

Feeding in Frogs

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I. INTRODUCTION

A major goal of functional morphology is to understand the evolution of functional differences among

animals. One aspect of this goal is to compare the function of the feeding apparatus across the major clades of tetrapod vertebrates. For each clade, the function of the feeding apparatus can be addressed by asking the following questions: (1) Which muscles are involved in producing feeding movements and what is the specific contribution of each? (2) What are the spatial and temporal patterns of muscle activation and how do they relate to movement? and (3) What are the neural mechanisms that are responsible for producing observed patterns of muscle activity?

Since the early 1990s, my research has focused on understanding the evolutionary relationships among morphology, biomechanics, and neural control of movement using prey capture of anurans as a model system. This chapter provides a summary of this work and a historical perspective on hypotheses concerning the mechanisms of anuran prey capture. The chapter begins by briefly reviewing the phylogeny and natural history of anurans (Section I). Subsequent sections describe the morphology (Section II) and function (Section III) of the anuran feeding apparatus, the neural control of prey capture movements (Section IV), and the evolution of mechanisms of tongue protraction and neural control of prey capture (Section V). The chapter ends with a summary of conclusions and a description of current and future directions. It is hoped that by describing the pitfalls that have been encountered in attempting to understand the mechanisms of prey capture in frogs, this chapter will help future workers avoid similar problems in the future. It is also hoped that our attempts to understand the biomechanics and neural control of prey capture in frogs will stimulate functional morphologists to undertake similar studies

in other groups of animals so that the generality of our results can be tested in other groups.

A. Phylogeny of Anurans

On superficial examination, frogs appear to be a morphologically homogeneous group. They are easily distinguished from other amphibians by their well-developed hind legs and the absence of a tail in adults. Frogs are, however, quite diverse morphologically, particularly in terms of their feeding apparatus, which has played an important role in anuran classification schemes for more than a century (Günther, 1859; Griffiths, 1963). Recent workers recognize 21–27 families of frogs (Duellman and Trueb, 1986; Ford and Cannatella, 1993). A number of phylogenetic hypotheses have been published for the anuran families, based on morphological (e.g., Ford and Cannatella, 1993) or genetic characters (e.g., Hillis *et al.*, 1993; Hay *et al.*, 1995). In these studies, the relationships of some anuran families are agreed upon generally, but relationships of the majority of families remain to be resolved definitively (Hillis *et al.*, 1993).

This chapter uses a recent phylogenetic hypothesis of anuran familial relationships (Fig. 5.1) that was developed using morphological characters by Ford and Cannatella (1993). In this hypothesis, the "archaeobatrachian" families (Ascaphidae, Leiopelmatidae, Bombinatoridae, and Discoglossidae) represent the most basal lineages of frogs. These families share many ancestral morphological characteristics, but are not closely related to each other and do not constitute a monophyletic group (Ford and Cannatella, 1993). On the basis of genetic characters, however, Hay *et al.* (1995) concluded that the Archaeobatrachia may, in fact, be monophyletic.

In Ford and Cannatella's (1993) phylogeny, the Mesobatrachia (Fig. 5.1) is a monophyletic group that includes two lineages: the pelobatoids (families Pelobatidae, Pelodytidae, and Megophryidae) and pipoids (families Pipidae and Rhinophrynidae). The remaining families are placed in the clade Neobatrachia. Within the Neobatrachia, the families Hylidae, Centrolenidae, and Pseudidae appear to form a clade, as do the ranoids (families Ranidae, Arthroleptidae, Hyperoliidae, Rhacophoridae, Dendrobatidae, Hemisotidae, and Microhylidae), although the relationships among ranoid families are unresolved. The placement of the dendrobatids remains controversial and some authors believe that they are more closely related to bufonids than to ranoids (Hass, 1995; Hay *et al.*, 1995; Ruvinsky and Maxson, 1996). The relationships among the other neobatrachian families are also unresolved (Fig. 5.1).

Most of the currently recognized anuran families

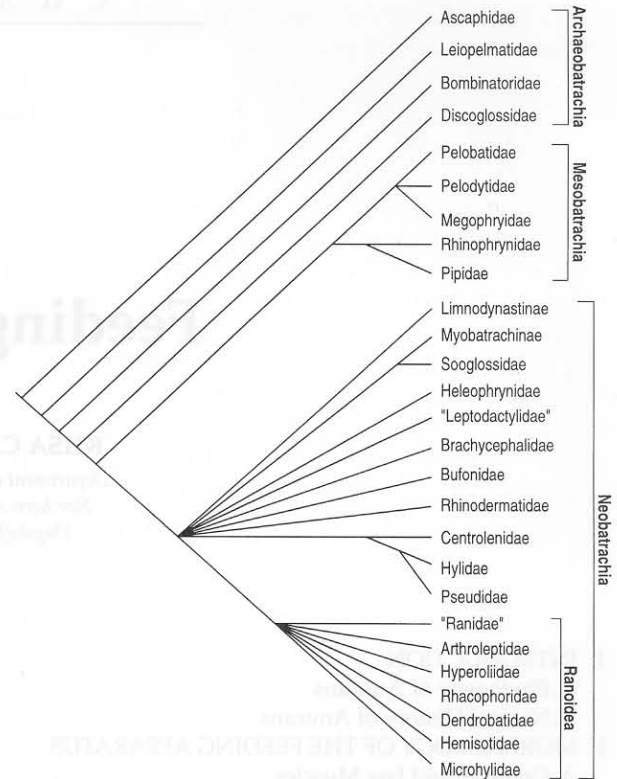


FIGURE 5.1. A phylogeny of the living anurans modified from Ford and Cannatella (1993). The archaeobatrachians are a grade group that share many ancestral characteristics but are not closely related to each other. The families *Leptodactylidae* and *Ranidae* are indicated in quotes because there is no evidence for their monophyly.

appear to be monophyletic, with the possible exception of *Myobatrachidae*, *Leptodactylidae*, and *Ranidae* (Ford and Cannatella, 1993). The family *Myobatrachidae* may not be monophyletic because its subfamily *Myobatrachinae* shares several characteristics with the family *Sooglossidae* that are absent in the subfamily *Limnodynastinae*. For the families *Ranidae* and *Leptodactylidae*, monophyly has been rejected, but the relationships of the subfamilies to other taxa remain to be resolved (Ford and Cannatella, 1993). At present, the unresolved relationships among neobatrachian frogs are a serious impediment to understanding anuran evolution.

B. Natural History of Anurans

Nearly all frogs are carnivorous after metamorphosis, and invertebrates are the most common prey, although there are reports of frogs that eat fruits (Silva *et al.*, 1989) and leaves (Das and Coe, 1994; Das, 1995, 1996). Most anurans are also feeding generalists, eating any prey that will fit into their mouths in proportions that match the relative abundance of prey in

nature (Toft, 1981). Dietary generalists tend to be wide-mouthed, sit-and-wait predators.

A few species of anurans are known to specialize on a narrower range of prey types (Toft, 1981). Some forest floor species, including the genus *Bufo* (Smith and Bragg, 1949; Inger and Marx, 1961; Berry and Bullock, 1962; Clarke, 1974; Zug and Zug, 1979; Toft, 1981), and many burrowing anurans, such as *Hemisus* (Emerson, 1976a), specialize on small prey such as ants, collembolans, termites, or mites (Simon and Toft, 1991; Toft, 1995; Caldwell, 1996), consuming them in greater proportions than their relative abundance in nature. Small prey specialists tend to lack teeth, have relatively narrow mouths, and search actively for prey (Toft, 1981). They also tend to have higher aerobic capacities and lower anaerobic capacities than dietary generalists (Taigen and Pough, 1983). Several anurans are known to consume rather peculiar types of prey, such as snails (Drewes and Roth, 1981), crabs (Premo and Atmowidjojo, 1987), fish (Knoepffler, 1976), or even other frogs (Emerson, 1985). However, these species also take a wide range of other prey types and so are not strict dietary specialists.

There have been relatively few attempts to correlate the morphology of the feeding apparatus with natural diets in anurans. Emerson (1985) and colleagues (Emerson and Voris, 1992, Emerson and Bramble, 1993; Emerson *et al.*, 1994) have studied the relationships among skull morphology, feeding behavior, and diet among diverse species. She found that frogs that eat relatively large prey have relatively longer jaws and wider skulls than those that eat small prey. In addition, the feeding cycle is longer and more asymmetrical (i.e., mouth closing takes longer than mouth opening) in species that eat large prey than in species that eat small prey. Gray (1997) compared the diets of sympatric hylid frogs with short vs long tongues. She found that there was overlap in the types of prey taken by the two species, but long-tongued species consumed a greater proportion of rapidly moving prey than short-tongued species. The ecological significance of differences among frogs in the morphology of the feeding apparatus is a topic that deserves further study.

II. MORPHOLOGY OF THE FEEDING APPARATUS

Feeding mechanisms of amphibians (frogs, salamanders, and caecilians) are extremely diverse. The tongues of caecilians are small and cannot be protruded from the mouth so jaw prehension is used to capture prey and some species possess a highly specialized jaw-closing mechanism (Bemis *et al.*, 1983; Nussbaum,

1983). In contrast to caecilians, terrestrial salamanders and frogs use lingual protraction to catch prey. They depend heavily on lingual adhesion for prey capture.

In salamanders, the articulated hyobranchial skeleton forms an internal support for the tongue, which leaves the mouth with the tongue during protraction (Lombard and Wake, 1976; Thexton *et al.*, 1977). Salamanders vary widely in their tongue morphology, especially with regard to projection distance, muscle attachment, and hyobranchial folding (Özeti and Wake, 1969; Regal, 1966; Wake, 1982; Lombard and Wake, 1977, 1987). In contrast to salamanders, the anuran tongue consists only of muscles and connective tissue, with no intrinsic cartilaginous or bony skeleton. The hyobranchial apparatus is an unarticulated plate formed from the ontogenetic fusion of the cartilaginous larval elements. It cannot be folded and does not leave the mouth with the tongue during feeding (Gans, 1961, 1962; Gans and Gorniak, 1982a,b; Roth *et al.*, 1990). Frogs also vary in their tongue morphology, especially with regard to the anatomy of the protractor muscle (Regal and Gans, 1976; Horton, 1982) and projection distance (Deban and Nishikawa, 1992; Nishikawa *et al.*, 1992).

Variation in the morphology of the feeding apparatus has been studied extensively in frogs (Magimel-Pelonner, 1924; Regal and Gans, 1976; Emerson, 1976b, 1985; Horton, 1982; Cannatella, 1985). Until recently, there have been few attempts to map morphological characteristics of the feeding apparatus onto a cladogram of anuran taxa, particularly in a functional context. In general, although the size and shape of elements of the feeding apparatus may differ dramatically among species, there is a great deal of overall similarity in the bones and muscles of the feeding apparatus among frogs (Figs. 5.2A–5.2C). The functional significance of anatomical variation remains unknown in most cases.

