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Neuromuscular control of prey capture in frogs

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While retaining a feeding apparatus that is surprisingly conservative morphologically, frogs as a group exhibit great variability in the biomechanics of tongue protraction during prey capture, which in turn is related to differences in neuromuscular control. In this paper, I address the following three questions. (1) How do frog tongues differ biomechanically? (2) What anatomical and physiological differences are responsible? (3) How is biomechanics related to mechanisms of neuromuscular control? Frog species use three non-exclusive mechanisms to protract their tongues during feeding: (i) mechanical pulling, in which the tongue shortens as its muscles contract during protraction; (ii) inertial elongation, in which the tongue lengthens under inertial and muscular loading; and (iii) hydrostatic elongation, in which the tongue lengthens under constraints imposed by the constant volume of a muscular hydrostat. Major differences among these functional types include (i) the amount and orientation of collagen fibres associated with the tongue muscles and the mechanical properties that this connective tissue confers to the tongue as a whole; and (ii) the transfer of inertia from the opening jaws to the tongue, which probably involves a catch mechanism that increases the acceleration achieved during mouth opening. The mechanisms of tongue protraction differ in the types of neural mechanisms that are used to control tongue movements, particularly in the relative importance of feed-forward versus feedback control, in requirements for precise interjoint coordination, in the size and number of motor units, and in the afferent pathways that are involved in coordinating tongue and jaw movements. Evolution of biomechanics and neuromuscular control of frog tongues provides an example in which neuromuscular control is finely tuned to the biomechanical constraints and opportunities provided by differences in morphological design among species.

Keywords: biomechanics; evolution; muscular hydrostats; tongues

1. INTRODUCTION

The comparative method is a powerful tool for discovering general principles of organization for at least two reasons. First, species that represent extremes of adaptation may reveal physiological processes that are too subtle to be readily apparent in less extreme forms. Second, groups of species that fall along a physiological continuum may also suggest hypotheses about underlying processes, especially when the species are relatively similar in other respects. The goal of this paper is to present the results of comparative studies on the neuromuscular control of prey capture in frogs. Frog species exhibit a continuum of variation in the biomechanics of the feeding apparatus, with extreme forms exhibiting nearly 90-fold variation among species in some aspects of feeding kinematics (table 1). At the same time, frogs are relatively conservative morphologically so that there are few confounding variables.

Although variation in animal morphology is readily apparent to even the most casual observer, variation in neuromuscular control among species is much less evident. Although there have been rather few comparative studies of neuromuscular control, there is little if any empirical evidence to support the idea that neuromuscular control differs significantly among morphologically divergent species. Comparative studies have tended to conclude, for example, that patterns of muscle activation are conserved during evolution (Peters & Goslow 1983; Wainwright *et al.* 1989). For example, all fishes and amphibians that have been studied show a similar pattern of rapid, simultaneous contraction of expansive phase muscles followed by contraction of compressive phase muscles during suction feeding (Lauder & Shaffer 1985; Lauder & Reilly 1988; Wainwright *et al.* 1989). The similarity in patterns of muscle activation among distantly related taxa led the authors to conclude that motor patterns evolve conservatively relative to morphology (Lauder 1981; Wainwright *et al.* 1989; Lauder & Shaffer 1993). However, as Smith (1994) points out, there is no reason to expect that muscle activity should change in such cases because homologous muscles in related taxa perform similar functions. Thus, a critical test of the 'motor conservatism hypothesis' requires examination of the evolution of neuromuscular control among taxa in which homologous muscles differ in function. Prey capture in frogs offers a unique opportunity to perform such a critical test.

2. MECHANISMS OF TONGUE PROTRACTION IN FROGS

Most frogs share several important features of the tongue: (i) it is attached anteriorly near the mandibular symphysis (figure 1); (ii) most of the fibres in both the protractor and retractor muscles are orientated nearly

Table 1. *A comparison of selected kinematic and behavioural characteristics of mechanical pullers* (Hyla, Discoglossus *and* Litoria), *inertial elongators* (Bufo *and* Phyllomedusa) *and hydrostatic elongators* (Hemisus *and* Dyscophus), *as well as aspects of neuromuscular control*

(Velocities and accelerations of the tongue tip are measured relative to the attachment of the tongue on the lower jaw.)

characteristics	mechanical pulling	inertial elongation	hydrostatic elongation
tongue movement	shortens	elongates to 180%	elongates to 200%
velocity ($\mathrm{cm\,s^{-1}}$)	15–50	250–400	*ca.* 24–240
acceleration ($\mathrm{m\,s^{-2}}$)	1.5–9.5	>310	*ca.* 3.5–145
tongue–jaw synchrony	no	yes	no
aiming	distance	head only	distance, azimuth, elevation
accuracy	*ca.* 95%	*ca.* 33%	>99%
on-line correction	yes	no	yes
feed-forward control	yes	yes	yes
feedback control	yes	no	yes
hypoglossal afferents	no	yes	no

parallel to the long axis of the tongue, so that their shortening either pulls the tongue pad toward the mental symphysis or toward the oesophagus (Horton 1982); (iii) the resting length of the tongue is approximately the length of the mandibles; and (iv) the mass of the tongue is *ca.* 1–2% of body mass. Yet, despite these similarities, comparative studies have identified three non-exclusive mechanisms that anurans use to protract their tongues during feeding (Nishikawa 1997, 1999). These are mechanical pulling, inertial elongation and hydrostatic elongation. It is important to note that the relative importance of these mechanisms differs among species, but all three mechanisms may occur to some extent in any given species.

In mechanical pulling (figure 2), the tongue shortens during protraction to *ca.* 60% of its resting length as the M. genioglossus contracts, pulling the tongue upward and forward toward the mandibular symphysis (Nishikawa & Cannatella 1991; Nishikawa & Roth 1991; Deban & Nishikawa 1992). The maximum reach of the shortening tongue is no more than a few millimetres beyond the tip of the jaws (figure 3). Because the tongue is short, mechanical pullers must lunge forward with their bodies to place their tongues on the prey (figure 3). Movements of the jaws and tongue are small compared with these lunging movements, and are also asynchronous (figure 4). The tongue tips of mechanical pullers reach moderate velocities (*ca.* 15–50 $\mathrm{cm\,s^{-1}}$) and accelerations (1.5–9.5 $\mathrm{m\,s^{-2}}$) during protraction, as measured from high-speed video in a coordinate system based at the attachment of the tongue to the lower jaw (table 1). Tongue movements can be corrected within the gape cycle but there is little if any ability to aim the tongue relative to the head in azimuth or elevation. Instead, aiming in these directions is achieved by turning the head toward the prey.

