

RESEARCH ARTICLE

Time-varying motor control of autotomized leopard gecko tails: multiple inputs and behavioral modulation

Timothy E. Higham^{1,*†} and Anthony P. Russell²

¹Department of Biological Sciences, Clemson University, 132 Long Hall, Clemson, SC 29634, USA and ²Department of Biological Sciences, University of Calgary, 2500 University Drive NW, Calgary, AB T2N 1N4, Canada

*Present address: Department of Biology, University of California, 900 University Avenue, Riverside, CA 92521, USA

†Author for correspondence (thigham@ucr.edu)

Accepted 24 October 2011

SUMMARY

Autotomy (voluntary loss of an appendage) is common among diverse groups of vertebrates and invertebrates, and much attention has been given to ecological and developmental aspects of tail autotomy in lizards. Although most studies have focused on the ramifications for the lizard (behavior, biomechanics, energetics, etc.), the tail itself can exhibit interesting behaviors once segregated from the body. For example, recent work highlighted the ability of leopard gecko tails to jump and flip, in addition to being able to swing back and forth. Little is known, however, about the control mechanisms underlying these movements. Using electromyography, we examined the time-varying *in vivo* motor patterns at four sites (two proximal and two distal) in the tail of the leopard gecko, *Eublepharis macularius*, following autotomy. Using these data we tested the hypothesis that the disparity in movements results simply from overlapping pattern generators within the tail. We found that burst duration, but not cycle duration, of the rhythmic swings reached a plateau at approximately 150 s following autotomy. This is likely because of physiological changes related to muscle fatigue and ischemia. For flips and jumps, burst and cycle duration exhibited no regular pattern. The coefficient of variation in motor patterns was significantly greater for jumps and flips than for rhythmic swings. This supports the conclusion that the different tail behaviors do not stem from overlapping pattern generators, but that they rely upon independent neural circuits. The signal controlling jumps and flips may be modified by sensory information from the environment. Finally, we found that jumps and flips are initiated using relatively synchronous activity between the two sides of the tail. In contrast, alternating activation of the right and left sides of the tail result in rhythmic swings. The mechanism underlying this change in tail behavior is comparable to locomotor gait changes in vertebrates.

Key words: tail autotomy, leopard gecko, central pattern generator, lizard, predator avoidance.

INTRODUCTION

Autotomy is the loss of an appendage (in whole, or part thereof) in response to mechanical and/or visual stimulation related to such factors as intraspecific competition or aggression, attempted predation or abiotic influences such as temperature extremes. Autotomy is clearly an effective strategy as it has evolved independently in diverse groups of animals including lizards (Dial and Fitzpatrick, 1983; Arnold, 1984; Zani, 1996; Bateman and Fleming, 2009), sea stars (Barrios et al., 2008), amphibians (Wake and Dresner, 1967), spiders (Eisner and Camazine, 1983; Amaya et al., 2001) and mammals (Dubost and Gasc, 1987). In many animals, the autotomized appendage is not notably active after it has been disconnected from the individual that releases it. In some lizards, however, the autotomized tail often moves (sometimes vigorously) for a substantial amount of time following its detachment (Rumping and Jayne, 1996; Higham and Russell, 2010). Although it is understood that tails can move following autotomy, we know little about the time-varying patterns of neuromuscular activity that induce these movements.

Tail autotomy in lizards is effective in distracting predators, either by providing a visual stimulus or by sacrificing a portion of the body that the predator can consume (Congdon et al., 1974; Vitt et al., 1977; Arnold, 1984; Cooper and Vitt, 1985; Maginnis, 2006; Bateman and Fleming, 2009). Once autotomized, the tails of some

lizards routinely move in a variety of ways, involving jumps and flips, as well as rhythmic swings (Higham and Russell, 2010). Most research focusing on autotomy in lizards has concentrated on the alteration of performance, energetics and/or behavior of the lizard, not the tail. For example, running speed may increase significantly following autotomy, which enhances the ability of the lizard to escape a predator (Daniels, 1983). But, conversely, the loss of the tail can impair jumping (Gillis et al., 2009), mid-air maneuvers (Jusufi et al., 2008) and stability while climbing (Jusufi et al., 2008), and can have social and fitness consequences such as altering reproductive abilities, survival potential, energetics and general behavior (Vitt et al., 1977; Maginnis, 2006). The benefits of distracting a predator apparently supersede these potential costs, and recent work has actually questioned the extent to which autotomy is costly (Fleming et al., 2009).

However, what about the tail following autotomy? Without influence from higher centers, the movement of the autotomized tail is likely driven primarily by central pattern generator (CPG) networks, which have been studied extensively in a variety of vertebrates and invertebrates (Brown, 1911; Harris-Warrick and Johnson, 1989; Harris-Warrick and Marder, 1991; Yakovenko et al., 2005; Chevallier et al., 2008; Whelan, 2010). Activation of CPG networks results in motoneuron output for rhythmic movements, such as those involved in respiration, mastication and locomotion

(Harris-Warrick, 2011). Although the basic principles regarding CPG networks are understood after countless studies, the modulation of locomotor behavior (e.g. switch between gaits) is still of great interest (Harris-Warrick and Marder, 1991; Crone et al., 2009). Although normal locomotor behavior can be triggered by the midbrain and the hindbrain, recent work has also indicated that the rhythmicity associated with locomotion can be triggered from activity in intrinsic spinal cells (Kiehn, 2011). Because of the lack of higher control, movements of autotomized lizard tails are an excellent system for studying CPG networks and the modulation of movement patterns.