The feeding apparatus of frogs consists of the cranium, mandibles, hyoid, and tongue, each of which is associated with a series of muscles. The morphology of each of these elements is described next, along with brief descriptions of hypothesized functions of the musculoskeletal elements and a brief review of diversity among taxa, where known. A more detailed examination of the function of the feeding apparatus is given in Section III.

A. Cranium and Jaw Muscles

The morphology of the anuran cranium was studied extensively by Trueb (1973), and a fairly detailed summary can be found in Duellman and Trueb (1986). Cranial morphology is highly variable among species,

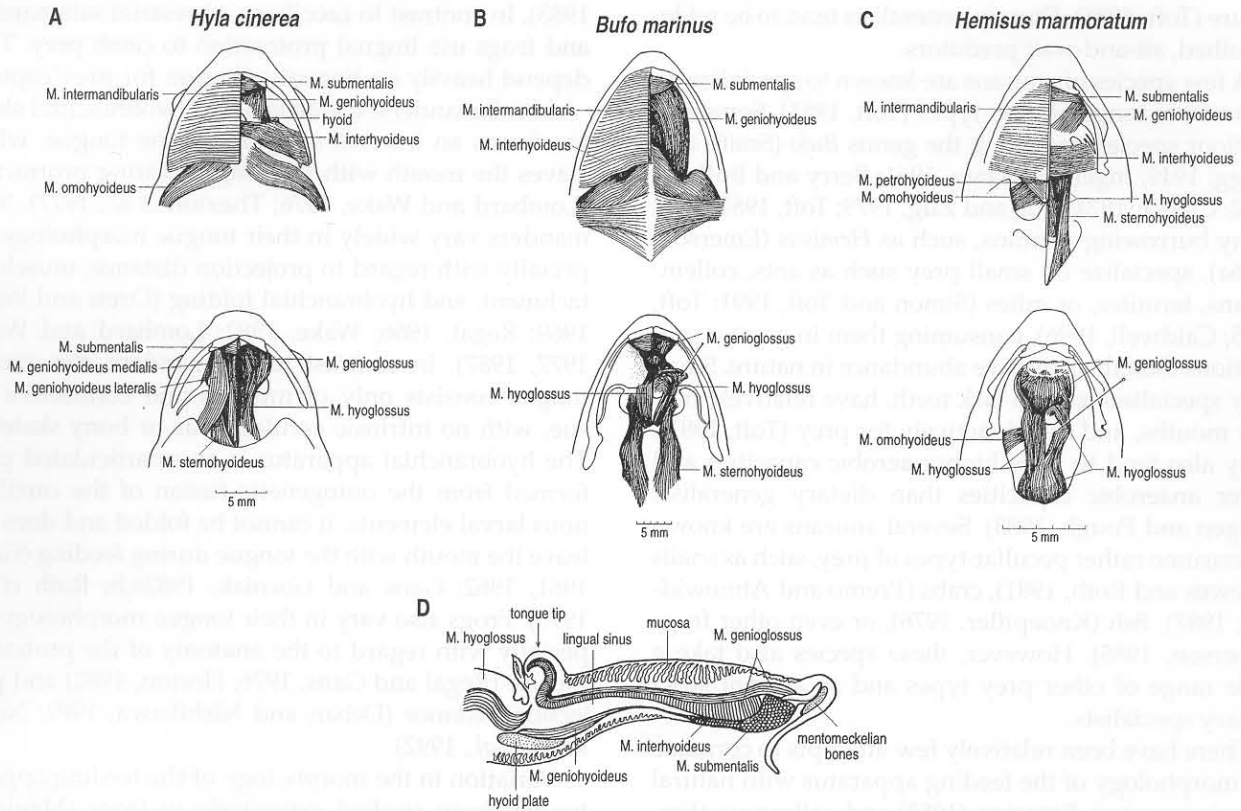


FIGURE 5.2. Musculature of the feeding apparatus in *Hyla cinerea* (A), *Bufo marinus* (B), and *Hemisus marmoratum* (C). Superficial muscles of the feeding apparatus include *M. intermandibularis*, *M. interhyoideus*, and *M. submentalis*. Deep muscles include the extrinsic tongue muscles *M. hyoglossus* and *M. genioglossus*, and the hyoid protractor *M. geniogyoides* and retractor *M. sternohyoideus*. A sagittal section of the tongue of *Hemisus* (D) shows the dorsoventral and longitudinal compartments of the *M. genioglossus*.

which exhibit a continuum from reduced ossification (e.g., *Ascaphus*) to hyperossification (e.g., pipid frogs). Reduction or loss of bones has occurred in numerous taxa, and a few taxa possess neomorphic cranial elements (Trueb, 1973).

Bones of the neurocranium include the sphenethmoid and the paired prootics and exoccipitals. The dermal roofing bones usually include only the nasals and the frontoparietals. The frontoparietals and prootics provide attachment sites for the *M. levator mandibulae anterior longus* and *M. levator mandibulae posterior longus* (= *M. temporalis*).

The bones of the palate include the paired vomers, which are often absent, and the parasphenoid, which is always present and covers the neurocranium ventrally. The prevomers, palatines, and pterygoids are absent in many taxa. Although quite variable in shape, the squamosal is always present. It acts as an important attachment site for the jaw levators. Maxillary arch bones always include the premaxilla and maxilla, and sometimes the quadratojugal. The premaxilla is highly

variable and is important in determining the shape of the snout (Trueb, 1973).

The teeth of frogs are reduced compared to most other vertebrates (Duellman and Trueb, 1986). Maxillary and premaxillary teeth are usually, but not always, present. Vomerine teeth are usually present if the vomers are present. No other bones of the upper jaw bear teeth in frogs. Small prey specialists, such as toads (family Bufonidae), lack teeth entirely (Duellman and Trueb, 1986).

The jaw muscles consist of one main depressor for opening the mouth and a complex of six levators (= adductors) for closing it. The *M. depressor mandibulae* originates from the dorsal fascia and/or otic capsule and inserts on the proximal tip of the mandible (Emerson, 1977), close to the jaw joint and therefore in a position of relatively low mechanical advantage. The muscles of the *M. levator mandibulae* complex extend from the otic capsules and squamosal to the mandible as follows: (1) the *M. levator mandibulae anterior longus* (= *M. pterygoideus*) originates on the frontoparietal

and prootic and inserts via a tendon on the medial side of the angulosplenic; (2) the massive *M. levator mandibulae posterior longus* (= *M. temporalis*) originates from the median raphe on the skull roof, the lateral surface of the frontoparietal, and the dorsal surface of the prootic and it inserts via a tendon on the medial side of the angulosplenic; (3) the *M. l. m. posterior lateralis* originates on the ventral arm of the squamosal and inserts on Meckel's cartilage and the lateral surface of the angulosplenic; (4) the *M. l. m. posterior articularis* originates on the quadrate and inserts on the mandible; (5) the *M. l. m. externus* originates on the zygomatic process of the squamosal and inserts laterally on the mandible; and (6) the *M. l. m. posterior subexternus* also originates on the zygomatic process of the squamosal and inserts on the posterior end of the mandible (Duellman and Trueb, 1986). All of the *Mm. levator mandibulae* insert farther from the jaw joint, in a position of relatively greater mechanical advantage, than the *M. depressor mandibulae*. The *Mm. levator*

mandibulae are innervated by the trigeminal nerve, whereas the *M. depressor mandibulae* is innervated by the facial nerve (Figs. 5.3D–5.3F).

Although there is much variation in the morphology of the skull and jaws of frogs (Trueb, 1973) and considerable variation among species in the jaw musculature (Starrett, 1968), the functional significance of interspecific differences remains largely unknown (Duellman and Trueb, 1986). James Birch (personal communication) is using morphometric methods to analyze the functional consequences of changes in anuran skull shape during development as well as differences among species.

B. Mandible and Buccal Floor Muscles

The mandibles of frogs generally consist of three paired bony elements associated with Meckel's cartilage: the angulosplenic, dentary, and mentomeckelian bones (which are absent in pipoids and a few other

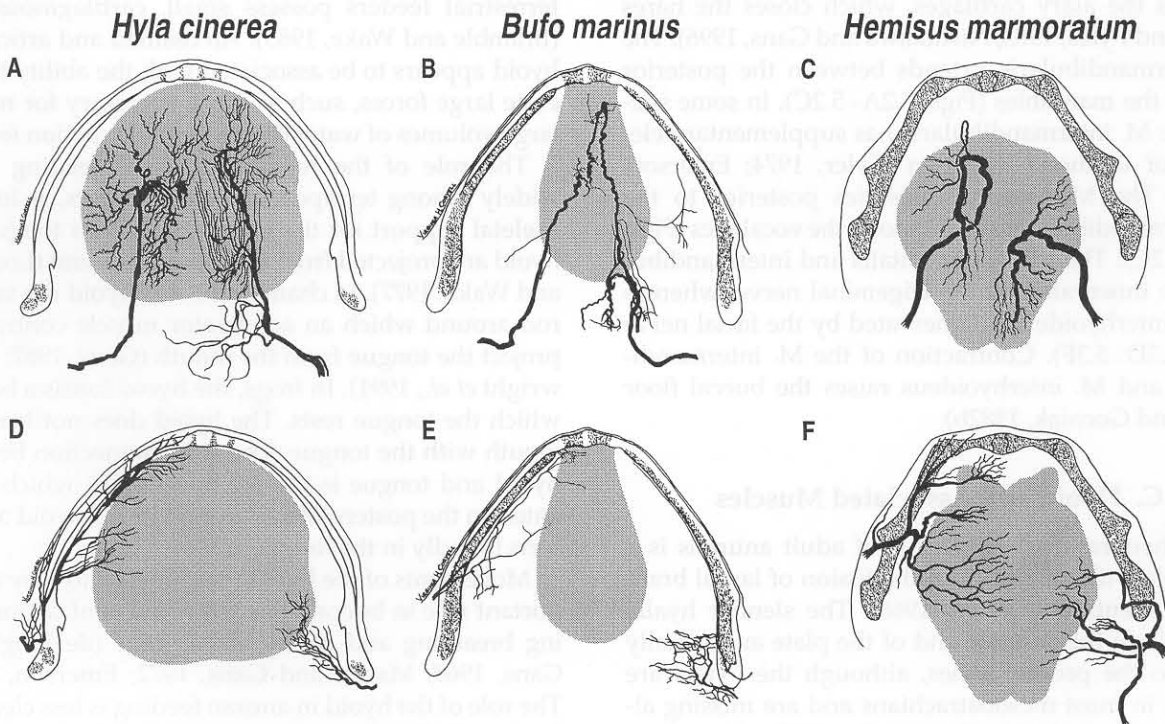


FIGURE 5.3. Camera lucida drawings of the peripheral nerves of adult *Hyla cinerea* (A,D), *Bufo marinus* (B,E), and *Hemisus marmoratum* (C,F) stained with Sudan black B. (Top row) The glossopharyngeal nerve is shown on the left and the hypoglossal nerve is shown on the right. (Bottom row) The trigeminal nerve is shown on the left and the facial nerve is shown on the right. The stippled area indicates the tongue pad. The glossopharyngeal nerve provides only sensory innervation of the tongue. The hypoglossal nerve innervates the *Mm. genioglossus basalis* and *medialis* (if present), the *M. hyoglossus*, and the *Mm. geniohyoideus*, *sternohyoideus*, and *omohyoideus*. The *M. genioglossus basalis* is innervated by the most proximal branches of the hypoglossal nerve at the base of the tongue, whereas the *M. genioglossus medialis* is innervated by the more distal branches. The trigeminal nerve crosses over the mandible and innervates the *M. intermandibularis* and *M. submental*. At the base of the mandible, the facial nerve innervates the *M. interhyoideus*.

species). The presence of a movable joint between the mentomeckelian and dentary is an unusual feature of the mandibles of most anurans (Regal and Gans, 1976; Nishikawa and Roth, 1991). In most species, depression of the mandibular tips results not only from downward movement of the mandibles relative to the cranium (mandibular depression), but also from downward movement of the mentomeckelian bones relative to the rest of the mandible (mandibular bending). Most frogs lack teeth on the mandible. Only one species (*Amphignathodon guentheri*) is known to possess mandibular teeth (Duellman and Trueb, 1986), although some species (e.g., *Ceratophrys*) possess tooth-like processes on the dentary.