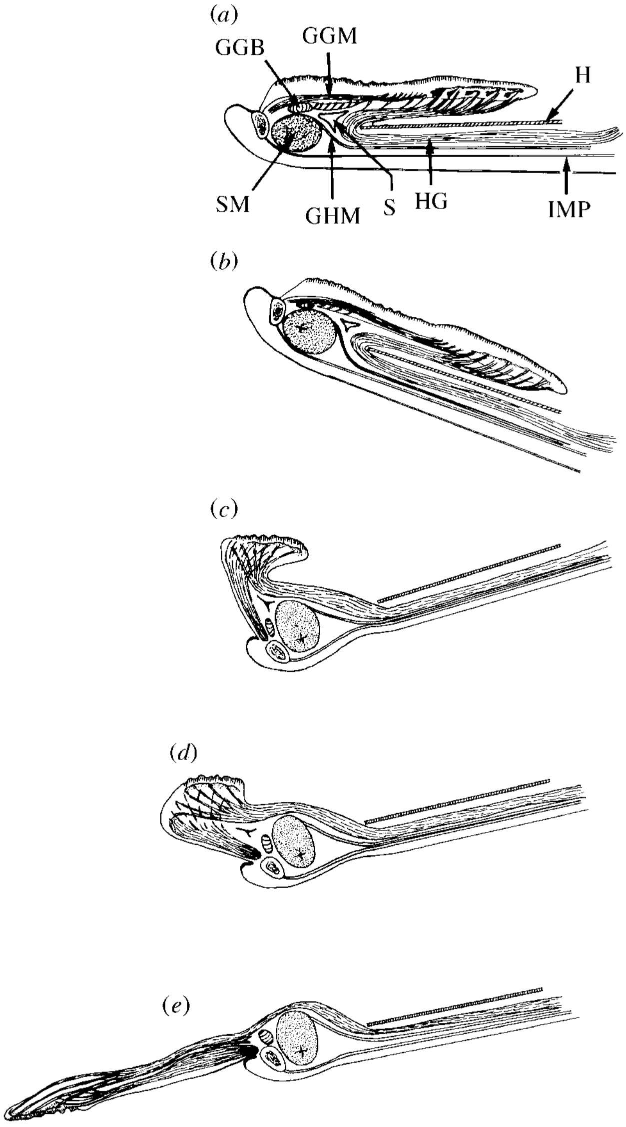
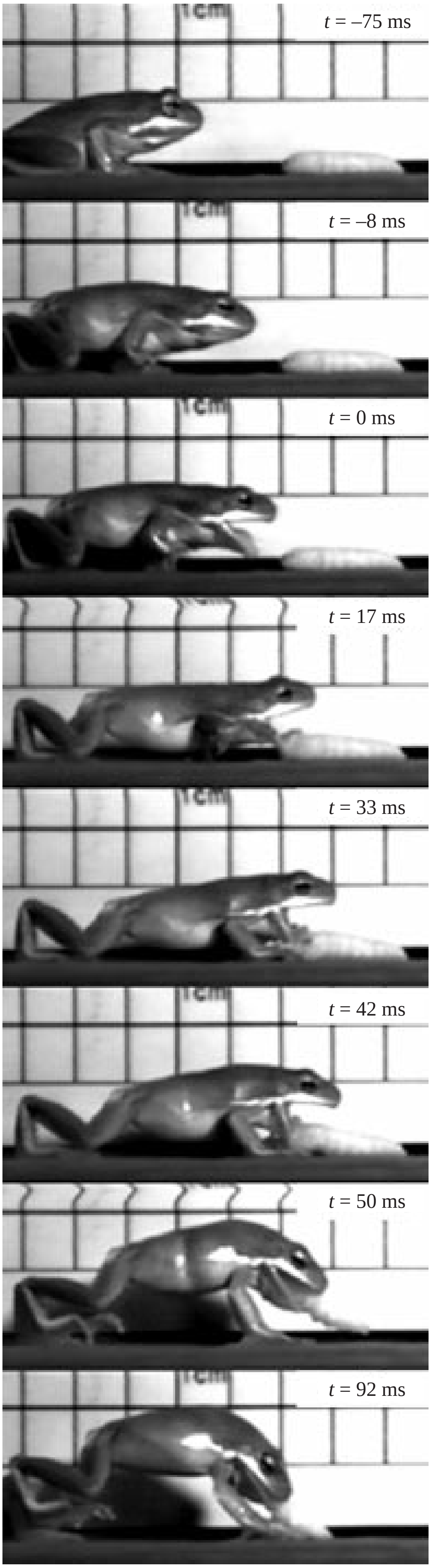


Figure 1. Schematic sagittal section through the tongue and lower jaw of a typical anuran (*B. marinus*) showing the anatomy of the tongue protractor (M. genioglossus = GG) and tongue retractor (M. hyoglossus = HG). The tongue at rest (*a*) is approximately as long as the lower jaw and is attached at the front of the mouth. During tongue protraction, the head is elevated (*b*), the mouth opens as the M. genioglossus contracts (*c*) and the tongue flips over the mandibles (*d*,*e*). Abbreviations: GGB, M. genioglossus basalis; GGM, M. genioglossus medialis; GHM, M. geniohyoideus medialis; SM, M. submentalis; S, lingual sinus; H, hyoid; IMP, M. intermandibularis posterior. Redrawn from Gans & Gorniak (1982).

In inertial elongators (figure 5), the initial stages of tongue protraction are similar to mechanical pullers. The tongue shortens at first as the M. genioglossus contracts and accelerates the tongue pad upward and forward. After the initial shortening phase, however, the tongue elongates to as much as 180% of its resting length primarily under the inertia produced by mouth opening (Gray & Nishikawa 1995; Nishikawa & Gans 1996).



During protraction, the tongue tip reaches velocities of more than 250–400 cm s^{-1} and accelerations of more than 310 m s^{-2}, over 30 times the acceleration due to gravity (table 1). Because tongue protraction is rapid and ballistic, tongue movements cannot be corrected within the gape cycle. There is also little if any ability to aim the tongue relative to the head. Instead, inertial elongators rely on movements of the head to aim the tongue at prey.

In inertial elongators, but not in mechanical pullers or hydrostatic elongators, the tongue tip follows a nearly straight line from mouth to prey (figure 6). Precise coordination of head, jaw and tongue movements produces the straight trajectory (Nishikawa & Gans 1996). Specifically, a large upward and forward acceleration of the tongue tip occurs simultaneously with a large downward acceleration of the mandibles and the vector summation of these large vertical movements produces the straight trajectory (figure 4).

In contrast to mechanical pullers and inertial elongators, the M. genioglossus of hydrostatic elongators consists of two compartments, one in which the muscle fibres are orientated parallel to the long axis of the tongue as in other frogs (M. genioglossus longitudinalis), and an additional one in which the fibres are orientated vertically within the tongue (M. genioglossus dorsoventralis, figure 7; Nishikawa *et al.* 1999). During protraction, the volume and width of the tongue remain constant. The tongue (figure 8) is able to double in length during protraction, due to both unfolding of the M. genioglossus longitudinalis and to shortening of the M. genioglossus dorsoventralis during protraction. Unfolding of the M. genioglossus longitudinalis increases tongue length by *ca.* 25%, and the remaining increase in tongue length is due to shortening of the M. genioglossus dorsoventralis to 60% of its resting length (Nishikawa *et al.* 1999).

Most muscular hydrostats possess muscle fibres that are orientated to allow active control of all dimensions: height, width and length. For example, the squid tentacle has both circular and transverse fibres (Van Leeuwen & Kier 1997). This allows the tentacle to increase in length by contracting in width and height simultaneously, causing a geometric increase in length as diameter decreases (i.e. the change in length is proportional to the square of the decrease in diameter; Kier & Smith 1985). *Hemisus* is unusual in possessing muscle fibres that are orientated in only two dimensions, longitudinal and vertical. Furthermore, a robust, transversely aligned connective tissue capsule that surrounds the dorsoventral muscle fibres resists lateral expansion so that the width of the tongue remains constant during tongue protraction. These factors limit the increase in length to a linear, rather than a geometric, function. This difference might in part explain why squid tentacles accelerate much faster (250 m s^{-2}, Van Leeuwen & Kier (1997)) than the tongues

Figure 2. (*Opposite*) Selected frames from a normal prey-capture sequence showing mechanical pulling in *Hyla cinerea*. The number in the top right-hand corner of each picture indicates the time (ms) from the frame in which mouth opening is first observed. Here, the mouth opens rapidly between frames −8 and 0 ms. The squares in the background are 1 cm × 1 cm. The short tongue can be seen at full protraction at $t = 17$ ms.

