

Flip, flop and fly: modulated motor control and highly variable movement patterns of autotomized gecko tails

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Many animals lose and regenerate appendages, and tail autotomy in lizards is an extremely well-studied example of this. Whereas the energetic, ecological and functional ramifications of tail loss for many lizards have been extensively documented, little is known about the behaviour and neuromuscular control of the autotomized tail. We used electromyography and high-speed video to quantify the motor control and movement patterns of autotomized tails of leopard geckos (*Eublepharis macularius*). In addition to rhythmic swinging, we show that they exhibit extremely complex movement patterns for up to 30 min following autotomy, including acrobatic flips up to 3 cm in height. Unlike the output of most central pattern generators (CPGs), muscular control of the tail is variable and can be arrhythmic. We suggest that the gecko tail is well suited for studies involving CPGs, given that this spinal preparation is naturally occurring, requires no surgery and exhibits complex modulation.

Keywords: tail autotomy; leopard gecko; central pattern generator; lizard; predator avoidance

1. INTRODUCTION

Autotomy is the process by which an appendage is voluntarily shed from the body of an animal and has arisen independently many times. It occurs in reptiles, amphibians, mammals and many groups of invertebrates (Dubost & Gasc 1987; Clause & Capaldi 2006). For over 100 years, lizard tail autotomy has captured the attention of scientists (Poulton 1895). It distracts predators during predator–prey interactions by providing a visual stimulus that entices the predator to attack the tail rather than the lizard (Arnold 1984; Bateman & Fleming 2009). In addition, tail loss can significantly increase the running speed, which also enhances the ability of a lizard to escape a predator (Daniels 1983), although it can also decrease the running speed in some taxa (Formanowicz *et al.* 1990). Whereas tail loss is beneficial to the lizard in terms of acute survival, several costs are also incurred. For example, tails are very important for jumping (Gillis *et al.* 2009), mid-air manoeuvres (Jusufi *et al.* 2008)

and for support while climbing (Jusufi *et al.* 2008), and tail loss significantly impairs these behaviours. The loss of a tail can also alter reproductive behaviour and output, survival and general behaviour (Maginnis 2006).

The ecological and functional costs and benefits of tail autotomy in lizards have a rich research history, but far less is known about tail function following autotomy. A single study using electromyography to examine muscle activity patterns of autotomized gecko (*Gekko gecko*) tails found that motor control is rhythmic, as are the outputs of most central pattern generators (CPGs) (Rumping & Jayne 1996). However, no study has quantified movement patterns of autotomized tails, and therefore no link between these and the underlying motor patterns has been established. In addition, qualitative observations suggest that tail movement can be elaborate and not simply rhythmic (Poulton 1895; Cooper *et al.* 2004). How can a tail that lacks higher control perform complex behaviours? Are complex motor patterns responsible? We quantified the three-dimensional movements and motor patterns of autotomized original tails (not previously autotomized) of *Eublepharis macularius* in order to determine whether tail movements and motor patterns are rhythmic and stereotyped, as is the case for other spinal preparations.

2. MATERIAL 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) 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., USA) (see Higham & Jayne 2004 for details), 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) and two distal (right and left) using 26-gauge hypodermic needles. Once the lizards had fully recovered, the base of the tail was lightly pinched to initiate maximal autotomy and the tail was placed immediately in the filming arena. Electromyographic (EMG) signals were amplified 1000 \times and the data were sampled at 5 kHz (BIOPAC Systems, Inc. MP150). Burst duration was measured as the duration from burst onset to burst offset. Rectified integrated area (RIA) was measured as the area enclosed by the absolute values of the digital voltages. Following experiments, tails were fixed and preserved and electrode locations verified.

A high-speed video camera (Photron APX-RS) captured the movements of the tail at 120 fps, which provided the capacity to record the initial 50 s following autotomy. The camera was orientated lateral to the filming arena, and a mirror (oriented at 45° above the arena) provided a dorsal view. In addition, a second camera (Casio EX-F1 Exilim Pro) was used to capture (at 30 fps) the entire bout of tail movement, which lasted as long as 30 min.