A series of three transversely oriented muscles form the floor of the buccal cavity: the *M. submentalis*, *M. intermandibularis*, and *M. interhyoideus* (Figs. 5.2A–5.2C). The *M. submentalis* connects the anterior ends of the mandibles. During feeding, it bends the mandibles downward by depressing their tips. During breathing, the *M. submentalis* closes the nares by lifting the mentomeckelian bones upward. This upward movement deforms the alary cartilages, which closes the nares (Gans and Pyles, 1983; Nishikawa and Gans, 1996). The *M. intermandibularis* extends between the posterior ends of the mandibles (Figs. 5.2A–5.2C). In some species, the *M. intermandibularis* has supplementary elements of unknown function (Tyler, 1974; Emerson, 1976b). The *M. interhyoideus* lies posterior to the *M. intermandibularis* and supports the vocal sacs (Figs. 5.2A–5.2C). The *Mm. submentalis* and *intermandibularis* are innervated by the trigeminal nerve, whereas the *M. interhyoideus* is innervated by the facial nerve (Figs. 5.3D–5.3F). Contraction of the *M. intermandibularis* and *M. interhyoideus* raises the buccal floor (Gans and Gorniak, 1982b).

C. Hyoid and Associated Muscles

The hyobranchial apparatus of adult anurans is a broad plate that forms from the fusion of larval branchial elements (De Jongh, 1968). The slender hyalia extend from the anterior end of the plate and usually attach to the prootic bones, although the hyalia are disjunct in most mesobatrachians and are missing altogether in pelodytids (Cannatella, 1985). Alary processes and posterolateral processes are usually present on the lateral margins of the hyoid plate, and postero-medial processes flank the larynx. In most anurans, only the postero-medial processes are ossified.

A pair of muscles, the *M. geniohyoideus* and *M. sternohyoideus*, serve to protract and retract the hyoid, respectively (Emerson, 1977; Gans and Gorniak, 1982b). The *M. geniohyoideus* originates on the pos-

terolateral processes of the hyoid and inserts near the mandibular symphysis (Figs. 5.2A–5.2C). In most species, it consists of separate medial and lateral compartments. The *M. sternohyoideus* originates on the sternum and inserts on the posterolateral edge of the hyoid plate (Figs. 5.2D–5.2F). The *Mm. petrohyoidei anterior et posteriores* and the *M. omohyoideus* elevate and depress the hyoid, respectively (de Jongh and Gans, 1969; Emerson, 1977). The glossopharyngeal nerve innervates the *M. petrohyoideus anterior* and the vagus nerve innervates the *Mm. petrohyoidei posteriores*, whereas the hypoglossal nerve innervates the *Mm. omohyoideus, sternohyoideus* and *geniohyoideus* (Figs. 5.3A–5.3C; Gaupp, 1896).

A great deal of variation in hyoid morphology is found among anurans (Duellman and Trueb, 1986). Aquatic suction feeders (e.g., *Hymenochirus*, family Pipidae) possess large, articulated, ossified hyoids, whereas terrestrial lingual feeders possess small, fused, cartilaginous hyoids. A similar pattern is found among aquatic and terrestrial turtles, in which suction feeders possess large, ossified, articulated hyoids whereas terrestrial feeders possess small, cartilaginous ones (Bramble and Wake, 1985). An ossified and articulated hyoid appears to be associated with the ability to generate large forces, such as those necessary for moving large volumes of water during aquatic suction feeding.

The role of the hyoid in lingual feeding varies widely among tetrapods. In salamanders, it forms a skeletal support for the tongue, and both tongue and hyoid are projected from the mouth as a unit (Lombard and Wake, 1977). In chameleons, the hyoid is a tapered rod around which an accelerator muscle contracts to project the tongue from the mouth (Gans, 1967; Wainwright *et al.*, 1991). In frogs, the hyoid forms a base on which the tongue rests. The hyoid does not leave the mouth with the tongue. The only connection between hyoid and tongue is the *M. hyoglossus*, which originates on the posterolateral process of the hyoid and inserts broadly in the tongue.

Movements of the hyoid plate appear to play an important role in buccal expansion and contraction during breathing and calling in anurans (de Jongh and Gans, 1969; Martin and Gans, 1972; Emerson, 1977). The role of the hyoid in anuran feeding is less clear (see Section III,B). Cineradiographic recordings of hyoid movement during feeding in *Bufo marinus* show that the hyoid is stabilized in a retracted position during the initial phase of tongue protraction and that it moves anteriorly during tongue protraction (Emerson, 1977). Based on these observations, Emerson (1977) hypothesized that the hyoid acts as a stable platform for the tongue during the initial stages of protraction, that it stores potential energy during intermediate stages,

and that the stored energy is imparted to the tongue during the final stages of protraction. However, this mechanism appears to be unlikely (see Section III,B).

In contrast to the neobatrachians that have been studied, the hyoid appears to play a more important role in feeding in mesobatrachians. Based on anatomical observations and muscle stimulation experiments, Trueb and Gans (1983) suggested that the hyoid plays an important role in tongue protraction during feeding in the termite-eating frog, *Rhinophrynus dorsalis*. This hypothesis remains to be tested experimentally in feeding animals. In the spadefoot toad (*Spea multiplicata*), another mesobatrachian, tongue movements were impaired after bilateral denervation of the M. geniohyoideus, suggesting that hyoid protraction is necessary for normal tongue protraction in this species (O'Reilly and Nishikawa, 1995).

The disjunct hyoid of mesobatrachians may be responsible for the greater role of hyoid protraction during feeding in this group. In most frogs, the cornua of the hyoid are fused to the prootic bones, which may limit forward excursion of the hyoid (Cannatella, 1985). In mesobatrachians, the cornua are continuous until metamorphosis, at which time a gap develops in the cornua, which frees the hyoid plate from its attachment to the skull (Ridewood, 1897), perhaps allowing the hyoid to move farther anteriorly during feeding than it can in other frogs.

D. Tongue and Associated Muscles

There are several problems that terrestrial frogs must overcome to capture prey successfully. These include contacting the prey with the tongue, ingesting prey, transporting it through the oral cavity, and finally swallowing it. In terrestrial anurans, the sticky tongue plays an important role in ingesting, transporting, and swallowing prey. There are no known instances of inertial feeding or transport among anurans, probably because they consume mostly small prey. Frogs do not masticate their food, and there is relatively little manipulation of the food by the tongue once it is in the oral cavity. Little is known about differences among anuran species in modes of oral transport and swallowing.

All anurans possess a relatively simple tongue that consists only of two pairs of extrinsic muscles: the M. genioglossus and M. hyoglossus (Gaupp, 1901; Regal and Gans, 1976). In contrast to most other terrestrial vertebrates, intrinsic muscles are absent in most species. The M. genioglossus originates near the mandibular symphysis and inserts posteriorly into the tongue pad (Figs. 5.2A–5.2C). In many anurans, the M. genioglossus is subdivided by connective tissue

into a number of different compartments, which vary widely among species (Horton, 1982). The M. hyoglossus originates on the posteromedial process of the hyoid and inserts along the lateral margin of the tongue pad, often interdigitating with the fibers of the M. genioglossus (Figs. 5.2A–5.2C). The Mm. genioglossus and hyoglossus are innervated by the hypoglossal nerve (Figs. 5.3A–5.3C).

In most frogs, the M. genioglossus is used to place the tongue on the prey (discussed in detail in Section III) and prey are returned to the mouth by the M. hyoglossus. In *Bombina*, *Bufo*, *Phrynomerus*, and *Hemisus*, denervation experiments demonstrate that the M. hyoglossus plays an important role in prey capture, oral transport, and swallowing (Ritter and Nishikawa, 1995; Tso *et al.*, 1995). Small prey are returned to the mouth and delivered to the esophagus by the tongue in a single movement, sometimes with the help of the forelimbs, whereas large prey are nearly always transported with the help of the forelimbs, presumably because lingual transport would be ineffective by itself (Gray *et al.*, 1997). Because most anurans retract the eyes into the orbit during swallowing, it has been suggested that the M. retractor bulbi also plays a role in anuran swallowing (Regal and Gans, 1976). However, this hypothesis has yet to be tested experimentally (Duellman and Trueb, 1986).

There have been three broadly comparative morphological studies of the tongue musculature of anurans. Magimel-Pelonnier (1924) studied 45 species, Regal and Gans (1976) studied 12 species, and Horton (1982) studied 63 species, predominantly from Australia. In all, 61 genera are represented. From these studies, three different patterns of tongue morphology have been described.

The first pattern consists of a round tongue that is broadly attached to the floor of the mouth, both anteriorly and posteriorly, so that there is no free flap posteriorly. In these tongues, the fibers of the M. hyoglossus radiate from the hyoid into the tongue pad and the ventralmost fascicles insert near the base of the tongue (Horton, 1982). The fibers of the M. genioglossus arise near the mandibular symphysis and radiate into the tongue, where they interdigitate with those of the M. hyoglossus (Regal and Gans, 1976; Horton, 1982). This morphology is found in all archaeobatrachians (i.e., *Ascaphus*, *Leiopelma*, *Bombina*, *Alytes*, and *Discoglossus*), some mesobatrachians (*Pelobates*, *Pelodytes*, and *Rhinophrynus*), and some neobatrachians, including *Telmatozbis*, *Litoria*, *Hyla*, *Gastrotheca*, *Rheobatrachus*, and several genera of limnodynastines (Magimel-Pelonnier, 1924; Regal and Gans, 1976; Horton, 1982; Trueb and Gans, 1983).

Based on their origins and insertions, Regal and

Gans (1976) hypothesized that, upon contraction, the *M. genioglossus* pulls the tongue toward the symphysis in these species, whereas the *M. hyoglossus* pulls the tongue toward the esophagus. These hypotheses have been confirmed by denervation of the *M. genioglossus* in *Bombina* (Nishikawa *et al.*, 1992), *Discoglossus* (Nishikawa and Roth, 1991), and *Hyla* (Deban and Nishikawa, 1992) and by denervation of the *M. hyoglossus* in *Bombina* (Tso *et al.*, 1995).