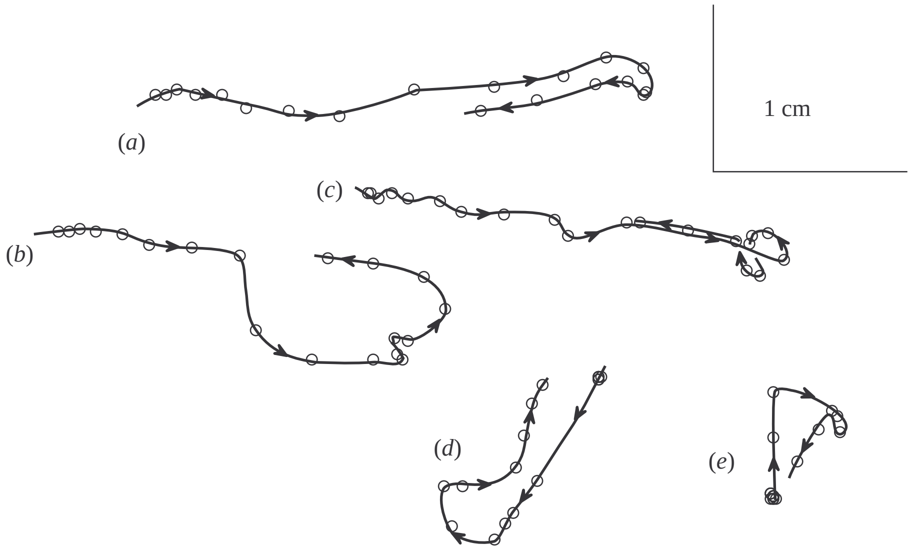


Figure 3. Movement trajectories of a mechanical puller (*Hyla cinerea*). Anterior is toward the right. Trajectories (*a*)–(*c*) begin at the same point in time and space, but are offset for clarity. Arrows show the direction of movement in each segment, and open circles indicate the position of each element in each video field. Trajectories of (*a*) the upper-jaw tip, (*b*) the lower-jaw tip and (*c*) the tongue tip relative to an external reference point. (*a*) The upper-jaw tip moves forward during the lunge and backward during body recovery. (*b*) The lower-jaw tip moves forward during the lunge, then downward as the mouth opens, and upward and back as the mouth closes during body recovery. (*c*) The tongue tip moves forward during the lunge, slightly upward during protraction and downward during retraction, then backward during body recovery. (*d*) Relative to the upper-jaw tip, the lower-jaw tip moves downward and backward during mouth opening, then upward and forward during mouth closing. (*e*) Relative to the lower-jaw tip, the tongue tip moves upward then forward relative to the lower-jaw tip, then down and back. The maximum movement of the tongue tip relative to the lower-jaw tip is less than 0.5 cm.

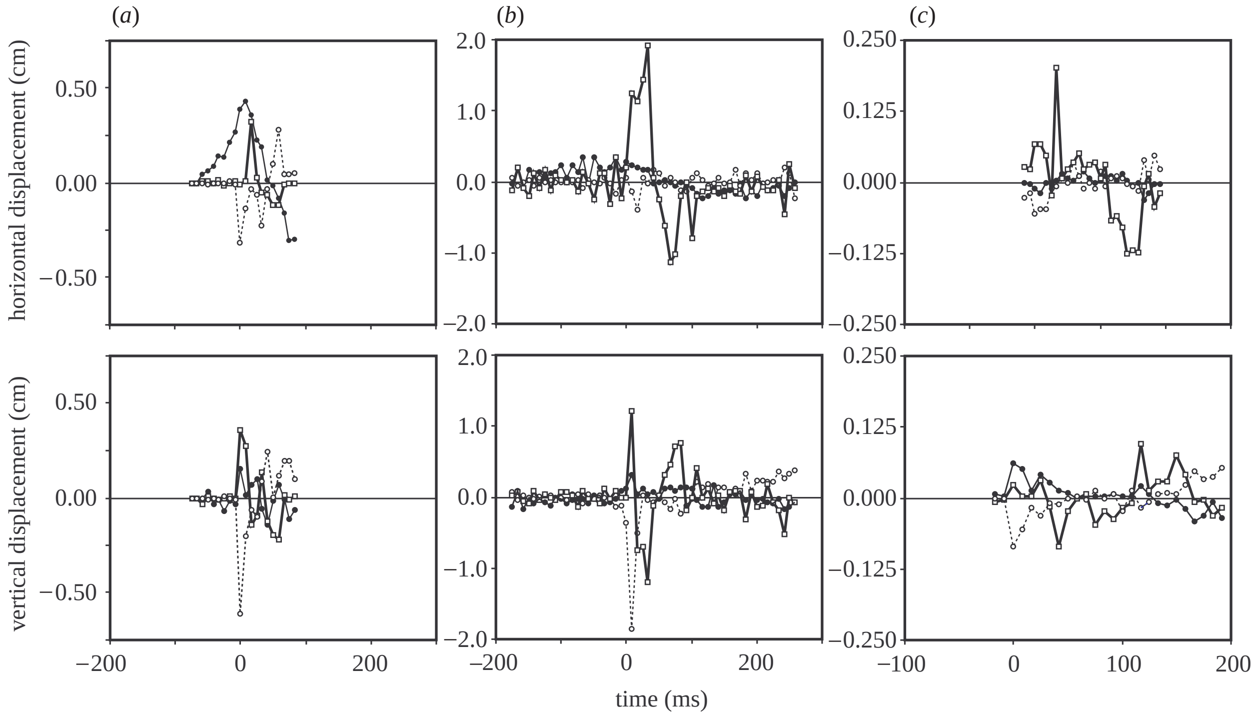
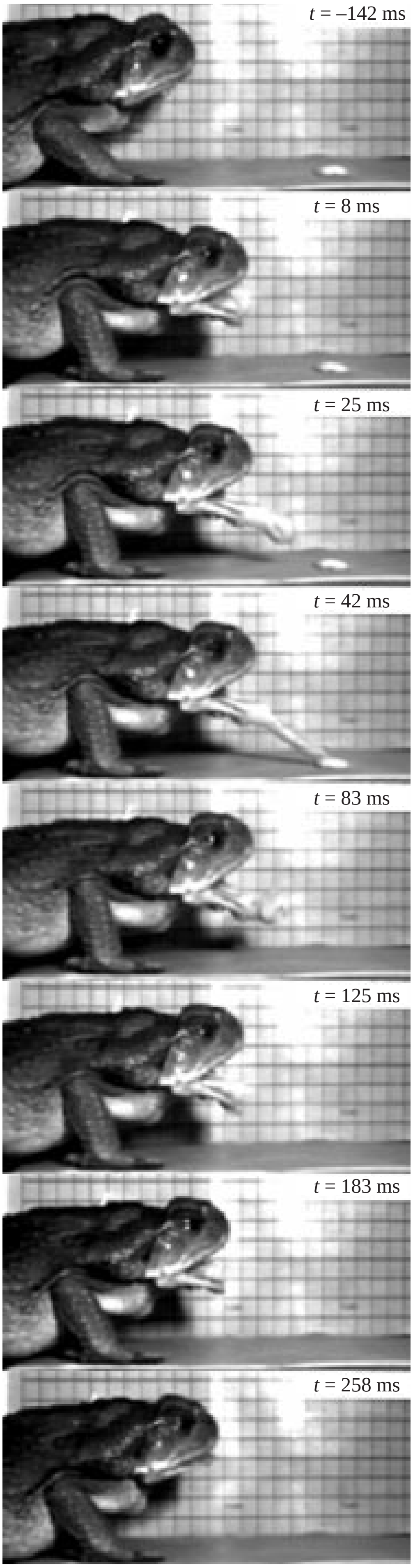


Figure 4. Horizontal (above) and vertical (below) displacements between successive frames for a mechanical puller (*a*) (*Hyla*), an inertial elongator (*b*) (*Bufo*) and a hydrostatic elongator (*c*) (*Hemisus*) (upper-jaw tip, closed circles; mandibular tip, open circles; lingual tip, open squares). For *Hyla*, horizontal displacements of the upper-jaw tips are greater than those of the mandibular and lingual tips, whereas for *Bufo* and *Hemisus*, the horizontal displacements of the lingual tip are greater than those of the upper-jaw and mandibular tips, and are positive during protraction and negative during retraction. In *Bufo*, the downward displacement of the mandible during mouth opening occurs simultaneously with a large upward displacement of the lingual tip, whereas the movements of the jaws and tongue are asynchronous in *Hyla* and *Hemisus*.



of *Hemisus* (3.5 m s^{-2}) and other hydrostatic elongators (table 1).