Two studies have examined muscle activity patterns using electromyography (EMG) in the autotomized tails of geckos (Rumping and Jayne, 1996; Higham and Russell, 2010). These studies revealed interesting differences between an arboreal gecko (Rumping and Jayne, 1996) and a desert-dwelling terrestrial gecko (Higham and Russell, 2010). Unlike the arboreal gecko, the tail of the terrestrial gecko exhibits complex motor patterns that result in diverse and highly variable movements. The origins of this complex movement pattern have yet to be determined, but might result from the interaction between multiple rhythm generators (Fig. 1), as occurs in the developing rat spinal cord (Demir et al., 2002). However, it is also quite possible that these complex motor patterns result from control mediated by independent neural pathways, at least one of which is sensitive to feedback from the external environment (Fig. 1). In this paper we explore the possibilities that were raised in an earlier study (Higham and Russell, 2010).

We quantified the time-varying patterns of motor activity at four different locations within autotomized tails of leopard geckos (*Eublepharis macularius* Blyth 1854) in order to address the following questions: (1) do the motor patterns underlying complex tail movements follow a pattern consistent with that of overlapping pattern generators (Fig. 1); (2) how do the motor patterns change with time following autotomy; and (3) does the coordination of motor patterns between EMG sites differ during complex behaviors compared with rhythmic movements?

MATERIALS AND METHODS

Four individuals of *E. macularius* (body mass: 5.2 ± 0.4 g; tail mass: 0.6 ± 0.1 g; snout–vent length: 61 ± 0.7 mm; tail length: 47 ± 0.8 mm) with original tails were anaesthetized *via* an intramuscular injection of ketamine (100 mg kg^{-1}). Bipolar stainless steel hook electrodes (0.05 mm diameter, California Fine Wire Co., Grover Beach, CA, USA) (for details, see Higham and Jayne, 2004), of sufficient length not to impede tail movement, were used. Once anaesthetized, electrodes were implanted percutaneously into four dorsolateral locations along the length of the tail, two proximal (right and left at 25% of the tail length) and two distal (right and left at 75% of the tail length), using 26-gauge hypodermic needles. Once each lizard had fully recovered, the base of the tail was lightly pinched to initiate maximal autotomy (i.e. at the proximal-most plane of autotomy) and the tail was placed immediately in the filming arena. Following experiments, tails were fixed and preserved, and electrode locations were verified.

Kinematics

A high-speed video camera (Photron APX-RS, San Diego, CA, USA) captured the movements of the tail at $120 \text{ frames s}^{-1}$, which provided the capacity to record the initial 50 s following autotomy. The camera was oriented lateral to the filming arena, and a mirror (oriented at 45 deg above the arena) provided a dorsal view. In addition, a second camera (Casio EX-F1 Exilim Pro, Dover City,

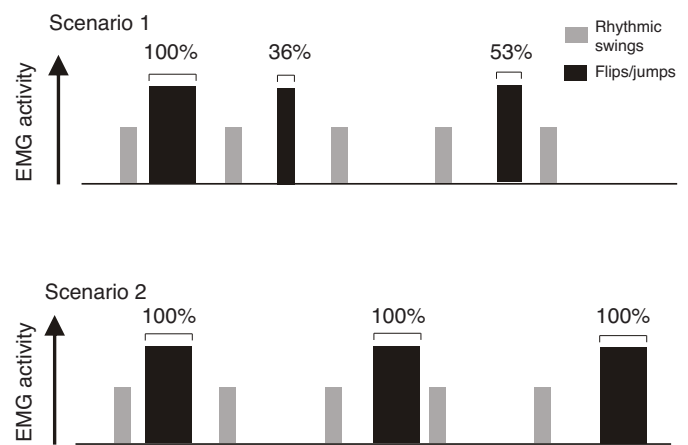


Fig. 1. Two potential scenarios leading to the patterns of electromyographic (EMG) activity that induce rhythmic swings and the more complex flips and jumps. The percentages above the bars indicate the duration (relative to the greatest duration) of each burst. Scenario 1 suggests that the rhythmic swings, but not the flips/jumps, arise from a central pattern generator. The origins of the bursts of activity that bring about the flips/jumps would be unknown in this scenario. Additionally, for this scenario, constant cycle duration is also unlikely for the impulses that drive the flips and jumps, as depicted. Ultimately, burst and cycle durations for the flips/jumps would have high coefficients of variation. Scenario 2 suggests that the flips/jumps and rhythmic swings result from independent but overlapping central pattern generators of different periodicity. For this scenario, the burst and cycle durations would likely be constant, resulting in low coefficients of variation.

NJ, USA) was used to capture (at 30 frames s^{-1}) the entire bout of tail movement, which lasted as long as 30 min. However, this was mainly for determining how long the tail moved following autotomy.

The tip and base of the tail were digitized in both the lateral and the dorsal view in order to determine how fast the tail moved, how much the tail moved and how high the tail moved during more complex behaviors. The two behaviors we identified previously (Higham and Russell, 2010) were confirmed as rhythmic swings (steady swinging within the x - z plane only) and more complex jumps and flips (unsteady movements with both horizontal and vertical components).