3. RESULTS AND DISCUSSION

Once autotomized, the tail tips swung rapidly back and forth (figure 1), commonly exceeding 250 cm s^{-1} . Interspersed with these rhythmic bouts were complex jumps, flips and lunges (figure 1). In contrast to the four to eight rhythmic movements per second, one to two complex movements typically occurred during the first 50 s following autotomy. Flips resulted in the tail being launched into the air by the tip of the tail pushing against the arena floor (figure 1). Almost all flips occurred in the absence of contact with the wall of the filming arena. However, the tails almost always lunged (rather than flipped) following contact with the arena wall by pushing with the tip and moving more horizontally than vertically.

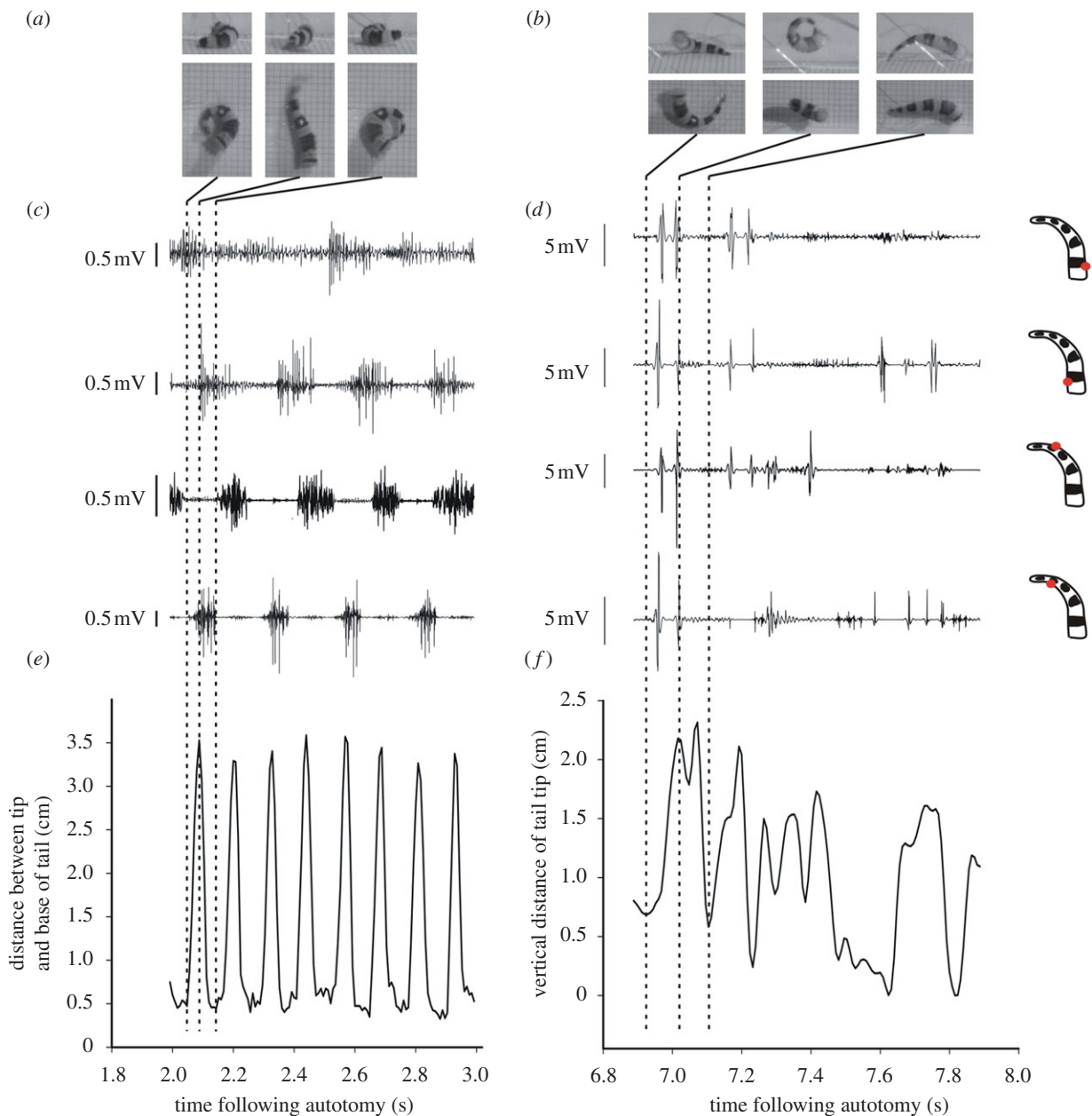


Figure 1. Motor patterns and movements (*a,c,e*) during rhythmic swinging and (*b,d,f*) during complex tail movements. (*a,b*) Images taken directly from video corresponding with the vertical dashed bars. (*c,d*) Representative EMG signals for each of the four sites in the tail (indicated by red dots on diagrams to the right of the graphs) for one individual. Note the difference in the vertical scale between (*c*) and (*d*). (*e*) Measured distance between the tip and base of the tail for eight consecutive rhythmic swings. (*f*) Measured vertical distance between the tip of the tail and the surface of the filming arena.