Some hydrostatic elongators (e.g. *Hemisus*) protract their tongues too slowly for inertia to play a role in tongue protraction, whereas others (e.g. *Dyscophus*) protract their tongues fast enough so that inertia may play a significant role in addition to hydrostatic elongation. In *Hemisus*, the tongue tip reaches maximum velocities of only 24 cm s^{-1} and accelerations of only 3.5 m s^{-2} (table 1). The tongue does not follow a straight line from mouth to prey during protraction (figure 9), but its trajectory can be controlled within the gape cycle in all three dimensions relative to the head (Ritter & Nishikawa 1995).

A phylogenetic analysis of tongue-protraction mechanisms was performed by mapping tongue-protraction modes onto an independently derived hypothesis of anuran phylogeny (Ford & Cannatella 1993). The most parsimonious interpretation of the observed character distribution (figure 10) is that (i) anurans primitively use mechanical pulling to protract their tongues; (ii) inertial elongation evolved several times independently from mechanical pulling; and (iii) hydrostatic elongation evolved once or twice from inertial elongation (Nishikawa 1997).

Results of these comparative studies demonstrate that anuran species differ by nearly 90-fold in the acceleration of the tongue tip during feeding (table 1). This observation raises two interesting questions about neuromuscular control, which will be addressed here: (i) what anatomical and physiological characteristics are responsible for differences in the acceleration of the tongue during protraction; and (ii) how do the tongue types differ in terms of neural control?

3. ANATOMICAL AND PHYSIOLOGICAL DIFFERENCES

On the basis of differences in tongue acceleration among species, we expected that inertial elongators would possess anatomical and physiological adaptations in the tongue muscles that would increase their maximum force and the rate of force development compared with mechanical pullers and hydrostatic elongators. Instead, comparative studies suggest that evolution of the biomechanics of the feeding apparatus between mechanical pullers and inertial elongators appears to have involved only relatively small changes in the anatomy and physiology of the tongue muscles. In contrast, hydrostatic elongators have evolved a new orientation of muscle fibres and a greater number of motor units (see below).

Most of the anatomical differences that have been described among frog tongues are of unknown functional significance (Horton 1982; Regal & Gans 1976). One difference among frog tongues that is related to the mechanism of tongue protraction is the amount of endomysial connective tissue they contain and the orientation

Figure 5. (*Opposite*). Selected frames from a normal prey-capture sequence for an inertial elongator, *B. marinus*. The number in the top right-hand corner of each picture indicates the time (ms) from the onset of mouth opening. The squares in the background are 1 cm × 1 cm. The tongue shortens at first ($t = 8$ ms) but then elongates by up to 180% of its resting length under its own momentum ($t = 25$–42 ms).

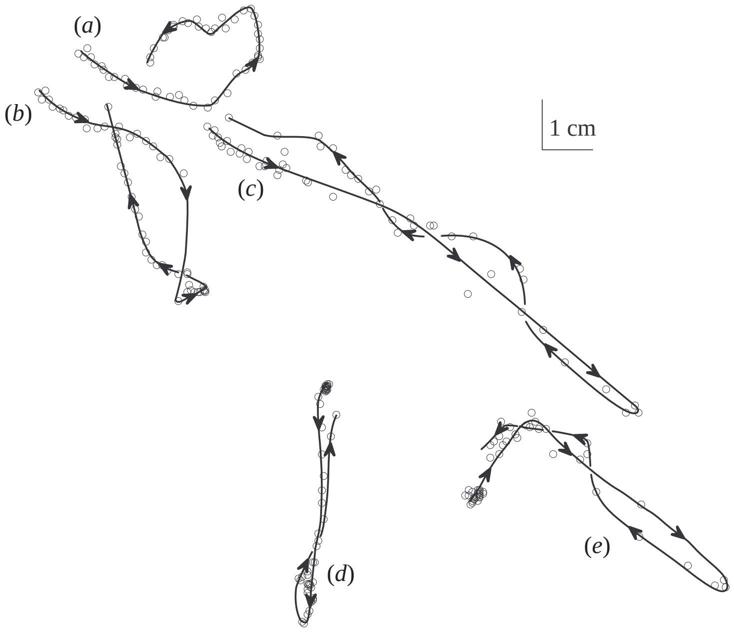


Figure 6. Movement trajectories of *B. marinus*, an inertial elongator. Anterior is toward the right. Trajectories (*a*)–(*c*) begin at the same point, but are offset for clarity. Arrows indicate the direction of movement in each segment of the trajectories, and open circles indicate the position of each element in each video field. Trajectories of (*a*) the upper-jaw tip, (*b*) the mandibular tip, and (*c*) the lingual tip relative to an external reference. The lingual tip follows a nearly straight trajectory from mouth to prey during protraction as it elongates by up to 180% of its resting length. Relative to an external reference point, the upper-jaw tip moves downward and forward during the lunge, then upward and back during body recovery. (*d*) Relative to the upper jaw tip, the movement of the lower jaw tip is mostly limited to the vertical plane. (*e*) The trajectory of the lingual tip relative to the mandibular tip is first upward and forward as the tongue shortens, but then changes abruptly to downward and forward as the tongue elongates and the lingual tip passes beyond the mandibles.

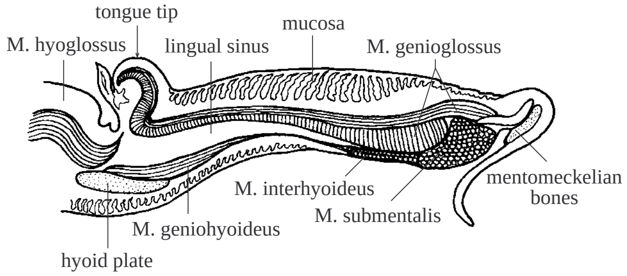


Figure 7. Camera lucida drawing of a sagittal section of the tongue of a hydrostatic elongator (*Hemisus marmoratum*) showing the dorsoventral and longitudinal compartments of the M. genioglossus.

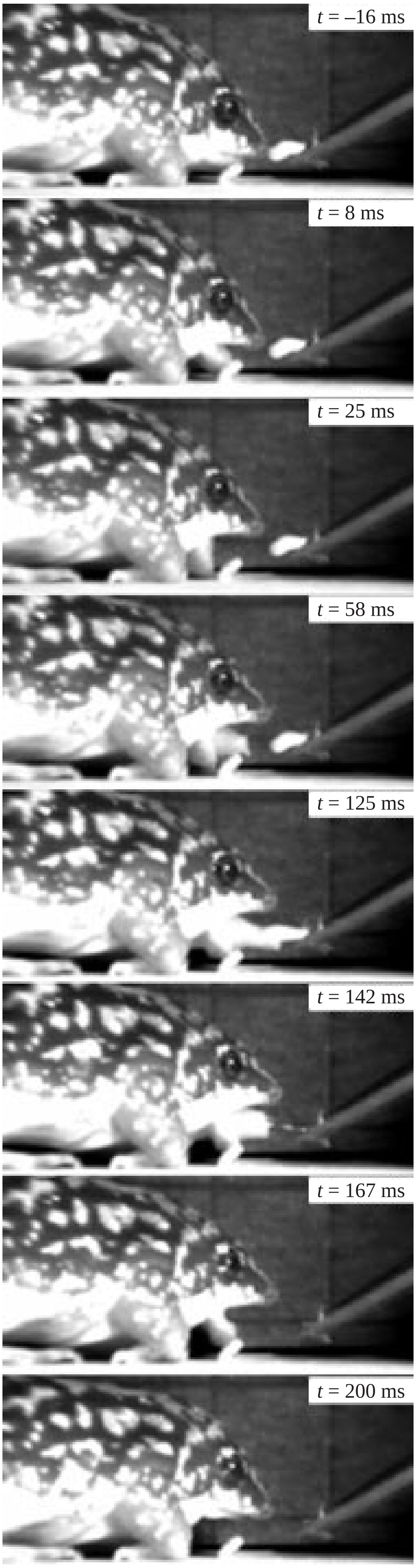
of these collagen fibres within the tongue (Webster 1996). Mechanical pullers have the most connective tissue, inertial elongators are intermediate, and hydrostatic elongators have the least. Parallel connective tissue fibres resist elongation of the tongue, whereas perpendicular fibres resist changes in tongue diameter. Mechanical pullers have the largest number of collagen fibres running parallel to the long axis of the tongue, inertial elongators are intermediate, and hydrostatic elongators have the fewest. In *Hemisus marmoratum*, a hydrostatic elongator, most of the collagen fibres are orientated perpendicular to the long axis of the tongue (Webster 1996; Nishikawa *et al.* 1999).

