Res.* **38**, 185-190.
- Libby, T., Moore, T. Y., Chang-Siu, E., Li, D., Cohen, D. J., Jusufi, A. and Full, R. J. (2012). Tail-assisted pitch control in lizards, robots and dinosaurs. *Nature* **481**, 181-184.
- Nauwelaerts, S. and Aerts, P. (2006). Take-off and landing forces in jumping frogs. *J. Exp. Biol.* **209**, 66-77.
- Norcross, M. F., Lewek, M. D., Padua, D. A., Shultz, S. J., Weinhold, P. S. and Blackburn, J. T. (2013). Lower extremity energy absorption and biomechanics during landing, part I: sagittal-plane energy absorption analyses. *J. Athl. Train.* **48**, 748-756.
- Prochazka, A., Schofield, P., Westerman, R. A. and Ziccone, S. P. (1977). Reflexes in cat ankle muscles after landing from falls. *J. Physiol. (Lond.)* **272**, 705-719.
- Santello, M. (2005). Review of motor control mechanisms underlying impact absorption from falls. *Gait Posture* **21**, 85-94.
- Santello, M. and McDonagh, M. J. N. (1998). The control of timing and amplitude of EMG activity in landing movements in humans. *Exp. Physiol.* **83**, 857-874.
- Schnyer, A., Gallardo, M., Cox, S. and Gillis, G. (2014). Indirect evidence for elastic energy playing a role in limb recovery during toad hopping. *Biol. Lett.* **10**.
- Wikstrom, E. A., Tillman, M. D., Schenker, S. M. and Borsa, P. A. (2008). Jump-landing direction influences dynamic postural stability scores. *J. Sci. Med. Sport* **11**, 106-111.
- Zug, G. R. (1985). Anuran locomotion – fatigue and jumping performance. *Herpetologica* **41**, 188-194.