EMG analysis

EMG signals were amplified $1000\times$ and the data were sampled at 5 kHz using an MP150 Data Acquisition System (BIOPAC Systems, Inc., Goleta, CA, USA). The onset and offset of EMG activity was determined using previously determined methods (Roberts and Gabaldon, 2008). Burst duration was measured as the duration from burst onset to burst offset (Fig. 1). Cycle duration was quantified as the time between successive burst onsets (Fig. 1). Muscle activity was recorded for the initial 5 min following autotomy, and the initial 50 s was synchronized with the high-speed video recordings using an external trigger that initiated video recording and sent a 5 V signal to the data acquisition system. Some of the EMG variables are presented in a previous publication (Higham and Russell, 2010); others are described in more detail herein.

Statistics

To determine whether burst duration and cycle duration are more variable for flips and/or jumps than for rhythmic swings, we calculated the coefficients of variation (CVs) for these two patterns during the initial 30 s following autotomy. For each individual, we determined the mean CV for each site. Differences in CV between

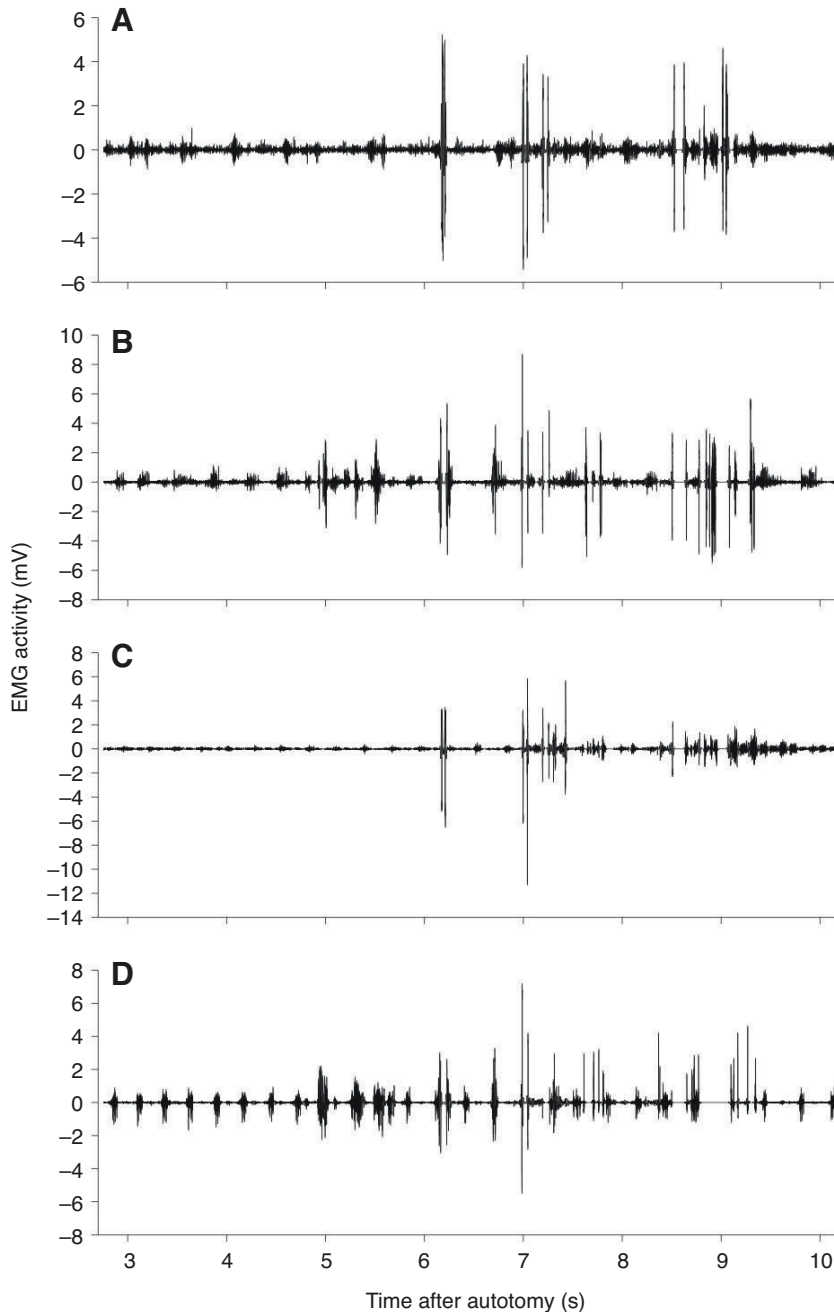


Fig. 2. Raw EMG traces for (A,B) the two proximal sites and (C,D) the two distal sites for approximately 8 s shortly after tail autotomy. A and C are from the left side of the animal, whereas B and D are from the right side. Note that these recordings include both rhythmic swings (initial seconds) and flips/jumps (after approximately 5 s).

the two categories of tail behavior were assessed using two-sample *t*-tests. To determine whether the coordination between EMG sites differed between rhythmic and complex tail movements, we calculated the delay in onset time between left and right sites at a given longitudinal station along the tail (i.e. proximal and distal). Using the means for each individual, differences in the delay were assessed using two-sample *t*-tests. A *P*-value of <0.05 was the criterion for statistical significance. For all analyses, the data were log-transformed in order to normalize them. Unless indicated, all values are presented as means \pm s.e.m.

RESULTS

Following autotomy, every tail exhibited both rhythmic swings and more complex jumps and flips, with distinct EMG bursts associated with each of these behaviors (Fig. 2). Unlike tail movement during

locomotion, which has a relatively low frequency [approximately 2 Hz in *E. macularius* (Fuller et al., 2011)], the autotomized tail exhibits a relatively high frequency of movement [approximately 8 Hz (Higham and Russell, 2010)]. The complex flips and jumps did not persist throughout the duration of tail movement, which can last up to 30 min, but instead typically ceased within the first few minutes.