The second pattern is found only among aquatic pipid frogs (e.g., *Xenopus*, *Pipa*, and *Hymenochirus*), which possess large articulated, ossified hyoids (Cannatella, 1985) and are secondarily tongueless (Cannatella and Trueb, 1988) although they possess vestiges of tongue musculature (Horton, 1982). These species use suction or ram feeding to ingest and transport prey (Sokol, 1969; Avila and Frye, 1977; O'Reilly *et al.*, 1999).

A third pattern consists of a muscular tongue that is attached anteriorly to the buccal floor, with a free posterior flap that varies in length among species (Regal and Gans, 1976) and varies to some extent among fixed specimens within a species (Magimel-Pelonnier, 1924). This type of tongue is found in some pelobatoids (*Scaphiopus*, *Spea*, and *Megophrys*) and some neobatrachians, such as *Hyla* and *Limnodynastes* (Magimel-Pelonnier, 1924; Regal and Gans, 1976; Horton, 1982). In these tongues, the fibers of the *M. hyoglossus* recurve to insert in the more distal parts of the tongue, rather than its anterior base.

In contrast to the *M. hyoglossus*, which is relatively homogeneous among species, the arrangement of the *M. genioglossus* varies widely (Magimel-Pelonnier, 1924; Regal and Gans, 1976; Horton, 1982). All species retain the interdigitating element that is found in species with round, broadly attached tongues, but several additional elements also may be present (Regal and Gans, 1976; Horton, 1982). These elements fall into two groups: those with fibers that run parallel to the long axis of the tongue [i.e., the ventral, dorsomedial and superficial elements of Horton (1982)] and those with transverse fibers [i.e., the *genioglossus basalis* of Gaupp (1901)]. At present, there is no information concerning the functional significance of this variation in the arrangement of the *M. genioglossus* (but see Section III,C). As in species with round, broadly attached tongues, retraction of the tongue is accomplished by contraction of the *M. hyoglossus* (Gans and Gorniak, 1982a,b; Ritter and Nishikawa, 1995; Tso *et al.*, 1995).

On the basis of their anatomy, the tongues of species with free posterior flaps are presumed to rotate over the mandibular symphysis so that the dorsal surface of the tongue at rest becomes the ventral surface of the fully protracted tongue, as has been shown to occur in *Rana* (Gans, 1961, 1962) and *Bufo* (Gans and Gorniak,

1982a,b). It has been hypothesized that these "flipping tongues" have evolved convergently several times among frogs (Regal and Gans, 1976), and this idea is supported by phylogenetic analysis (Section V,A).

Despite the variation in tongue morphology, most frogs (with the exception of pipids) share several important features of the tongue: (1) it is attached anteriorly near the mandibular symphysis; (2) most of the fibers in both the protractor and the retractor muscles are oriented nearly parallel to the long axis of the tongue so that their shortening would pull the tongue pad either toward the symphysis or toward the esophagus (Horton, 1982); (3) those fibers that are transverse (i.e., *genioglossus basalis*) are relatively short and are associated with large amounts of connective tissue (Horton, 1982); (4) the resting length of the tongue approximates the length of the mandibles; and (5) the mass of the tongue is approximately 0.5–1.0% of body mass, which is about as large in relative terms as the human heart.

III. FUNCTION OF THE FEEDING APPARATUS

This section first gives an overview of methods that can be used to study the function of any morphological system, in this case the feeding apparatus. It next discusses previously published hypotheses for the mechanism of tongue protraction in anurans, including an analysis of which methods were informative, which were uninformative, and which were positively misleading. The section ends with a discussion of functional diversification of the mechanism of tongue protraction among anuran species.

A. Methods for Studying the Function of the Feeding Apparatus

Before undertaking a comparative and functional analysis of feeding, it is important to ask what types of experiments and observations can best be used to understand the function of the feeding apparatus. Obviously, the necessary data include a description of anatomy as well as a description of movement patterns, which usually involves some type of kinematic analysis. These often are supplemented with information about muscular and neural activity. Traditional methods include recordings of electrical activity from relevant muscles and nerves as well as electrical stimulation experiments.

Kinematic studies are of three types: (1) description of films or still photos; (2) analysis of kinematic profiles in which values of kinematic variables, such as gape angle, are plotted over time (Fig. 5.4); and (3) trajectory

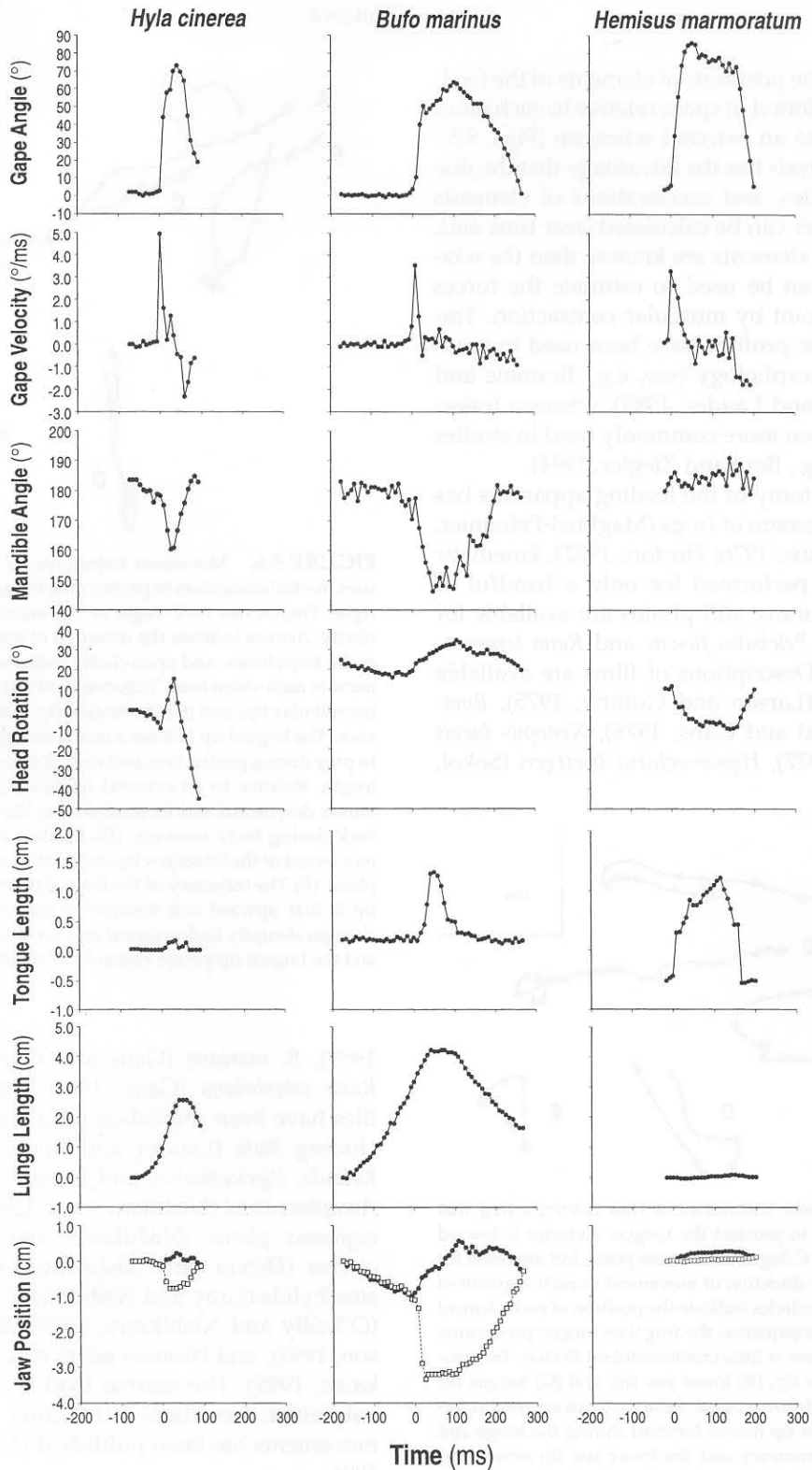


FIGURE 5.4. Kinematic profiles for *Hyla cinerea*, *Bufo marinus*, and *Hemisus marmoratum* showing gape angle ($^{\circ}$), gape velocity ($^{\circ}/\text{msec}$), mandible angle ($^{\circ}$), head rotation ($^{\circ}$), tongue length (cm), lunge length (cm), and jaw position (cm) as a function of time. Mandible angle is the angle subtended by the jaw joint and the tip of the mandibles, with the midpoint of the mandible at the vertex. It is approximately 180° at rest and bends downward to approximately 140° under the contraction of the M. submentalis. Head rotation is the angle formed between a line connecting the jaw joint and upper jaw tips and the horizon line and measures the change in head position relative to the horizon. In this sequence, *H. cinerea* uses jaw prehension to capture the prey, and the head is rotated downward to an angle of 45° below the horizon. Lunge length is the horizontal position of the upper jaw tip in each field. Jaw position shows the vertical position of the upper and lower jaw tips in each field.

analysis, in which the positions of elements of the feeding apparatus are plotted in space relative to each other as well as relative to an external reference (Figs. 5.5–5.7). Trajectory analysis has the advantage that the displacements, velocities, and accelerations of elements relative to each other can be calculated over time and, if the masses of the elements are known, then the relative accelerations can be used to estimate the forces produced at each joint by muscular contraction. Traditionally, kinematic profiles have been used in studies of functional morphology (see, e.g., Bramble and Wake, 1985; Reilly and Lauder, 1989), whereas trajectory analysis has been more commonly used in studies of motor control (e.g., Bout and Ziegler, 1994).

Whereas the anatomy of the feeding apparatus has been studied in 61 genera of frogs (Magimel-Pelonnier, 1924; Regal and Gans, 1976; Horton, 1982), kinematic studies have been performed for only a handful of genera. Among anurans, still photos are available for *Discoglossus pictus*, *Pelobates fuscus* and *Rana temporaria* (Vences, 1988). Descriptions of films are available for *Ascaphus truei* (Larsen and Guthrie, 1975), *Bombina orientalis* (Regal and Gans, 1976), *Xenopus laevis* (Avila and Frye, 1977), *Hymenochirus boettgeri* (Sokol,

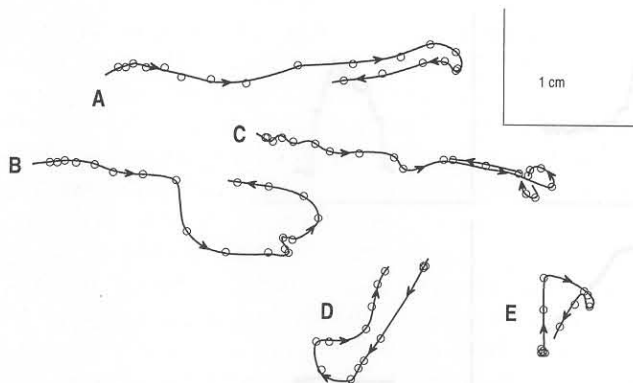


FIGURE 5.5. Movement trajectories of *Hyla cinerea*, a frog that uses mechanical pulling to protract the tongue. Anterior is toward the right. Trajectories A–C begin at the same point, but are offset for clarity. Arrows show the direction of movement in each segment of the trajectories, and open circles indicate the position of each element in each video field. In this sequence, the frog uses tongue prehension to capture the prey so there is little craniovertebral flexion. Trajectories of (A) the upper jaw tip, (B) lower jaw tip, and (C) tongue tip relative to an external reference point. Relative to an external reference point, the upper jaw tip moves forward during the lunge and backward during body recovery and 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. (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 tongue shortens during protraction and never protrudes more than a few millimeters beyond the tips of the mandibles.