The only other anatomical differences among tongue-protraction mechanisms are (i) an increase in the relative length of muscle fibres in the M. genioglossus and M. hyoglossus and a change in insertion of the M. hyoglossus from the anterior to the posterior part of the tongue pad in inertial elongators compared with mechanical pullers (Horton 1982); and (ii) the addition of the dorsoventral compartment in the M. genioglossus (described above) in hydrostatic elongators (figure 7), which elongates the tongue when it contracts (Nishikawa *et al.* 1999).

Peters & Nishikawa (1999) recently conducted a comparative study of the isometric contractile properties of the tongue muscles in anuran species representing each of the tongue-protraction mechanisms, including a mechanical puller (*Litoria caerulea*), an inertial elongator (*Bufo marinus)* and a hydrostatic elongator (*Dyscophus guinetti*). Several contractile properties were measured, including force–stimulus frequency, force–stimulus duration and length–tension relationships, fatigue, twitch, tetanic and passive forces, and contraction (time from stimulus onset to peak force) and half-relaxation times for the protractor and retractor muscles of each species (table 2). The species were similar in the physiological cross-sectional area of the M. genioglossus (table 2).

Contrary to our predictions, the results showed that the maximum twitch and tetanic forces and the time to reach peak force of the protractor muscles (table 2) are more similar among species than we expected based on the nearly 90-fold differences in acceleration of the tongue tip among species (table 1). Anuran species differ by only 20–30% in the maximum force produced and contraction times of the protractor muscles. Furthermore, given the slow contraction and half-relaxation times of the M. genioglossus, how is it that these muscles can develop force fast enough to account for the rapid movements of the tongue during protraction that have been observed kinematically in inertial elongators?

The results of our comparative studies suggest that differences among species in tongue acceleration are due not to differences in the anatomy and physiology of the tongue protractor M. genioglossus, but rather to differences in the inertia transferred from the mandibles to the tongue during mouth opening. Furthermore, differences in the amount of tongue elongation during protraction are due primarily to differences in the passive resistance of the tongue tissues to elongation (figure 11), which presumably is mediated by the amount and orientation of endomysial connective tissues associated with the tongue muscles (Peters & Nishikawa 1999; Webster 1996). Passive resistance is about four times greater in mechanical pullers than it is in inertial and hydrostatic elongators at the longest tongue lengths (figure 11).



In fact, a recent study showed that anuran species differ markedly in the velocity of mouth opening during prey capture, with inertial elongators opening their mouths substantially faster than other frogs (O'Reilly 1998). A biomechanical model of jaw and tongue movements in an inertial elongator (the marine toad, *B. marinus*) shows that the mouth-opening torque is seven times greater than the mouth-closing torque during feeding, although the mouth-opening muscle (M. depressor mandibulae) is smaller in mass and cross-sectional area than the mouth-closing muscle (M. levator mandibulae) (Nishikawa *et al.* 1997).

This and other evidence (see below) suggests that a catch mechanism may facilitate the extremely rapid mouth opening observed in inertial elongators, which appears to be the major force that elongates the tongues of these species. Specifically, we believe that co-contraction of the M. levator mandibulae while the M. depressor mandibulae develops force, followed by rapid relaxation of the M. levator mandibulae, allows for rapid opening of the mouth and inertial elongation of the tongue.

Further evidence that supports the idea of a catch mechanism comes from muscle denervation and stimulation studies (Nishikawa & Gans 1992). In spinal-pithed frogs, stimulation of the M. depressor mandibulae does not produce mouth opening because it is resisted by tonic contraction of the M. levator mandibulae. If the M. levator mandibulae is denervated, however, then stimulation of the M. depressor mandibulae produces mouth opening as expected. This tonic contraction of the M. levator mandibulae, if it occurs during feeding and is followed by sudden relaxation, may serve as a catch mechanism that increases the opening force produced by the M. depressor mandibulae during feeding. This hypothesis is currently being tested using low-frequency electromyography to detect tonic muscle activity and *in vitro* physiological experiments to measure the contraction and relaxation rates of muscle fibres in the M. levator mandibulae.

The fact that both the tongues and jaws of inertial elongators show adaptations associated with the mechanism of tongue protraction demonstrates the importance of considering the feeding apparatus as a multijoint system in which torques acting at one joint may be produced at another joint. Single-joint models as well as inverse dynamic models may overlook these important effects.

4. DIFFERENCES IN NEURAL CONTROL

We have also conducted comparative studies to determine how neural control differs among mechanical pullers, inertial elongators and hydrostatic elongators. These studies have demonstrated that the neural circuits that control feeding behaviour have evolved considerably so that both inertial elongators and hydrostatic elongators possess specialized neurological features that are adapted to the constraints and opportunities associated with their particular mechanisms of tongue protraction.

Figure 8. (*Opposite*) Selected frames from a normal prey-capture sequence for a hydrostatic elongator (*Hemisus marmoratum*). The number in the top right-hand corner of each picture indicates the time (ms) from the onset of mouth opening. The squares in the background are 1 cm × 1 cm. The tongue elongates slowly during protraction (*t* = 25–125 ms).

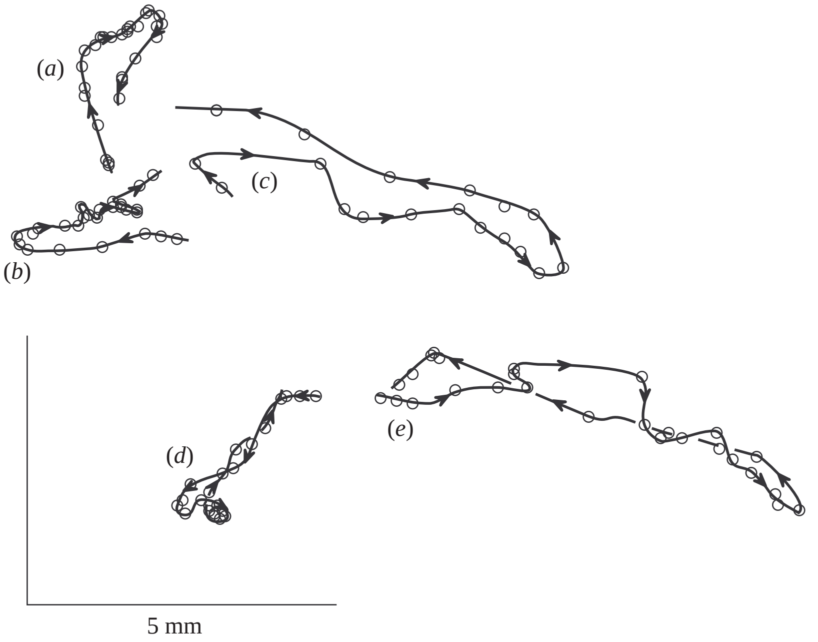


Figure 9. Movement trajectories of a hydrostatic elongator (*Hemisus marmoratum*). Anterior is toward the right. Trajectories (*a*)–(*c*) begin at the same point, but are offset for clarity. Arrows indicate the direction of movement in each segment of the trajectories, and open circles indicate the position of each element in each video field. Trajectories of (*a*) the upper-jaw tip, (*b*) the mandibular tip, and (*c*) the lingual tip relative to an external reference. There is relatively little head movement during feeding, although the head moves slightly upward and forward, then down and back during feeding. (*d*) The lower-jaw tip is both depressed and retracted during mouth opening, and retraction of the lower jaw counteracts the upward rotation of the tongue tip relative to the mandibles, so that the initial trajectory of the tongue (*c*) is straight out of the mouth. (*e*) Unlike inertial elongators, the tongue does not follow a straight line from mouth to prey during protraction.