The mean burst duration of rhythmic tail movements was approximately 0.05 s immediately following autotomy (Fig. 3A). However, this quickly increased, reaching a duration of approximately 0.13 s at approximately 120 s following autotomy. Burst duration eventually settled at a plateau after approximately 150 s following autotomy, and maintained a relatively constant burst duration (approximately 0.16 s) for the remainder of time following autotomy. Mean cycle duration increased for the 5 min that we

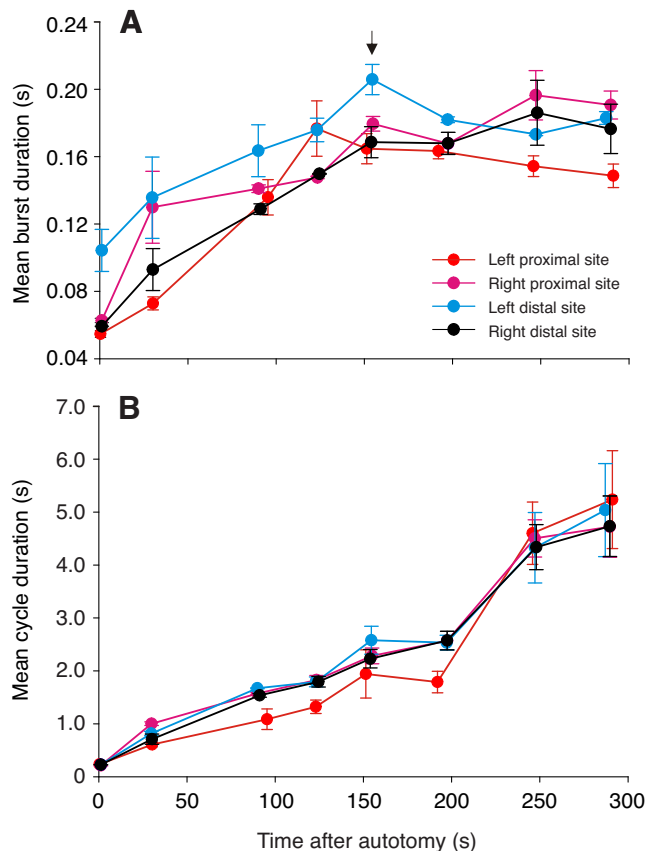


Fig. 3. Mean (\pm s.e.m.) burst (A) and cycle (B) durations of the rhythmic swings for the first 300 s following tail autotomy. Note that burst duration reaches a plateau at approximately 150 s (arrowhead), whereas cycle duration continues to increase with time. $N=4$ individuals.

recorded following autotomy, starting at approximately 0.2 s and reaching approximately 5 s at 300 s following autotomy (Fig. 3B). Cycle duration also became more variable over time (Fig. 3B).

Burst duration (two-sample t -test, $P=0.001$; Fig. 4) and cycle duration (two-sample t -test, $P<0.001$; Fig. 4) were both significantly more variable (as indicated by higher values of CV) for flips/jumps than they were for rhythmic swings. For example, the mean CV was approximately three times greater for burst duration and almost 10 times greater for cycle duration for flips/jumps than for rhythmic swings (Fig. 4).

For the initial 30 s following autotomy at the proximal two sites, the onset delay between the left and right EMG sites was approximately 130 ms for rhythmic tail movements and 20 ms for flips/jumps (two-sample t -test, $P<0.001$; Fig. 5A). For this same time period at the distal two sites, the onset delay between the left and right EMG sites was approximately 90 ms for rhythmic tail movements and 15 ms for flips/jumps (two-sample t -test, $P=0.002$; Fig. 5B). Thus, contralateral sites at the same station were co-activated (recruited almost simultaneously) during flips/jumps, but exhibited no overlap in activity during rhythmic swings.

DISCUSSION

We explored the time-varying motor patterns at four sites in the tail following autotomy in the leopard gecko, *E. macularius*. The results reveal interesting changes in burst and cycle duration along this time course. A key result is that the burst and cycle durations are

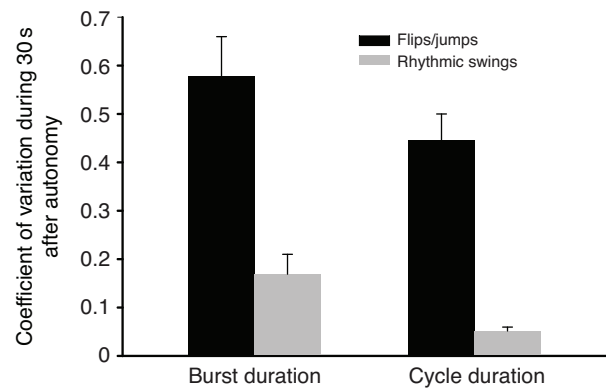


Fig. 4. Mean (\pm s.e.m.) coefficients of variation during the initial 30 s following tail autotomy for burst (left bars) and cycle (right bars) duration during flips/jumps (black) and rhythmic swings (gray). These data are combined from all four sites. Note that for burst and cycle durations, the coefficients of variation do not result from the activities of overlapping pattern generators (Fig. 6). Instead, it appears that the movements associated with rhythmic swings are controlled by a CPG, but those controlling jumps and flips emanate from an alternative, but unknown, neural circuit that could potentially respond to sensory information in the environment or to feedback from muscle proprioceptors. These results are discussed in more detail below.

more variable for jumps and flips than they are for rhythmic swings. This, coupled with the fact that the relative timing of muscular activation among sites differs markedly between tail movement behaviors, suggests that the complex tail movements following autotomy do not result from the activities of overlapping pattern generators (Fig. 6). Instead, it appears that the movements associated with rhythmic swings are controlled by a CPG, but those controlling jumps and flips emanate from an alternative, but unknown, neural circuit that could potentially respond to sensory information in the environment or to feedback from muscle proprioceptors. These results are discussed in more detail below.