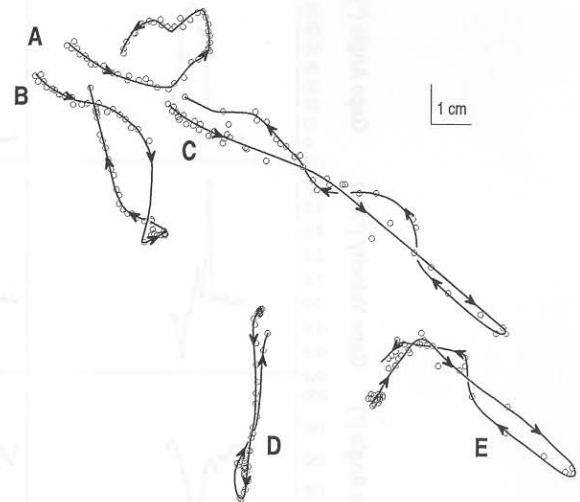


FIGURE 5.6. Movement trajectories of *Bufo marinus*, a frog that uses inertial elongation to protract the tongue. Anterior is toward the right. Trajectories A–C begin at the same point, but are offset for clarity. Arrows indicate the direction of movement in each segment of the trajectories, and open 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 moves 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.

1969), *B. marinus* (Gans and Gorniak, 1982a,b), and *Rana catesbeiana* (Gans, 1961, 1962). Kinematic profiles have been published for a handful of genera, including *Bufo* (Lauder and Reilly, 1994), *Rana*, *Bufo*, *Kaloula*, *Pyxicephalus*, and *Dyscophus* (Emerson, 1985), *Ascaphus truei* (Nishikawa and Cannatella, 1991), *Discoglossus pictus* (Nishikawa and Roth, 1991), *Hyla cinerea* (Deban and Nishikawa, 1992), phyllomedusine hylids (Gray and Nishikawa, 1995), *S. multiplicata* (O'Reilly and Nishikawa, 1995), *Rana pipiens* (Anderson, 1993), and *Hemisis marmoratum* (Ritter and Nishikawa, 1995). The marine toad *B. marinus* is the only amphibian for which a trajectory analysis of feeding movements has been published (Nishikawa and Gans, 1996).

Kinematic profiles (Fig. 5.4) are useful for analyzing the timing of movements of different elements of the feeding apparatus relative to each other. However, as a method for quantifying movement, kinematic profiles are limited by the fact that displacements are plotted in time rather than space. Important information about

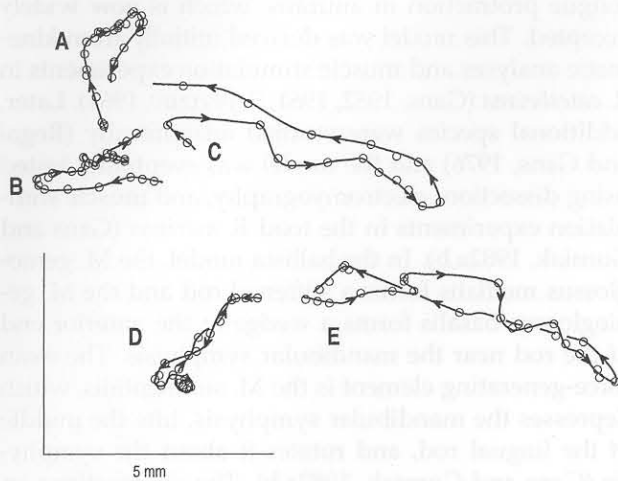


FIGURE 5.7. Movement trajectories of *Hemisus marmoratum*, a frog that uses hydrostatic elongation to protract its tongue. Anterior is toward the right. Trajectories A–C begin at the same point, but are offset for clarity. Arrows indicate the direction of movement in each segment of the trajectories, 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.

head, jaw, and tongue movements and their coordination can often be obtained by performing a trajectory analysis. For example, from kinematic profiles, we can observe that the skull typically begins to rotate upward as the mouth opens during feeding in *Hyla* and *Bufo* (Fig. 5.4). By plotting the trajectory of the mandibular tip relative to the tip of the upper jaw, we also see that mouth opening involves nearly pure depression of the mandibles in *Bufo* (Fig. 5.6), whereas the mandibles are both depressed and retracted to some extent in *Hyla* (Fig. 5.5) and *Hemisus* (Fig. 5.7). From the trajectory analysis, we can see that in *Bufo* the upward rotation of the head during mouth opening balances the retraction of the mandibles, which is an inevitable consequence of downward rotation of the mandibles, whereas the retraction of the mandibles is not entirely balanced by upward head rotation in *Hyla* and *Hemisus*.

As a second example, we can examine tongue movements during prey capture. Kinematic profiles (Fig. 5.4) show that anuran species protract their tongues to different degrees and at different rates of speed. In addition, trajectory analyses show that the tongue tip of *Bufo* (Fig. 5.6) follows a straight line from mouth to

prey, whereas the tongues of *Hyla* (Fig. 5.5) and *Hemisus* (Fig. 5.7) do not. This straight trajectory can be seen to emerge from the precise coordination of head, jaw, and tongue movements (Fig. 5.6).

Electromyographic (EMG) recordings coupled with kinematic analyses may help generate hypotheses about the roles that individual muscles play during feeding (Gans and Gorniak, 1982a,b). For anurans, EMG studies of feeding behavior have been performed only in the toads *B. marinus* (Gans and Gorniak, 1982a,b) and *B. japonicus* (Matsushima *et al.*, 1985) and the frog *R. pipiens* (Anderson and Nishikawa, 1993). Gans and Gorniak (1982a,b) obtained records of EMG activity from several muscles in freely behaving toads feeding on natural prey. Matsushima *et al.* (1985) stimulated the optic tectum with implanted electrodes to elicit tongue flipping in freely behaving animals.

In addition to EMG recordings, muscle stimulation has often been used to study the function of muscles believed to be involved in feeding behavior. It is often possible to perform muscle stimulation on uncooperative species that refuse to eat in captivity (Bemis *et al.*, 1983; Trueb and Gans, 1983). Among anurans, muscle stimulation experiments have been performed only in *B. marinus* (Emerson, 1977; Gans and Gorniak, 1982a,b) and *R. dorsalis* (Trueb and Gans, 1983).

In addition to these traditional techniques, a variety of other techniques may provide additional information that may be used to understand the roles of particular elements of the feeding apparatus. One method is to denervate individual muscles by surgically transecting the nerves that innervate them in order to study how movements change after a muscle or set of muscles has been inactivated. This technique can be used to demonstrate that a particular muscle is either necessary or sufficient for performing a given movement (Nishikawa and Roth, 1991). However, because most peripheral nerves contain both sensory and motor fibers, it is important to consider the possibility that some observed effects of nerve transection may be due to deafferentation rather than to muscle denervation (Nishikawa and Gans, 1992).

B. Hypotheses for the Mechanism of Tongue Protraction

Historically, numerous mechanisms have been proposed to explain tongue flipping in anurans (for a review, see Gans and Gorniak, 1982b). Two relatively recent hypotheses include the hyoid model of Emerson (1977) and the ballista model of Gans and Gorniak (1982a,b). Both of these studies used a variety of techniques to study feeding in the marine toad, *B. marinus*. Both studies proposed relatively complex mechanisms

for tongue protraction and, although based on accurate and repeatable observations, both have been shown to have problems with some aspects of data interpretation (Nishikawa and Gans, 1992, 1996). It is useful to describe these hypotheses and the evidence on which they were based in order to determine which techniques were helpful, which were relatively uninformative, and which were misleading in terms of understanding the mechanism of tongue protraction in anurans.

Emerson (1977) used dissection, cineradiography, and electrical stimulation to develop a biomechanical model of tongue protrusion in toads. Cineradiographic observations revealed that the hyoid is held in the retracted position during mouth opening, moves downward and forward during tongue protraction, and upward and backward during retraction. When stimulated electrically, the tongue protractor muscle *M. genioglossus* "positioned the tongue in the preflip condition but did not cause the tongue to leave the mouth." Stimulation of the *M. depressor mandibulae* did not cause the jaws to open, although stimulation of the *Mm. geniohyoideus* and *sternohyoideus* resulted in mouth opening. From these and other observations, Emerson (1977) hypothesized that the hyoid plays a static role during mouth opening and a dynamic role during protraction and retraction of the tongue. Specifically, she proposed that the hyoid retractor *M. sternohyoideus* stabilizes the hyoid in a retracted position in the floor of the mouth and stores potential energy during the early stages of mouth opening, which she presumed to be caused by contraction of the hyoid muscles *Mm. geniohyoideus* and *sternohyoideus*. As the mouth opens more fully under the contraction of the *M. depressor mandibulae* and the *M. sternohyoideus* stops contracting, potential energy is released as the hyoid moves anteriorly, and this released energy is imparted to the tongue as kinetic energy. Posterior movement of the hyoid, perhaps due to elastic recoil, would initiate retraction of the tongue, which would then be fully retracted by contraction of the *M. hyoglossus*. When the hyoid is fully retracted, it is once again held in place by the action of the *M. sternohyoideus*.

Emerson's (1977) model was refuted by Gans and Gorniak (1982a,b) who showed that (1) the pattern of EMG activity in the muscles of the hyoid and tongue is inconsistent with the model; (2) the tongue is stiff rather than flaccid when protracted; and (3) when the hyoid is wired to the sternum, and thus can impart no kinetic energy to the tongue, toads were observed to feed normally.

As an alternative to Emerson's hyoid model, Gans and Gorniak (1982a,b) offered their ballista model of

tongue protraction in anurans, which is now widely accepted. This model was derived initially from kinematic analyses and muscle stimulation experiments in *R. catesbeiana* (Gans, 1952, 1961; Severtzov, 1961). Later, additional species were studied anatomically (Regal and Gans, 1976) and the model was eventually tested using dissection, electromyography, and muscle stimulation experiments in the toad *B. marinus* (Gans and Gorniak, 1982a,b). In the ballista model, the *M. genioglossus medialis* forms a stiffened rod and the *M. genioglossus basalis* forms a wedge at the anterior end of the rod near the mandibular symphysis. The main force-generating element is the *M. submentalis*, which depresses the mandibular symphysis, lifts the middle of the lingual rod, and rotates it about the symphysis (Gans and Gorniak, 1982a,b). The observations on which the model was based include: (1) electromyographic data showing that the *M. submentalis* and *Mm. genioglossus basalis* and *medialis* are active during tongue protraction and (2) the observation that stimulation of the *M. genioglossus basalis* resulted in rotation of the base of the tongue toward the mandibular symphysis, whereas stimulation of the *M. genioglossus medialis* resulted in stiffening of the tongue with no anterior movement.