Prey capture in frogs is a goal-orientated, prehensile movement that shares many features of neuromuscular control with other prehensile movements such as reaching in humans (Gottlieb *et al.* 1989; Flanders *et al.* 1992) or pecking in pigeons (Bermejo & Ziegler 1989). Performance of these goal-orientated prehensile tasks requires sensory information about the target as well as sensory information about the animal's internal state, both of which are used to modulate motor activity. Relevant information about the target is obtained visually in frogs (Ewert 1987) and includes target position in three dimensions (distance, azimuth and elevation), size, shape and velocity (Valdez & Nishikawa 1997). Relevant information about the animal's internal state is obtained through proprioceptive sense organs distributed throughout the body and includes the length and mass of musculoskeletal elements, the physiological properties and mechanical advantage of the muscles, the position of musculoskeletal elements before and during movement, and the action of forces such as gravity and inertia (Gielen & Denier van der Gon 1989).

Prey capture requires the planning and execution of precisely coordinated movements of the head, jaws and tongue (Nishikawa & Gans 1996). To capture prey successfully, a frog must detect and recognize prey (Ewert 1987), locate it in space (Ingle 1983), and analyse its relative size, shape and speed of movement (Valdez & Nishikawa 1997). Once prey is detected and located, a frog must respond to prey before it escapes, place its tongue accurately on the prey, apprehend it, and bring it back to the mouth.

Motor control differs in several ways among frog species that use different mechanisms to protract their tongues. The first difference is that inertial elongators use only feed-forward open-loop control to coordinate jaw and tongue movements. In inertial elongators, there is no opportunity for on-line feedback correction after the tongue is launched because tongue protraction is ballistic (Nishikawa & Gans 1996). In contrast, mechanical pullers and hydrostatic elongators can rely on both feed-forward and feedback control of tongue movements because there is no ballistic stage of tongue elongation.

A second difference in motor control is that in inertial elongators, accurate placement of the tongue on the prey requires precise coordination of the extremely rapid, simultaneous movements of the tongue and jaws. This precise coordination of tongue and jaw movements is not necessary in mechanical pullers because the movement of the short tongue pad relative to the lower jaw is restricted to a few millimetres, so that the tongue pad will always end up in nearly the same location as the tips of the mandibles. Precise tongue–jaw coordination is also unnecessary in hydrostatic elongators because the tongue does not depend on inertia for elongation, but instead elongates under the contraction of the M. genioglossus dorsoventralis.

In inertial elongators, tongue afferents that are innervated by the hypoglossal nerve have evolved convergently in at least four independent lineages for precise coordination of tongue and jaw movements (figure 12). Small changes in the central and peripheral connections of cranial (*Bufo*) or spinal (*Rana*) mechanosensory afferents have led to the emergence of novel functions in coordinating feeding behaviour in inertial elongators, including modulating the phase of activity in jaw muscles and influencing motor programme choice during feeding (Nishikawa 1997, 1999).

Finally, the three-dimensional aiming ability of hydrostatic elongators implies several changes in neural control that have yet to be investigated. For both three-dimensional aiming and high accuracy, we would expect that motor units should be smaller and more numerous in hydrostatic elongators than in other species.

Our comparative studies have focused on how visual and proprioceptive input is used to modulate prey-capture movements. Methods that have been used to investigate the neural control of prey capture include behavioural studies, deafferentation experiments, electrophysiological recording and neuroanatomical tracing. These studies have focused on the modulatory effects of visual analysis of prey features, the modulatory effects of proprioceptive tongue afferents, and the interaction between vision and proprioception in controlling feeding movements.

Figure 10. Cladogram illustrating the evolution of tongue-protraction mechanisms among frogs. The cladogram was derived from a consensus of morphological and molecular characters (see Ford & Cannatella 1993). Tongue-protraction mechanisms were then mapped onto the cladogram. The most parsimonious hypothesis is as follows: (i) mechanical pulling is the ancestral condition; (ii) inertial and hydrostatic elongation are derived conditions; (iii) inertial elongation evolved several times independently among frogs; and (iv) hydrostatic elongation evolved once from inertial elongation.

(a) *Visual guidance of prey-capture movements*

Frogs are visual predators, and the neurophysiology of the anuran visual system has been a major topic of neuroethological research for many years (Lettvin *et al.* 1959; Ewert 1987). In my laboratory, we have investigated how prey-capture movements are modulated in response to prey characteristics (Anderson 1993; Anderson & Nishikawa 1996; Valdez & Nishikawa 1997). Because they depend heavily upon lingual adhesion in order to capture prey, frogs use different strategies to capture prey of different sizes (Anderson 1993). Small prey are captured with the tongue and are transported to the oesophagus without contacting the jaws (tongue prehension), whereas large prey are contacted with the tongue first, the head then rotates downward and the prey are captured in the closing jaws and transported into the oral cavity with the

Table 2. *A comparison of selected isometric contractile properties of the tongue protractor muscles* (*M. genioglossus*) *in a mechanical puller* (L. caerulea), *an inertial elongator* (B. marinus) *and a hydrostatic elongator* (D. guinetti) (*from Peters & Nishikawa 1999*)

(The *p*-value comes from an analysis of covariance with tongue mass as the covariate. Fatigue index as in Peters & Nishikawa (1999). PCSA, physiological cross-sectional area.)

variables	*Litoria*	*Bufo*	*Dyscophus*	difference (%)	*p*
mean PCSA (cm^2)	0.0675	0.0649	0.0873	25.7	—
twitch force (mN)	36.3 ± 0.4	47.1 ± 0.5	36.3 ± 0.6	22.9	n.s.[a]
tetanic force (mN)	383.0 ± 35.4	241.6 ± 19.6	242.6 ± 19.6	36.9	n.s.
contraction time (ms)	55.5 ± 1.8	44.2 ± 1.6	36.4 ± 1.2	34.4	<0.05
half-relaxation time (ms)	43.7 ± 1.3	27.5 ± 1.3	32.6 ± 2.0	37.1	<0.05
fatigue index	53.9 ± 0.6	59.5 ± 2.8	62.8 ± 2.0	14.2	<0.05

[a] n.s. = non-significant.

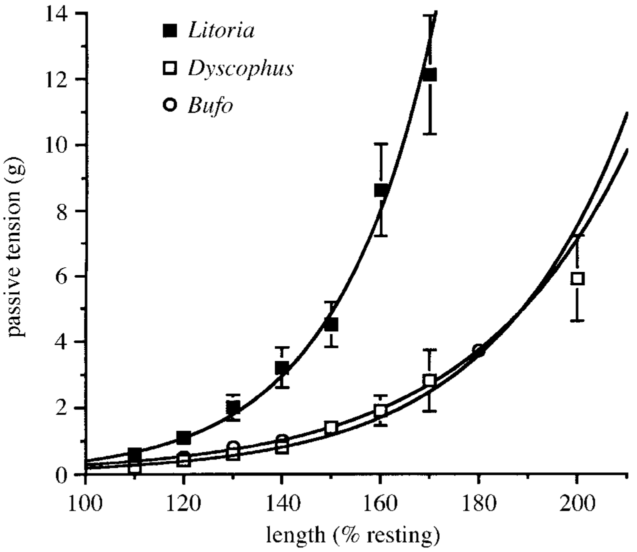


Figure 11. Passive force produced by elongating the tongue from resting length (L_0) to 200% of L_0 in a mechanical puller (*L. caerulea*; solid squares), an inertial elongator (*B. marinus*; open circles) and a hydrostatic elongator (*D. guinetti*; open squares). The passive force is greater in the mechanical puller than in the other species at all lengths. From Peters & Nishikawa (1999).

forelimbs (jaw prehension). During tongue prehension, the head remains more nearly level with respect to the horizon, lunge distance is shorter, the tongue is protracted farther and the mouth remains open for a longer time than during jaw prehension.