For regular rhythmic swings, EMG bursts alternated from side to side and signals were propagated anteriorly (figure 1). Activity on one side typically ceased prior to the onset of bending in the opposite direction (figure 1). Whereas EMG duration was not influenced by the type of behaviour ($p > 0.05$, t -test), jumps and flips exhibited a significantly higher RIA compared with rhythmic swings (figure 2; $p < 0.05$, t -test), indicating that they require a significantly higher level of motor unit recruitment than do rhythmic motions. This suggests that not all of the tail's motor units are recruited during regular rhythmic motions, but probably are during more vigorous movements. An emergent question from this is why the tail does not simply recruit all of the motor units available and perform more ballistic movements from the onset of autotomy? One benefit is that

the tail is able to move for a much longer period of time by not recruiting all of the available motor units (and thus avoiding muscle fatigue).

Previous work revealed that autotomized tails of *G. gecko* exhibit rhythmic motor patterns with a very low coefficient of variation (Rumping & Jayne 1996). However, it is unclear whether the movements of the tails were strictly rhythmic. One explanation for the potential differences between studies could be that only some species exhibit complex tail movements post-autotomy. Previous work indicates that species occupying more exposed habitats tend to experience higher frequencies of autotomy (Bateman & Fleming 2009). As such, species that live in more exposed and two-dimensional habitats (leopard geckos occupy exposed desert habitats, as opposed to the trees