Results of muscle denervation experiments and detailed kinematic analyses have shown that the ballista hypothesis for tongue protraction also requires substantial revision (Nishikawa and Gans, 1996). Specifically, denervation of the *M. submentalis*, which is the major force-producing element in the ballista hypothesis, had no effect on tongue protraction in *B. marinus*, whereas denervation of the *Mm. genioglossus basalis* and *medialis* reduced tongue protraction significantly. From these experiments, Nishikawa and Gans (1996) concluded that the *M. genioglossus medialis* not only stiffens the tongue during protraction, but also is the main force-generating element that pulls the tongue forward out of the mouth.

We can now examine why the models of Emerson (1977) and Gans and Gorniak (1982a,b), although based on accurate and repeatable observations, failed to identify the muscles that are responsible for tongue protraction in toads. First, neither study described the kinematics of tongue protraction in toads with either kinematic profiles or trajectory analyses, so both studies overlooked the fact that the tongue normally elongates by approximately 180% of its resting length during protraction (Nishikawa and Gans, 1996). Second, EMG studies were relatively uninformative because numerous muscles are activated simultaneously during feeding (Gans and Gorniak, 1982b), which makes it difficult to understand how each contributes to feeding movements. Furthermore, electromyographic data

were positively misleading because some muscles that are active during tongue protraction (i.e., the *M. submentalis*) appear to have little or no effect on tongue movements as demonstrated by surgical denervation experiments (Nishikawa and Gans, 1996).

Finally, the results of muscle stimulation experiments were also positively misleading. At least three repeatable results were misinterpreted by Emerson (1977), Gans and Gorniak (1982a,b), or both. First, Emerson (1977) reported accurately that stimulation of the *M. depressor mandibulae* is insufficient to open the mouth of a spinal pithed toad. The explanation for this result, however, is not that the force produced by the muscle is insufficient to open the mouth, but rather that, even in spinal pithed toads, tonic contractions of the *Mm. levator mandibulae* resist mouth opening (Nishikawa and Gans, 1992). During normal feeding, this tonic activity is inhibited during mouth opening so that the *M. depressor mandibulae* does not have to overcome the additional force produced by tonic activity. When the *M. levator mandibulae* is denervated, stimulation of the *M. depressor mandibulae* results in rapid opening of the mouth (Nishikawa and Gans, 1992).

Second, Emerson (1977) accurately reported that stimulation of the *M. geniohyoideus* causes the mouth to open. Once again, however, the explanation is rather complex. In this case, the hypoglossal nerve runs through the body of the *M. geniohyoideus* and it contains sensory fibers from the tongue that, when stimulated, inhibit tonic contractions of the *M. levator mandibulae* (Nishikawa and Gans, 1992). When the *M. geniohyoideus* is stimulated, the hypoglossal nerve is also stimulated, and tonic contractions of the *M. levator mandibulae* are inhibited. In this case, stimulation of the *M. geniohyoideus* causes the mouth to open, but it takes less force to open the mouth because the tonic contractions of the *M. levator mandibulae* are inhibited by electrical stimulation of the hypoglossal nerve that runs through the belly of the *M. geniohyoideus*. When the hypoglossal nerve is transected before it enters the *M. geniohyoideus*, stimulation of the *M. geniohyoideus* no longer produces mouth opening because the tonic contractions of the *M. levator mandibulae* are no longer inhibited (Nishikawa and Gans, 1992).

Both of these examples illustrate the fact that muscle stimulation experiments can be positively misleading because the neural pathways, both sensory and motor, may remain intact even after spinal pithing and affect the force necessary to achieve a given movement. In muscle stimulation experiments, tonic muscle activity may be present that is not present during normal behavior in the intact animal. Furthermore, electrical stimuli may activate not only muscle fibers but also

nearby nerve fibers. In turn, stimulation of sensory nerve fibers may activate central neural circuits that modulate tonic activity of other muscles, thereby changing the amount of force that is necessary to achieve a given movement. For these reasons, the results of muscle stimulation experiments should always be interpreted with caution.

Finally, both Emerson (1977) and Gans and Gorniak (1982b) noted that stimulation of the *Mm. genioglossus* in a spinal pithed toad does not result in protraction of the tongue. Based on this and other observations, Emerson (1977) hypothesized that the hyoid played an important role in tongue protraction, whereas Gans and Gorniak (1982a,b) hypothesized that the *M. submentalis* was the major force-generating element for tongue protraction. In contrast, denervation experiments suggest that the *Mm. genioglossus* are the major force-generating elements for tongue protraction during feeding (Nishikawa and Gans, 1996). The resolution of these conflicting observations seems to be that the dynamics of tongue protraction, which in toads involves large, simultaneous displacements of the jaws and tongue in as little as 35 msec (Nishikawa and Gans, 1996), cannot be duplicated under the static conditions in which muscle stimulation experiments necessarily are conducted.

In my opinion, our current understanding of the feeding mechanisms of anurans has come mostly from detailed anatomical descriptions, kinematic analyses of movement, including both kinematic profiles and trajectory analyses, and experimental denervation of feeding muscles. In the case of anuran feeding behavior, both electromyographic studies and muscle stimulation experiments have been mostly uninformative and sometimes even misleading. An understanding of the biomechanics of complex anatomical systems can only be achieved by using as many techniques as possible to develop and test hypotheses about function.

C. Functional Diversification among Anuran Taxa

Over the past several years, my students and I, along with several collaborators, have used many different techniques to study the function of the anuran feeding apparatus. Detailed studies have been published for several anuran species, including *D. pictus* (Nishikawa and Roth, 1991); *S. multiplicata* (O'Reilly and Nishikawa, 1995); *Hyla cinerea* (Deban and Nishikawa, 1992); *Pachymedusa dacnicolor* (Gray and Nishikawa, 1995); *B. marinus* (Nishikawa and Gans, 1996); *Dendrobates*, *Phylllobates*, and *Epipedobates* (Wiltenmuth and Nishikawa, 1994); *R. pipiens* (Anderson, 1993); *H. marmoratum* (Ritter and Nishikawa, 1995); and

Phrynomerus bifasciatus (Jaeger and Nishikawa, 1993; Meyers *et al.*, 1996).

From these comparative studies, we have identified three different mechanisms that anurans use to protract their tongues during feeding in terrestrial environments. These mechanisms are mechanical pulling, inertial elongation, and hydrostatic elongation, and each is described in detail in the following sections. All of the nearly 150 species that have been examined so far fall into one of these categories, although additional mechanisms, such as hyoid pushing in mesobatrachians (see Section II,C; O'Reilly and Nishikawa, 1995), may also be present.

1. Mechanical Pulling

The first mechanism of tongue protraction is mechanical pulling, here exemplified by *H. cinerea* (Fig. 5.8). It is found in all archaeobatrachian lineages, including *Ascaphus* (Ascaphidae) (Nishikawa and Cannatella, 1991), *Leiopelma* (Leiopelmatidae), *Bombina* (Bombinatoridae), and *Discoglossus* (Discoglossidae) (Nishikawa and Roth, 1991), as well as in some mesobatrachians (e.g., *Pelobates* and *Spea*) and some neobatrachians (e.g., *Hyla*). Anatomically, the tongues of mechanical pullers tend to be round in shape, broadly attached to the floor of the mouth, and there is much interdigitation of the *M. hyoglossus* and *M. genioglossus medialis* throughout the tongue pad (Magimel-Pelonnier, 1924; Regal and Gans, 1976; Horton, 1982). The ventralmost fibers of the *M. hyoglossus* insert near the anterior tip of the tongue (Horton, 1982).

In mechanical pullers, the function of the tongue protractor muscle *M. genioglossus* is most like that of typical vertebrate skeletal muscle. Both the *M. genioglossus* and the tongue as a whole shorten during protraction as the fibers of the *M. genioglossus* contract and pull the tongue tip toward the mandibular symphysis (Fig. 5.8). This mechanism is essentially similar to that proposed by Regal and Gans (1976). In mechanical pullers, the resting length of the tongue is approximately equal to the length of the mandibles (Figs. 5.3A–5.3C). The tongue shortens as the *M.*

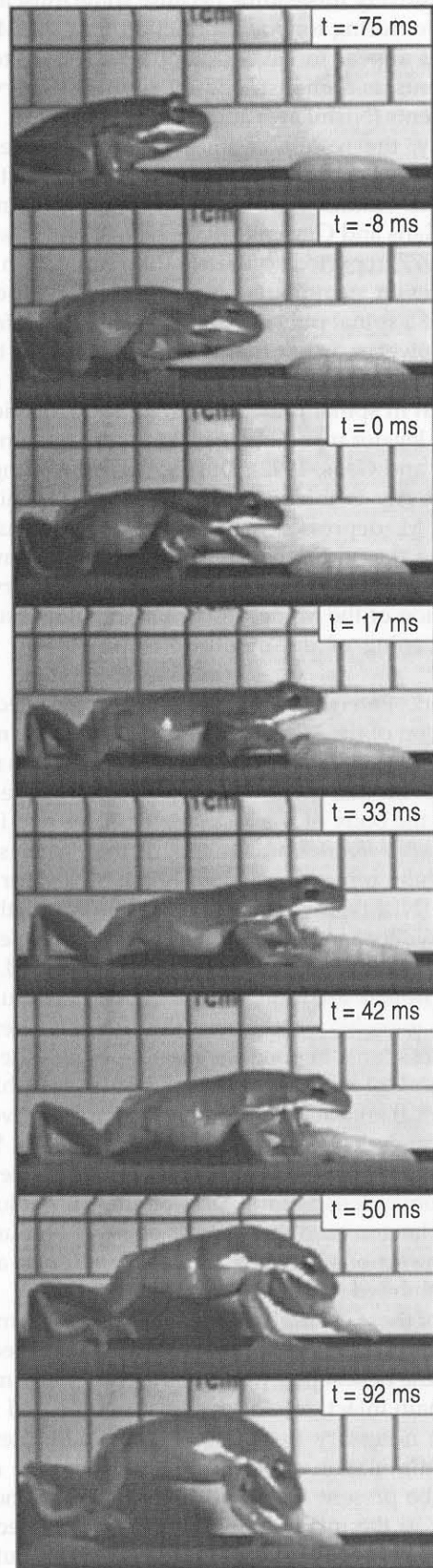


FIGURE 5.8. Selected frames from a normal prey-capture sequence for *Hyla cinerea*, showing mechanical pulling. The number in the right-hand corner of each picture indicates the time (msec) from the onset of mouth opening. The squares in the background are 1×1 cm. The short tongue can be seen at full protraction at $t = 17$ msec. In this sequence, the frog uses jaw prehension to capture the waxworm. The craniovertebral joint is flexed downward between $t = 42$ and $t = 92$ msec, and at $t = 92$ msec, the jaws close on the prey.