Multiple neural pathways?

What are the origins of the signals driving the complex tail movements? Our results support the idea that a minimum of two independent neural circuits are active in the tail (Fig. 6). One provides the source of the regularly repeating rhythmic signals that are present throughout the duration of tail movements following autotomy. The other is transient and actuates the complex flips and jumps. The rhythmic signal appears to be the one that dominates in the lizard species that have been studied (Rumping and Jayne, 1996). Such a rhythmic signal is characteristic of CPGs in other vertebrates (Chevallier et al., 2008), associated with lateral undulatory patterns along the long axis of the body, and is interpreted here as the primitive condition. The alternative signal, driving the flips and jumps, is more erratic and is possibly sensitive to feedback (external or internal). In addition, it appears that it likely innervates primarily fast-twitch glycolytic fibers that are capable of high-power bursts given that complex flips and jumps, unlike rhythmic swings, do not persist for the duration of tail movement following autotomy. Indeed, the complex flips and jumps essentially are only evident for the first 80–120 s (2 min) following autotomy, whereas the rhythmic swings persist, at diminishing intensity, for as long as 1800 s (30 min).

A key unanswered question is how the additional neural pathway is activated. Three potential explanations are as follows: (1) random firing until fatigued, (2) the pathway is sensitive to environmental input and is thus modulated or (3) the pathway is sensitive to muscle proprioceptors (muscle spindles or golgi tendon organs) and is thus modulated. The latter could be determined if tail movements were recorded while simultaneously monitoring the activity of afferent

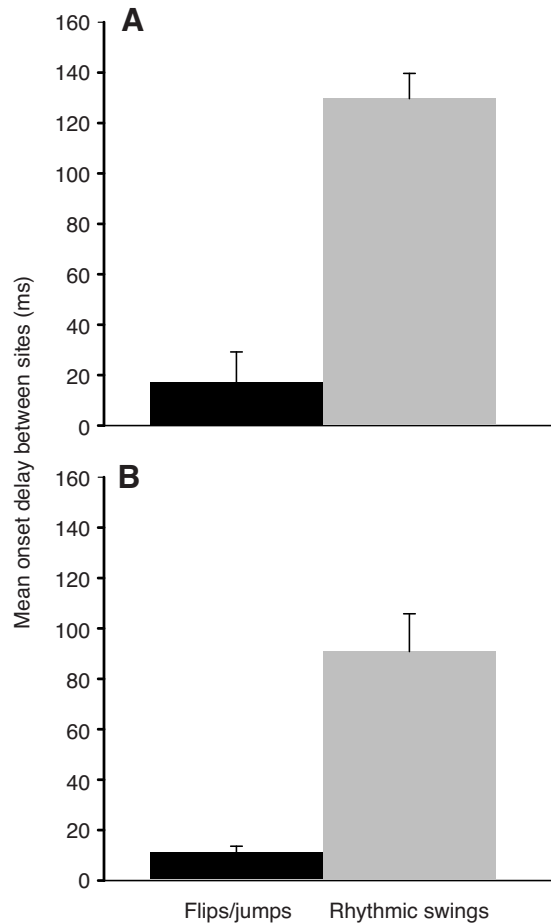


Fig. 5. Mean (\pm s.e.m.) delay in the time of EMG onset between the left and right (A) proximal and (B) distal sites. Note that a time of 0 ms would indicate the simultaneous activation of both sides. There was a significantly longer delay in activation between the two sides of the tail for rhythmic swings than flips/jumps. $N=4$ individuals.

sensory neurons originating from the surface of the tail. Epidermal sensory organs are likely present on the surface of the tail, and mechanical deformation of the surface of the skin would initiate their firing (Maclean, 1980). It is known that some geckos with specialized tails bear appropriately situated cutaneous mechanoreceptors that are sensitive to environmental disturbances (Russell and Bauer, 1987).

Regional coordination of motor patterns

To swing back and forth, as is typical of undulatory locomotion in vertebrates (Jayne and Lauder, 1995), an autotomized tail exhibits

alternating patterns of recruitment between the left and right sides (Higham and Russell, 2010). However, we found that during flips and jumps there is a significant period of co-activation between the left and right sides of the tail at a given station along the length of the tail (i.e. proximal and distal). In addition, there was only a short delay (<20 ms) between the onset of EMG activity on one side relative to the other (Fig. 5). What are the functional ramifications of such a recruitment pattern? Given that our electrodes were inserted dorsal to the horizontal septum, it is possible that this co-activation is one that results in activation of the epaxial muscles on both sides of the tail essentially simultaneously (in a given segment), resulting in a dorsal arching. This could also be the case for hypaxial muscles (separate recordings from epaxial and hypaxial muscle blocks in the same segment would permit determination of the periodicity of intrasegmental epaxial/hypaxial muscle activation patterns). Such simultaneous contralateral contractions would provide the motive power that permits the tail to push off from the substrate (initiating a jump).