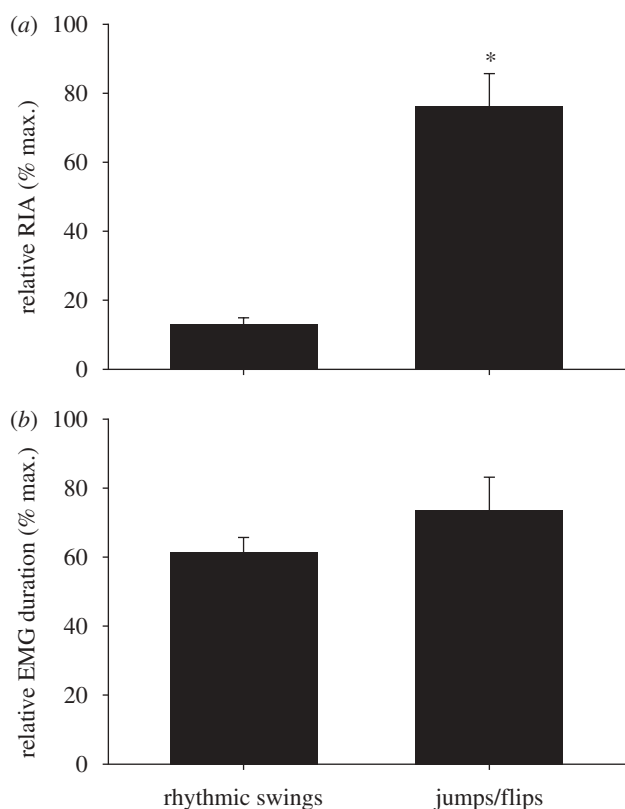


Figure 2. Tail behaviour and motor patterns. (a) Mean RIA (relative to maximum observed for each individual) for rhythmic swings and complex behaviours (jumps and flips) for the right distal electrode location, $n = 4$ individuals. (b) Mean EMG duration (relative to maximum observed for each individual) for rhythmic swings and complex behaviours (jumps and flips) for the right distal electrode location. These patterns were comparable in all four electrode locations. Values are mean \pm s.e.m. * $p < 0.05$ for differences between tail movement categories (t -test).

occupied by Tokay geckos) might also exhibit more complex tail movement, as seen in our study, because the nature of the terrain is more conducive to the employment of such kinematically complex behaviours. In addition to ecological differences, the two species are phylogenetically disparate (Gamble *et al.* 2008). Thus, tails of species of *Gekko* may lack the ability to perform more dynamic behaviours such as jumping and flipping. Future work examining tail behaviour and motor control in a comparative context will aid in our understanding of the evolution of post-autotomic tail behaviour.

Tail behaviour following autotomy in *Eublepharis* exhibits several features that maximize distraction of a predator. First, the high-speed movements of the tail tip makes it stand out relative to the surrounding environment, which enhances the likelihood that the tail, rather than the lizard, will be pursued by a visually oriented predator. Although a predator will be able to hone in on the rhythmic movements of a tail over time, interspersing more complex movements, such as a jump or flip, will increase the unpredictability of tail movement, also decreasing the probability of capture. Finally, the complex flips result in considerable displacement of the tail over a short period of time, enabling the tail to maximize the use of space in the

environment and ultimately occupy the attention of the predator longer (Cooper *et al.* 2004). In addition to distracting a predator, which autotomized tails do (Dial & Fitzpatrick 1983), selection may have favoured the complex movements observed here so that the tail could completely evade the predator. This would allow a lizard to return to the site of autotomy and ingest the severed tail, as observed in the lab and field by Clark (1971). This would potentially compensate for the loss of high levels of lipids that are typically stored in the tails of geckos (Clark 1971).

The ability of an animal, or part of an animal, to move without the active control of higher centres in the brain is well known. This results from a network of neurons located within the spinal cord that is able to trigger a rhythmic pattern of motor output (i.e. CPG), which can be modulated by proprioceptive and/or exteroceptive sensory feedback (Gottschall & Nichols 2007). A key, and as yet unanswered, question is what the source of the stimulus is that initiates complex tail movements in leopard geckos? The most plausible explanation is a CPG that relies on sensory feedback from the environment. While this is probably the case, it appeared that many (if not most) of the jumps and flips occurred without any obvious cue from the environment. Thus, it is possible that the seemingly random signal is intrinsic and does not rely on environmental cues. Instead, the complex signal might be a result of the interaction between multiple rhythm generators, as occurring in the developing rat spinal cord (Demir *et al.* 2002). Future work exploring the origin of the signal and the mechanosensory receptivity of the isolated tail will provide insight into the generator involved in complex tail movements.

Studying CPGs generally involves surgically eliminating the link between the brain and spinal cord, yielding a spinal preparation (Sherrington 1909). Examples of spinal animals include cats (Gottschall & Nichols 2007), lamprey (Wallen & Williams 1984) and dogfish (Mos *et al.* 1990). All of these cases, however, exhibit rhythmic patterns of motion and have not been subjected to selection because the spinal preparation lacks an environmentally important biological role (Bock & von Wahlert 1965). Compared with these preparations, the gecko tail is ideal for studies of feedback mechanisms associated with CPGs because it is a naturally occurring, self-initiated spinal preparation resulting from selectively important self-mutilation rather than surgical invasion (Rumping & Jayne 1996). The autotomized gecko tail may be an excellent model for understanding the spontaneous activity that is sometimes observed following partial and complete spinal cord injury (Zijdewind & Thomas 2001).

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