TABLE 5.1 Characteristics of the Different Mechanisms of Tongue Protraction

Characteristics	Mechanical pulling	Inertial elongation	Hydrostatic elongation
Example	<i>Hyla cinerea</i>	<i>Bufo marinus</i>	<i>Hemidus marmoratum</i>
Tongue movement	Tongue shortens	Tongue elongates 180%	Tongue elongates 200%
Velocity (cm/sec)	79	286	24
Acceleration (m/sec ²)	66	310	3.5
Tongue/jaw synchrony	No	Yes	No
Aiming	Distance	None	Distance, azimuth, elevation
Accuracy	95%	33%	>99%
On-line correction	Yes	No	Yes
Feedforward control	Yes	Yes	Yes
Feedback control	Yes	No	Yes
Hypoglossal afferents	No	Yes	No

genioglossus contracts, pulling the tongue pad upward and forward toward the symphysis (Figs. 5.4, 5.5E, and 5.8). Thus, in mechanical pullers, the tongue is shorter at full protraction than it is at rest in the floor of the mouth. In *H. cinerea*, for example, the length of the tongue at maximum protraction is approximately 60% of its resting length (Fig. 5.4).

Movements of the head, jaws, and tongue are small and rather asynchronous (Fig. 5.11) in mechanical pullers. Because the tongue shortens during protraction, the frogs must lunge forward with their entire bodies in order to place the tongue on the prey (Figs. 5.4, 5.5A, and 5.8). When capturing relatively large prey, the frogs also exhibit head flexion in order to bring the tongue down onto the prey, and the prey are apprehended with the jaws (Figs. 5.4 and 5.8). For small prey, tongue prehension is used for prey capture and there is less flexion of the head (Fig. 5.5A).

During feeding, the lower jaw tip is depressed and retracted slightly relative to the upper jaw tip (Fig. 5.5D). The short tongue can hardly be moved independently of the lower jaw (Fig. 5.5D) and the maximum reach of the tongue beyond the jaws typically is not more than a few millimeters (Fig. 5.4; Deban and Nishikawa, 1992). Relative to the lower jaw tip, to which the tongue is attached, the tongue reaches moderate velocities (79 cm/sec) and accelerations (66 m/sec²) during protraction (Table 5.1). Tongue movements can be corrected in progress within a single gape cycle and there is little, if any, ability to aim the tongue relative to the head (Deban and Nishikawa, 1992). In the two species of mechanical pullers that have been studied (Gray, 1997), prey capture success ranges from 95% in *H. cinerea* to 68% in *H. arenicolor* when feeding on relatively small, slow-moving prey such as waxworms.

2. Inertial Elongation

In contrast to mechanical pullers whose tongues shorten during protraction, the tongues of many frogs elongate during protraction (Figs. 5.9 and 5.10). Given the fact that muscles can only contract to do work, and given that all frogs exhibit rather similar morphologies of the extrinsic tongue muscles in which most fibers run parallel to the long axis of the tongue, it is rather surprising that the tongues of these frogs can elongate beyond resting length during protraction. What mechanisms are responsible for tongue elongation and which muscles are responsible?

Many anurans use inertia to elongate the tongue during protraction. Inertial elongation is found among several anuran lineages, including some leptodactylid leptodactylids (*Physalaemus* and *Pleurodema*), some eleutherodactylid leptodactylids (*Eleutherodactylus*), all bufonids, all phyllomedusine hylids, and all ranoids except hemisotids and microhylids (Nishikawa *et al.*, 1992). This chapter uses the marine toad, *B. marinus*, as an example of a typical inertial elongator (Fig. 5.9).

The tongues of inertial elongators are similar morphologically to those of mechanical pullers, except that the fibers of the protractor and retractor muscles are relatively longer, which produces a posterior flap that is free from the floor of the mouth (Magimel-Pelonner, 1924; Regal and Gans, 1976; Horton, 1982). In addition, there is less interdigitation between the M. hyoglossus and the M. genioglossus in the tongue pad, and the ventralmost fibers of the M. hyoglossus recurve to insert in the posterior, rather than the anterior, part of the tongue (Horton, 1982). The relative mass of the tongue is typically smaller in inertial elongators (0.5%) than in mechanical pullers (1.0%).

The initial stages of tongue protraction are similar in mechanical pullers and inertial elongators. Inertially elongated tongues shorten at first as the *M. genioglossus medialis* contracts and accelerates the tongue pad upward and forward. In inertial elongators, however, the tongue elongates by as much as 180% of its resting length under its own inertia after the initial shortening phase (Nishikawa and Gans, 1996).

Inertial elongation appears to be the fastest and least accurate mechanism of tongue protraction in anurans. In toads (*B. marinus*), the tongue tip reaches velocities of up to 270 cm/sec and accelerations of 310 m/sec² (more than 30 times gravity) relative to the tips of the mandibles during protraction (Nishikawa and Gans, 1996). These velocities and accelerations are several times greater than those of mechanical pullers (Table 5.1). Toads are also much less accurate (30%) at capturing prey than mechanical pullers (Table 5.1; Gray, 1997). Because tongue protraction is rapid and ballistic, tongue movements cannot be corrected within the gape cycle (Nishikawa and Gans, 1996). Like mechanical pullers, toads possess little, if any, ability to aim the tongue relative to the head.

The complexity of tongue and jaw movements during feeding in inertial elongators is demonstrated by the trajectories of the upper jaw tip, mandibular tip, and lingual tip (Fig. 5.6), which show how the individual movements of these elements contribute to tongue protraction (Nishikawa and Gans, 1996). A remarkable feature that emerges from this analysis is that the lingual tip follows an almost straight line from mouth to prey, despite rotation of the tongue over the mandibular symphysis during protraction, from top to bottom as well as rear to front, and despite substantial changes in the shape of the tongue during protraction (Fig. 5.9).

The straight-line trajectory of the lingual tip relative to an external reference is the sum of the relative trajectories of all the elements to which the tongue is attached: (1) the trajectory of the upper jaw tip relative to an external reference, which is first downward and forward, then upward and back (Fig. 5.6A); (2) the trajectory of the mandibular tip relative to that of the upper jaw tip, which is mostly restricted to the vertical plane

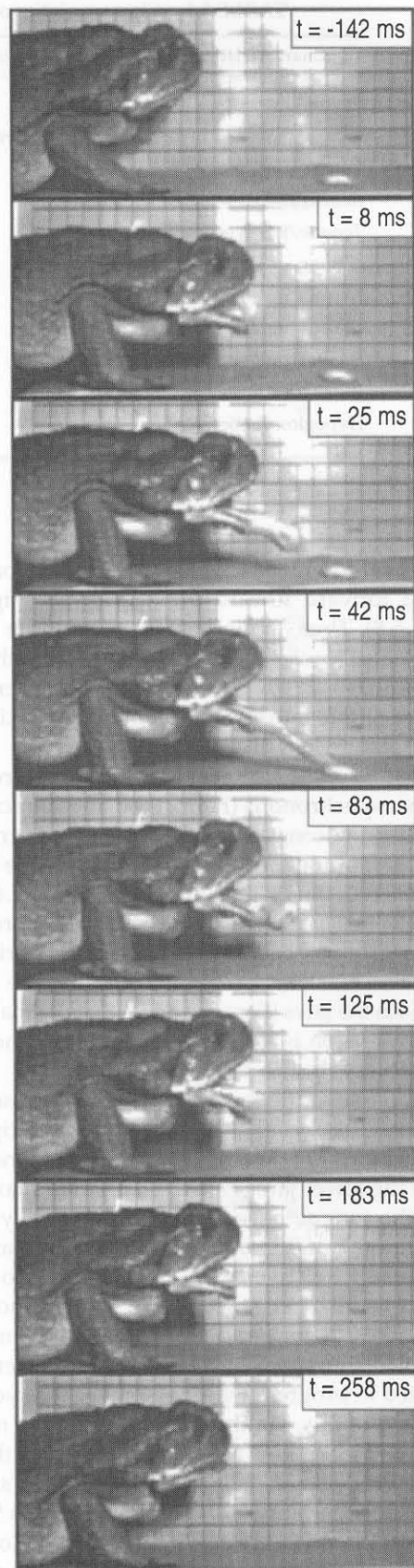
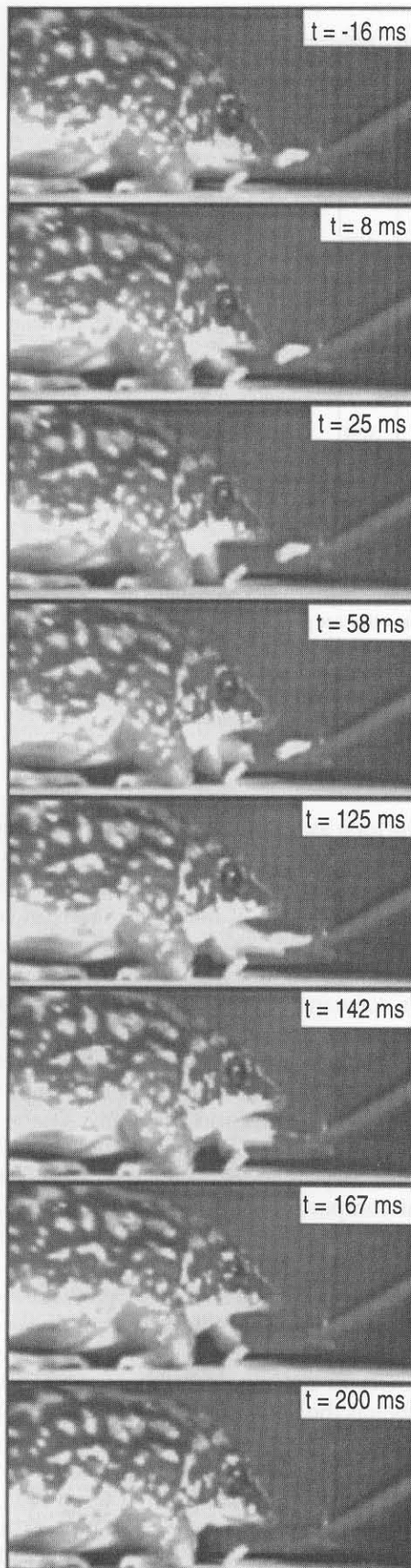


FIGURE 5.9. Selected frames from a normal prey-capture sequence for *Bufo marinus*, showing inertial elongation. The number in the right-hand corner of each picture indicates the time (msec) from the onset of mouth opening. The squares in the background are 1 × 1 cm. The tongue shortens at first ($t = 8$ msec) but then elongates by up to 180% of its resting length under its own momentum ($t = 25$ – 42 msec).



(Fig. 5.6D); and (3) the trajectory of the lingual tip relative to the mandibular tip, which first rises as the tongue shortens and moves forward, but then changes direction abruptly as the lingual tip passes beyond the oral cavity and moves downward and forward as the tongue elongates (Fig. 5.6E).