Changes in motor patterns with time

Why would the burst duration, but not cycle duration, reach a plateau (Fig. 3)? It is understood that single motor unit discharge frequency diminishes shortly after the onset of maximum contractions. This has been termed 'muscle wisdom', based upon the observation that the firing rate of the motoneuron coincides with the decreased contractile speed of muscle (Marsden et al., 1983). Whether cycle duration can increase in order to match decreases in muscle function in an autotomized tail remains unknown. Alternatively, passive responses to changes in peripheral muscle function (fatigue) are likely. Acute peripheral fatigue can occur at any of the steps involved in excitation–contraction coupling, but also as a result of the acute effects of metabolic changes on contractile protein function (Westerblad and Allen, 2002). Specifically, fatigue in the autotomized tail could result from a build up of metabolic byproducts (Westerblad et al., 2002) or altered ionic concentrations and fluxes (Fitts, 1994). This could alter cell excitability and result in the continual increase in cycle duration that we observed (Fig. 3). However, future work assessing these variables will provide further details regarding the mechanisms underlying the changes in motor pattern.

Potential link between lizard tails and gait change in vertebrates

Animals commonly shift gaits as they change their speed of locomotion (Hoyt and Kenagy, 1988; Alexander, 1989; Gillis and Biewener, 2001; Korsmeyer et al., 2002; Vanhooydonck et al., 2002; Nudds et al., 2011). For example, a diverse array of vertebrate species, both aquatic and terrestrial, switch from alternating limb or fin movements at slower speeds to synchronous limb or fin movements at higher speeds (Alexander, 1989). Interestingly, mice typically use a single gait (trotting) over a range of speeds (Herbin et al., 2007).

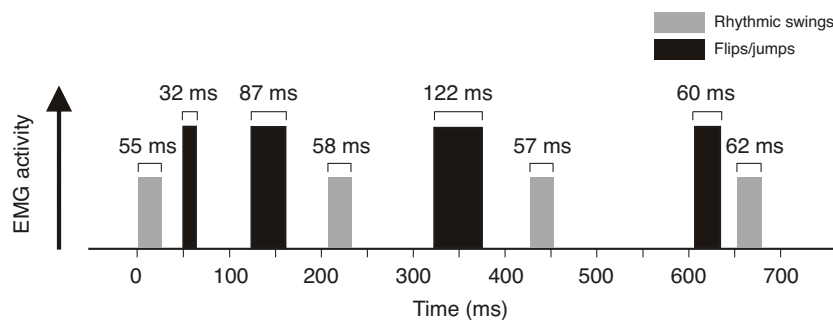


Fig. 6. A schematic that includes representative EMG burst and cycle durations (shown above each bar) from a proximal site in the tail of one individual during the initial 700 ms following autotomy. Other individuals and sites show similar results. These results support scenario 1 (see Fig. 1), providing evidence that the rhythmic swings, but not the flips/jumps, arise from a central pattern generator. Both the burst and cycle durations for the flips/jumps have high coefficients of variation compared with the rhythmic swings.

Using this system's employment of a single gait over a range of speeds, recent work has highlighted the important role played by interneurons in the spinal cord in the speed-dependent change in gait (Crone et al., 2009). The latter study utilized transgenic mice in which V2a interneurons were ablated. These mice exhibited normal trotting gaits at slower speeds, but, unlike normal mice, switched to a galloping gait at higher speeds (Crone et al., 2009). Although normal mice are quite capable of switching from a trot to a gallop at higher speeds (Heglund and Taylor, 1988), Crone et al. (Crone et al., 2009) likely did not observe this change because of the limited speed range examined in their study. Despite this, Crone et al. (Crone et al., 2009) observed a change in gait at a slower speed in their experimental animals when compared with the normal mice.

Typically, the relative activity of excitatory and inhibitory interneuron pathways determines the gait used by an animal (Kullander et al., 2003). For example, this likely triggers the different sets of spinal neurons that are recruited during different gaits in zebrafish. The muscular activity patterns underlying the two different behaviors in the autotomized tails of our study exhibit striking similarities to those patterns found in different locomotor gaits of vertebrates. During slower movements, the left and right sides of the tail exhibit alternating contractions (comparable to a trot in terrestrial vertebrates), resulting in the rhythmic swinging behavior. The complex jumps and flips exhibit relatively synchronous activity of the left and right sides of the tail, which is characteristic of a galloping, or bounding, gait in terrestrial vertebrates. We hypothesize that the underlying switch between these two 'gaits' of the gecko tail is similar to the switch found in other vertebrates during gait transitions. Lizards use a trotting gait over their range of locomotor speeds (McElroy et al., 2008). Given this lack of gait change, it is interesting that the autotomized tail undergoes a physiological change in gait that is never evident in the intact animal.

Future directions

The autotomized tail, which contains a portion of the spinal cord, is a self-initiated preparation and is ostensibly harmless to the lizard. The neural pathways have not been characterized, but this is a next logical step. In addition, the tail regenerates following autotomy. Are the complex neural pathways re-formed in the regenerated tail? Original and re-formed neural pathways could be characterized using immunocytological and gross histological techniques employing confocal microscopy (Thorsen and Hale, 2007). In addition, motor pools in the spinal cord could be visualized using fluorescent retrograde labeling (Thorsen and Hale, 2007). By determining the anatomical arrangements of the neural pathways in the tail, and what controls the tail once it is separated from the lizard's body, we will begin to understand how complex tail movements can be modulated in the absence of higher control.