Tongue prehension is more effective for capturing small prey than jaw prehension because the prey is transported to the oesophagus in a single movement, which offers less chance for escape. On the other hand, tongue prehension is effective only if the weight of the prey is less than the maximum force of adhesion between tongue and prey. Thus, jaw prehension is more effective for capturing large prey (Anderson & Nishikawa 1996; Valdez & Nishikawa 1997). The distinction between 'small' versus 'large' prey is relative to the size of the frog. Larger frogs switch behaviour patterns at larger prey sizes than smaller frogs.

Use of jaw versus tongue prehension is based on a visual analysis of prey size (Anderson & Nishikawa 1993). When offered pieces of earthworm ranging in size from 1.5–4.5 cm, adult frogs (*Rana pipiens*) always use tongue prehension to capture 1.5 cm prey and jaw prehension to capture 2.0 cm and larger prey. Another study compared prey-capture movements across five different types of live prey (earthworms, waxworms, newborn mice, crickets and termites) in the Australian frog, *Cyclorana novaehollandiae* (Valdez & Nishikawa 1997). This study showed that frogs modulate their feeding movements in response not only to prey size, but also to shape and speed of movement. The ability to use a visual analysis of prey characteristics to modulate feeding movements is widespread among frogs because distantly related species with different tongue morphologies (i.e. *R. pipiens* and *Cyclorana novaehollandiae*) use tongue prehension to capture small prey and jaw prehension to capture large prey.

(b) *Modulation of prey-capture movements by tongue afferents*

Comparative studies of the proprioceptive control of prey capture have shown that inertial elongators possess a novel circuit for coordinating tongue and jaw movements (Nishikawa 1997, 1999; Nishikawa *et al.* 1992, 1993) that is absent in mechanical pullers and hydrostatic elongators (figure 12). Most inertial elongators that have been studied have been found to possess mechanosensory afferents in the tongue, innervated by the hypoglossal nerve, which serve a variety of functions in feed-forward (i.e. open-loop, planned in advance) control of jaw and tongue movements during prey capture (Anderson 1993; Anderson & Nishikawa 1993, 1996, 1997; Nishikawa & Gans 1992). These afferents respond phasically to mechanical stimulation of the tongue and are postulated to monitor changes in the position of the tongue in the oral cavity during breathing and feeding.

One function of these tongue afferents is to modulate the phase of activity in the mouth-opening and -closing muscles of inertial elongators (Nishikawa & Gans 1992; Anderson & Nishikawa 1993). In intact adult frogs (*Rana* and *Bufo*), the mouth-opening muscles are activated *ca.* 90 ms before the mouth-closing muscles. After bilateral transection of the hypoglossal nerves, however, the mouth remains closed when the frogs attempt to feed because the M. levator mandibulae and the M. depressor mandibulae are activated simultaneously. Thus, sensory input from the tongue afferents coordinates jaw muscle activity by sending an afferent signal to the brain that delays activity of the jaw levators. This signal is produced before the onset of mouth opening and probably

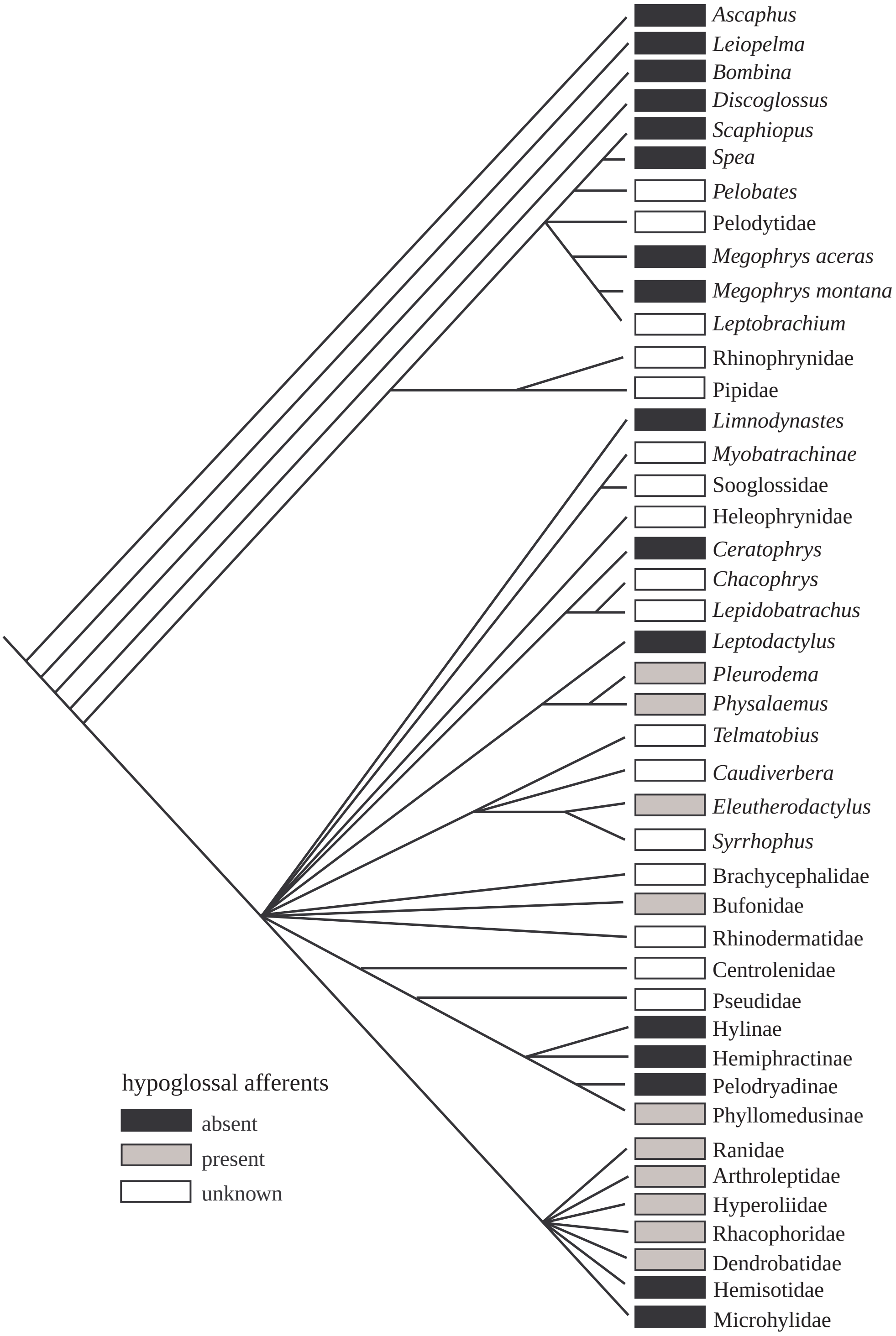


Figure 12. Cladogram illustrating the evolution of tongue afferents among frogs. These afferents are ancestrally absent among frogs. They have evolved several times independently, but only in frogs that use inertial elongation to protract the tongue. These afferents appear to have been lost in hydrostatic elongators (families Hemisotidae and Microhylidae).

results from stimulation of tongue mechanoreceptors by retraction of the hyoid during the preparatory stage of feeding. In intact frogs and toads, this afferent signal coordinates the simultaneous acceleration of the tongue and mandibles, which ensures that the lingual trajectory will fall on a straight path from mouth to prey (Nishikawa & Gans 1996).