ACKNOWLEDGEMENTS

We thank Melina Hale for discussing some of the ideas presented in this manuscript. Members of the Higham Laboratory also helped with animal care.

FUNDING

This study was funded using start-up funds from Clemson University to T.E.H.

REFERENCES

Alexander, R. M. (1989). Optimization and gaits in the locomotion of vertebrates. *Physiol. Rev.* **69**, 1199-1227.
 Amaya, C. C., Klawinski, P. D. and Formanowicz, D. R., Jr (2001). The effects of leg autotomy on running speed and foraging ability in two species of wolf spider (*Lycosidae*). *Am. Midl. Nat.* **145**, 201-205.
 Arnold, E. N. (1984). Evolutionary aspects of tail shedding in lizards and their relatives. *J. Nat. Hist.* **18**, 127-169.

Barrios, J. V., Gaymer, C. F., Vasquez, J. A. and Brokordt, K. B. (2008). Effect of degree of autotomy on feeding, growth, and reproductive capacity in the multi-armed sea star *Helaster helianthus*. *J. Exp. Mar. Biol. Ecol.* **361**, 21-27.
 Bateman, P. W. and Fleming, P. A. (2009). To cut a long tail short: a review of lizard caudal autotomy studies carried out over the last 20 years. *J. Zool.* **277**, 1-14.
 Brown, T. G. (1911). The intrinsic factors in the act of progression in the mammal. *Proc. R. Soc. Lond. B* **84**, 308-319.
 Chevillier, S., Ijspeert, A. J., Ryzcko, D., Nagy, F. and Cabelguen, J. M. (2008). Organisation of the spinal central pattern generators for locomotion in the salamander: biology and modelling. *Brain Res. Rev.* **57**, 147-161.
 Congdon, J. D., Vitt, L. J. and King, W. W. (1974). Geckos: adaptive significance and energetics of tail autotomy. *Science* **184**, 1379-1380.
 Cooper, W. E., Jr and Vitt, L. J. (1985). Blue tails and autotomy: enhancement of predation avoidance in juvenile skinks. *Z. Tierpsychol.* **70**, 265-276.
 Crone, S. A., Zhong, G., Harris-Warrick, R. and Sharma, K. (2009). In mice lacking V2a interneurons, gait depends on speed of locomotion. *J. Neurosci.* **29**, 7098-7109.
 Daniels, C. B. (1983). Running: an escape strategy enhanced by autotomy. *Herpetologica* **39**, 162-165.
 Demir, R., Gao, B., Jackson, M. B. and Ziskind-Conhaim, L. (2002). Interactions between multiple rhythm generators produce complex patterns of oscillation in the developing rat spinal cord. *J. Neurophysiol.* **87**, 1094-1105.
 Dial, B. E. and Fitzpatrick, L. C. (1983). Lizard tail autotomy: function and energetics of postautotomy tail movement in *Scincella lateralis*. *Science* **219**, 391-393.
 Dubost, G. and Gasc, J.-P. (1987). The process of total tail autotomy in the South-American rodent, *Proechimys*. *J. Zool.* **212**, 563-572.
 Eisner, T. and Camazine, S. (1983). Spider leg autotomy induced by prey venom injection: an adaptive response to "pain"? *Proc. Natl. Acad. Sci. USA* **80**, 3382-3385.
 Fitts, R. H. (1994). Cellular mechanisms of muscle fatigue. *Physiol. Rev.* **74**, 49-94.
 Fleming, P. A., Verburg, L., Scantlebury, M., Medger, K. and Bateman, P. W. (2009). Jettisoning ballast or fuel? Caudal autotomy and locomotor energetics of the cape dwarf gecko *Lygodactylus capensis* (Gekkonidae). *Physiol. Biochem. Zool.* **82**, 756-765.
 Fuller, P. O., Higham, T. E. and Clark, A. J. (2011). Posture, speed, and habitat structure: three-dimensional hindlimb kinematics of two species of padless gecko. *Zoology* **114**, 104-112.
 Gillis, G. B. and Biewener, A. A. (2001). Hindlimb muscle function in relation to speed and gait: *in vivo* patterns of strain and activation in a hip and knee extensor of the rat (*Rattus norvegicus*). *J. Exp. Biol.* **204**, 2717-2731.
 Gillis, G. B., Bonvini, L. A. and Irschick, D. J. (2009). Losing stability: tail loss and jumping in the arboreal lizard *Anolis carolinensis*. *J. Exp. Biol.* **212**, 604-609.
 Harris-Warrick, R. M. (2011). Neuromodulation and flexibility in central pattern generator networks. *Curr. Opin. Neurobiol.* **21**, 685-692.
 Harris-Warrick, R. M. and Johnson, B. R. (1989). Motor pattern networks: flexible foundations for rhythmic pattern production. In *Perspectives in Neural Systems and Behavior* (ed. T. J. Carew and D. B. Kelley), pp. 51-71. New York: Liss.
 Harris-Warrick, R. M. and Marder, E. (1991). Modulation of neural networks for behavior. *Annu. Rev. Neurosci.* **14**, 39-57.
 Heglund, N. C. and Taylor, C. R. (1988). Speed, stride frequency and energy cost per stride: how do they change with body size and gait? *J. Exp. Biol.* **138**, 301-318.
 Herbin, M., Hackert, R., Gasc, J.-P. and Renous, S. (2007). Gait parameters of treadmill versus overground locomotion in mouse. *Behav. Brain Res.* **181**, 173-179.
 Higham, T. E. and Jayne, B. C. (2004). *In vivo* muscle activity in the hindlimb of the arboreal lizard, *Chamaeleo calyptratus*: general patterns and effects of incline. *J. Exp. Biol.* **207**, 249-261.
 Higham, T. E. and Russell, A. P. (2010). Flip, flop and fly: modulated motor control and highly variable movement patterns of autotomized gecko tails. *Biol. Lett.* **6**, 70-73.
 Hoyt, D. F. and Kenagy, G. J. (1988). Energy costs of walking and running gaits and their aerobic limits in golden-mantled ground squirrels. *Physiol. Zool.* **61**, 34-40.
 Jayne, B. C. and Lauder, G. V. (1995). Red muscle motor patterns during steady swimming in largemouth bass: effects of speed and correlations with axial kinematics. *J. Exp. Biol.* **198**, 1575-1587.
 Jusufi, A., Goldman, D. I., Revzen, S. and Full, R. J. (2008). Active tails enhance arboreal acrobatics in geckos. *Proc. Natl. Acad. Sci. USA* **105**, 4215-4219.
 Kiehn, O. (2011). Development and functional organization of spinal locomotor circuits. *Curr. Opin. Neurobiol.* **21**, 100-109.
 Korsmeyer, K. E., Steffensen, J. F. and Herskin, J. (2002). Energetics of median and paired fin swimming, body and caudal fin swimming, and gait transition in parrotfish (*Scarus schlegelii*) and triggerfish (*Rhinecanthus aculeatus*). *J. Exp. Biol.* **205**, 1253-1263.
 Kullander, K., Butt, S. J., Lebre, J. M., Lundfald, L., Restrepo, C. E., Rydstrom, A., Klein, R. and Kiehn, O. (2003). Role of EphA4 and EphrinB3 in local neuronal circuits that control walking. *Science* **299**, 1889-1992.
 Maclean, S. (1980). Ultrastructure of epidermal sensory receptors in *Amphibolurus barbatus* (Lacertilis: Agamidae). *Cell Tissue Res.* **210**, 435-445.
 Maginnis, T. L. (2006). The costs of autotomy and regeneration in animals: a review and framework for future research. *Behav. Ecol.* **17**, 857-872.
 Marsden, C. D., Meadows, J. C. and Merton, P. A. (1983). "Muscular wisdom" that minimizes fatigue during prolonged effort in man: peak rates of motoneuron discharge and slowing of discharge during fatigue. *Adv. Neurol.* **39**, 169-211.
 McElroy, E. J., Hickey, K. L. and Reilly, S. M. (2008). The correlated evolution of biomechanics, gait and foraging mode in lizards. *J. Exp. Biol.* **211**, 1029-1040.
 Nudds, R. L., Folkow, L. P., Lees, J. J., Tickle, P. G., Stokkan, K. A. and Codd, J. R. (2011). Evidence for energy savings from aerial running in the Svalbard rock ptarmigan (*Lagopus muta hyperborea*). *Proc. R. Soc. Lond. B* **278**, 2654-2661.
 Roberts, T. J. and Gabalton, A. M. (2008). Interpreting muscle function from EMG: lessons learned from direct measurements of muscle force. *Integr. Comp. Biol.* **48**, 312-320.
 Rumping, J. M. and Jayne, B. C. (1996). Muscle activity in autotomized tails of a lizard (*Gekko gekko*): a naturally occurring spinal preparation. *J. Comp. Physiol. A* **179**, 525-538.

- Russell, A. P. and Bauer, A. M.** (1987). Caudal morphology of the knob-tailed geckos, genus *Nephurus* (Reptilia: Gekkonidae), with special reference to the tail tip. *Aust. J. Zool.* **35**, 541-551.
- Thorsen, D. H. and Hale, M. E.** (2007). Neural development of the zebrafish (*Danio rerio*) pectoral fin. *J. Comp. Neurol.* **504**, 168-184.
- Vanhooydonck, B., Van Damme, R. and Aerts, P.** (2002). Variation in speed, gait characteristics and microhabitat use in lacertid lizards. *J. Exp. Biol.* **205**, 1037-1046.
- Vitt, L. J., Congdon, J. D. and Dickson, N. A.** (1977). Adaptive strategies and energetics of tail autotomy in lizards. *Ecology* **58**, 326-337.
- Wake, D. B. and Dresner, I. G.** (1967). Functional morphology and evolution of tail autotomy in salamanders. *J. Morphol.* **122**, 265-305.
- Westerblad, H. and Allen, D. G.** (2002). Recent advances in the understanding of skeletal muscle fatigue. *Curr. Opin. Rheumatol.* **14**, 648-652.
- Westerblad, H., Allen, D. G. and Lannergren, J.** (2002). Muscle fatigue: lactic acid or inorganic phosphate the major cause? *News Physiol. Sci.* **17**, 17-21.
- Whelan, P. J.** (2010). Shining light into the black box of spinal locomotor networks. *Philos. Trans. R. Soc. Lond. B* **365**, 2383-2395.
- Yakovenko, S., McCrea, D. A., Stecina, K. and Prochazka, A.** (2005). Control of locomotor cycle duration. *J. Neurophysiol.* **94**, 1057-1065.
- Zani, P. A.** (1996). Patterns of caudal-autotomy evolution in lizards. *J. Zool.* **240**, 201-220.