Experiments also demonstrate that stimulation of the hypoglossal nerve, which innervates tongue mechanoreceptors, inhibits tonic activity in the M. levator mandibulae (Nishikawa & Gans 1992). Thus, we hypothesize that a second function of these tongue mechanoreceptors is related to the catch mechanism for rapid opening of the mouth during feeding that was proposed above. Specifically, it seems likely that these tongue afferents provide the signal that releases the 'catch' by inhibiting both tonic and phasic activation of the M. levator mandibulae during feeding, allowing the mouth to open rapidly, transferring inertia to the stretchable tongue, which then elongates under this inertial load.

A phylogenetic analysis was performed to investigate the evolution of tongue afferents among anurans. For this analysis, individuals representing 57 species, 39 genera and 15 families were filmed during feeding before and after bilateral transection of the hypoglossal nerves (Nishikawa *et al.* 1993), and the presence–absence of these afferents in each taxon was mapped onto an independently derived phylogeny (Ford & Cannatella 1993). Hypoglossal afferents that modulate the phase of activity in the jaw muscles are absent in all mechanical pullers and all hydrostatic elongators (figure 12). All inertial elongators possess hypoglossal afferents that modulate the phase of activity in the jaw muscles, and it appears that these afferents have evolved convergently at least four times independently: (i) in *Pleurodema* and *Physalaemus* (family Leptodactylidae); (ii) in phyllomedusine hylids; (iii) in bufonids; and (iv) in ranoids except for hemisotids and microhylids, in which hypoglossal afferents appear to have been lost or, alternatively, may never have been present.

Although the function of these afferents is very similar across species at the behavioural level, both cladistic analyses and comparative neuroanatomical studies show that the circuits are convergent rather than homologous in different anuran lineages (Nishikawa *et al.* 1993; Anderson & Nishikawa 1997). Frogs primitively lack afferents in the hypoglossal nerve, as do most vertebrates (Ariens-Kappers *et al.* 1936). In toads of the family Bufonidae, sensory fibres from the glossopharyngeal nerve have invaded the tongue via the hypoglossal nerve and these fibres ascend to higher brain centres in the solitary tract (Nishikawa *et al.* 1993). In frogs of the family Ranidae, large myelinated afferents of the most anterior cervical spinal nerve have invaded the tongue via the hypoglossal nerve (Anderson & Nishikawa 1997). These fibres ascend and descend in the dorsomedial funiculus and project to the granular layer of the cerebellum and the medial reticular formation. In frogs, a variety of evidence points to the medial reticular formation as a possible site of the central pattern generator for prey capture (Matsushima *et al.* 1989; Weerasuriya 1989). The source of hypoglossal afferents remains unknown in leptodactylids and hylids.

During invasions of new territory in inertial elongators, tongue afferents have changed both their peripheral pathways and their central connections, although the location of their cell bodies and the basic class of cutaneous mechanoreceptors that they innervate appear to have been conserved. Future studies in my laboratory will explore in greater detail how these convergent neural circuits differ anatomically and physiologically.

(c) *Interactions between vision and proprioception*

Afferent input from the tongue interacts with visual input in controlling prey-capture movements in inertial elongators. In the leopard frog (*R. pipiens*), the modulatory effect of tongue afferents depends upon attributes of the visual stimulus that are presented to elicit feeding (Anderson & Nishikawa 1993). When presented with small prey, deafferented frogs attempt to use tongue prehension to capture prey and the mouth remains closed, as noted above. When the same deafferented frogs are presented with large prey, they use jaw prehension to capture prey and their mouths open normally. This result demonstrates that the effect of tongue afferents on feeding movements is modulated by visual input. In other words, visual input has a gating effect on tongue afferents.

Tongue afferents also interact with visual input during motor programme choice in *R. pipiens* (Anderson & Nishikawa 1996). As mentioned above, intact adult frogs use tongue prehension to capture 1.5 cm pieces of earthworm, but switch to jaw prehension for 2.0 cm and larger prey. Based on the results of the deafferentation experiments described above, we would expect that the mouth would never open for 1.5 cm prey and always open for 2.0 cm and larger prey. When the tongue afferents are transected, the mouth never opens for 1.5 cm prey and always opens for 2.5 cm and larger prey. However, the frogs alternate randomly between tongue prehension and jaw prehension when 2.0 cm prey are offered. Thus, the ability to choose between motor programmes for tongue prehension and jaw prehension is impaired by hypoglossal transection.

(d) *Organization of motor units in hydrostatic elongators*

Because a muscular hydrostatic system allows for precise, localized, and diverse movements, as demonstrated by the ability of hydrostatic elongators to aim the tongue in three dimensions relative to the head, one would expect that the dorsoventral compartment of the M. genioglossus should be composed of a large number of relatively small motor units compared with mechanical pullers and inertial elongators. In hydrostatic elongators, independent recruitment of portions of a muscle is necessary for precise, localized movement, and sequential recruitment during tongue protraction may help to support the tongue against gravity. In contrast, the M. genioglossus of inertial elongators, such as *B. marinus* or *R. pipiens*, should be composed of a small number of large motor units that are activated simultaneously to produce a large instantaneous acceleration when the tongue is launched from the mouth. Gradual and modulated protraction also confers the advantage that the tongue trajectory can be corrected on-line within a gape cycle. In contrast, the tongue trajectory of inertial elongators is determined at launch, is not corrected in flight, and is constrained to fall on a straight line (Nishikawa & Gans 1996). Thus, we would expect a larger number of motor units in hydrostatic elongators than in inertial elongators. As predicted, approximately 250 motor neurons innervate the M. genioglossus of an inertial elongator, *R. pipiens* (Stuesse *et al.* 1983), whereas approximately 950 motor neurons innervate the M. genioglossus of a hydrostatic elongator, *Hemisus marmoratum* (Anderson *et al.* 1998).

5. CONCLUSIONS

Prey capture in frogs has proven to be an informative model system for studying the relationship between biomechanics and neural control of movement. Despite the morphological conservatism of the feeding apparatus, frog species differ in the biomechanics of tongue protraction during feeding. In mechanical pullers, the function of the tongue muscles is most like that of typical vertebrate skeletal muscle, in which muscle fibres contract to do work. Inertial elongators have specialized in using the inertia developed by mouth opening to elongate their tongues, and this has involved a modification of the connective tissues of the tongue to decrease the passive resistance to elongation as well as the evolution of a catch mechanism in the jaw muscles that increases the speed of mouth opening and thus the inertia transferred to the tongue to effect elongation. In hydrostatic elongators, a new compartment of the tongue protractor muscle M. genioglossus has evolved that contracts to produce tongue elongation directly by changing the shape of the tongue. Like inertial elongators, hydrostatic elongators also possess modifications of the connective tissues of the tongue to decrease the resistance to elongation. The evolution of this new muscle compartment allows the tongue to be protracted at slow or fast speeds, as well as to be aimed in three dimensions relative to the head.

These comparative studies demonstrate that neural control of prey capture has evolved in concert with these changes in the biomechanics of tongue protraction. Inertial elongators have evolved novel afferents in the tongue that play several different roles in the feed-forward control of their ballistic prey-capture movements. Both anatomical studies and phylogenetic analyses suggest that tongue afferents with behaviourally similar functions have evolved multiple times in different anuran lineages. The afferents differ not only in their peripheral pathways but also in their central connections, which implies that the neural circuits for controlling ballistic tongue movements have evolved considerably from those controlling the tongues of mechanical pullers.

In contrast to inertial elongators, hydrostatic elongators have specialized in fine control of tongue movements, and this ability has resulted in a nearly fourfold increase in the number of motor units, and probably a change in the pattern of recruitment, in their protractor muscles compared with other frogs.

The evolutionary diversity exhibited by anuran species demonstrates that the neural circuits that control prey capture are finely rather than broadly tuned to the biomechanics of the feeding apparatus, and that many aspects of motor systems can become specialized to serve different functions during evolution.

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