Trajectory analysis demonstrates that precise coordination among head, jaw, and tongue movements is responsible for the straight trajectory of the tongue tip from mouth to prey. First, the downward and forward and then the upward and back movement of the head counteracts the tendency for mouth opening to produce retraction of the lower jaw, which would occur without compensatory head movements because the jaw tip must transcribe a circular path about the jaw joint. Furthermore, a large upward acceleration of the lingual tip occurs simultaneously with a large downward acceleration of the mandibular tips (Fig. 5.11). The acceleration of the tip of the mandibles relative to that of the upper jaw is oriented downward, whereas the acceleration of the lingual tip relative to that of the mandibles is oriented upward and forward. These large, synchronous, partially opposed jaw and tongue movements add together precisely to generate the straight lingual trajectory (Nishikawa and Gans, 1996).

Nishikawa and Gans (1996) used a simple matrix model to demonstrate that the linear trajectory of the tongue depends on the simultaneous accelerations of tongue and jaws. In this model, the relative timing of displacements of the jaws and tongue was varied systematically and the change in tongue trajectory was measured. This analysis showed that changes in the relative timing of the displacements had only a small effect on the horizontal position of the tongue tip. However, the vertical position of the lingual tip strongly depends on the simultaneous displacement of the mandibular and lingual tips. If the vertical displacements of the lingual tip are added to the vertical displacements of the upper jaw and mandibular tips 8 msec (i.e., one video field) earlier than they actually occur, then the trajectory of the lingual tip would intersect that of the upper jaw (i.e., the tongue would contact the palate). If the lingual displacements occur 8 msec too late, then the lingual tip would drop with the mandible before accelerating upward, which would

FIGURE 5.10. Selected frames from a normal prey-capture sequence for *Hemissus marmoratum*, showing hydrostatic elongation. The number in the right-hand corner of each picture indicates the time (msec) from the onset of mouth opening. The squares in the background are 1×1 cm. The tongue elongates slowly during retraction ($t = 25$ – 125 msec).

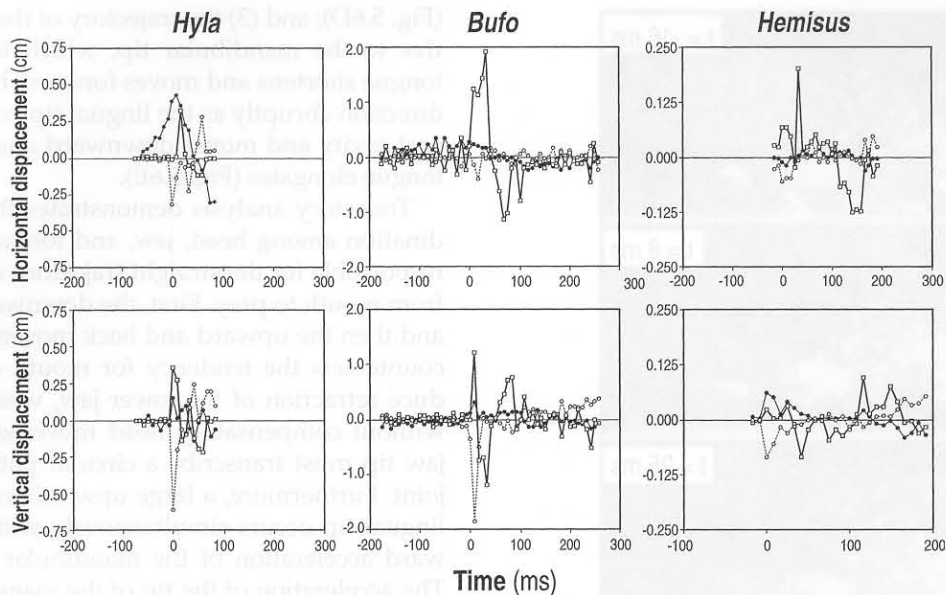


FIGURE 5.11. Horizontal (above) and vertical (below) displacements between successive frames for *Hyla*, *Bufo*, and *Hemisus* (upper jaw tip, closed circles; mandibular tip, open circles; lingual tip, open squares). For *Hyla*, horizontal displacements of the upper jaw tips are greater than those of the mandibular and lingual tips, whereas for *Bufo* and *Hemisus*, 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 movements of the jaws and tongue are asynchronous in *Hyla* and *Hemisus*.

produce a nonlinear trajectory that deviates from the observed trajectory by more than 1 cm (approximately 20% of tongue length). Thus, the synchrony of the large displacements of the tongue and mandibles is necessary for successful prey capture in inertial elongators, but not in mechanical pullers (Table 5.1).

3. Hydrostatic Elongation

The third mechanism of tongue protraction, hydrostatic elongation, is possessed only by members of the families Hemisotidae and Microhylidae. This chapter uses *Hemisus marmoratum* as a representative hydrostatic elongator (Fig. 5.10). *Hemisus* may elongate its tongue up to 200% of resting length (Ritter and Nishikawa, 1995). However, it protracts its tongue too slowly to use an inertial mechanism. The tongue tip reaches maximum velocities of 15 cm/sec (nearly 20 times slower than inertial elongators) and accelerations of 0.5 m/sec² (more than 600 times slower than inertial elongators, Table 5.1). Instead of inertia, a hydrostatic mechanism is used to protract the tongue (Nishikawa *et al.*, 1995).

In hydrostatic elongators, the tongue protractor muscle (M. genioglossus) consists of two compartments, one in which the muscle fibers are oriented par-

allel to the long axis of the tongue as in other frogs and one in which the fibers are oriented vertically (Nishikawa *et al.*, 1995; Fig. 5.2D). During protraction, the volume and the width of the tongue remain constant. When the vertical fibers contract, they decrease the thickness of the tongue and, because the volume of the tongue is constant, this change in shape is translated directly into tongue elongation (Nishikawa *et al.*, 1995). A decrease in tongue thickness of 50% (from 2 to 1 mm) is translated into a 100% increase in tongue length (from 5 to 10 mm). Ritter and Nishikawa (1995) favored a hydraulic mechanism of tongue elongation in *Hemisus* because they overlooked the presence of the dorsoventral compartment of the M. genioglossus in *H. marmoratum*. The presence is apparent only in sections, and not in gross dissection.

In contrast to inertial elongators, which *must* protract their tongues rapidly in order to achieve elongation, hydrostatic elongators may protract their tongues either slowly or rapidly. In terms of prey capture, *H. marmoratum* is the slowest and most accurate of the anuran species that have been studied to date (Ritter and Nishikawa, 1995). Other hydrostatic elongators, such as *Dyscophus insularis*, protract their tongues more rapidly than *Hemisus*. Hydrostatic elongators exhibit high accuracy of prey capture (99%; Gray, 1997) and on-line

correction of tongue movements within a gape cycle (Table 5.1).

In contrast to both mechanical pullers and inertial elongators, there is very little head movement during feeding in hydrostatic elongators, although the head moves slightly upward and forward and then down and back during feeding (Fig. 5.7A). The lower jaw tip is both depressed and retracted during mouth opening (Fig. 5.7D), 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 is straight out of the mouth, rather than upward and forward as in inertial elongators (Fig. 5.7C). In contrast to inertial elongators, the tongue does not follow a straight line from mouth to prey during protraction (Fig. 5.7E). As in mechanical pullers, movements of the head, jaws, and tongue are asynchronous (Fig. 5.11).

All anurans studied to date can aim their heads relative to their bodies and do so readily during feeding. In addition, some mechanical pullers can modulate tongue protraction distance in response to prey distance (Deban and Nishikawa, 1992; O'Reilly and Nishikawa, 1995). All hydrostatic elongators can modulate tongue protraction distance in response to prey distance, and in addition are the only anurans that can aim their tongues relative to their heads in dimensions other than distance (Ritter and Nishikawa, 1995; Jaeger and Nishikawa, 1993; Meyers *et al.*, 1996). *Phrynomerus bifasciatus* (family Microhylidae) aims its tongue relative to the head in distance and azimuth (Jaeger and Nishikawa, 1993; Meyers *et al.*, 1996), whereas *H. marmoratum* aims its tongue relative to its head in distance, azimuth, and elevation (Ritter and Nishikawa, 1995).

Insight into the mechanism of tongue aiming comes from denervation experiments in *Hemismus* (Ritter and Nishikawa, 1995) and *Phrynomerus* (Meyers *et al.*, 1996). In both species, when unilateral denervation of the M. genioglossus is performed, the tongue bends toward the inactivated side. In *Phrynomerus*, the tongue deviates by up to 90° from the target, whereas in *Hemismus* it deviates by more than 180°. These experiments are consistent with the proposed hydrostatic mechanism of tongue protraction, in which the tongue bends toward the inactivated side to equalize tensile stresses in the tongue. They also suggest that microhylids and hemisotids may regulate the azimuth of the tongue by differential recruitment of the right and left sides of the M. genioglossus (Ritter and Nishikawa, 1995). In contrast, the amplitude of tongue movement is reduced after unilateral denervation of the M. genioglossus in *B. marinus*, but the direction of tongue protraction is unaffected (personal observation).

Finally, *H. marmoratum* is the only frog that is known to possess a truly prehensile tongue. In other frogs, the

tongue sticks to prey by wet adhesion. In *Hemismus*, the tongue not only sticks to prey but actually grasps it (Ritter and Nishikawa, 1995). If a termite is held with forceps, the tongue of *H. marmoratum* can generate enough tensile force to tear it in half. Muscle denervation experiments demonstrate that activation of the M. hyoglossus is necessary for this prehensile function. The M. hyoglossus sends a fascicle into each lobe of the bilobed tongue and, when inactivated, prehension is eliminated, although the frogs can still capture prey using lingual adhesion (Ritter and Nishikawa, 1995; Tso *et al.*, 1995). These experiments also demonstrate that the M. hyoglossus plays an important role in swallowing. Intact *Hemismus* always ingests, transports, and swallows termites in a single movement, whereas the tongue is often protracted with a previously captured termite still adhering to it after M. hyoglossus denervation.

IV. NEURAL CONTROL OF PREY CAPTURE

Until the 1970s, when *in vitro* intracellular recording techniques became feasible in the intact vertebrate central nervous system, patterns of motor output were widely believed to result from a chain of reflex-like interactions between sensory and motor neurons (Delcomyn, 1980). Since then, however, *in vitro* and deafferentation studies in a large number of animals, ranging from leeches to primates, have shown that intrinsic patterns of motor output are produced in the absence of sensory input (Delcomyn, 1980; Grillner, 1985). The neurons responsible for producing this output have been termed central pattern generators (CPGs). These CPGs are implicated in the production of numerous behavior patterns, including breathing, swimming, walking, and feeding. In frogs, a variety of evidence points to the medial reticular formation as a possible site of the CPG for prey capture (Matsushima *et al.*, 1989; Weerasuriya, 1989).

Unlike a spinal cord in a dish, however, all behaving animals must produce varied patterns of motor output that are exquisitely appropriate to the animal's changing conditions. Adaptive behavior involves the production of a motor response that is appropriate in the context of incoming sensory stimuli. In order to understand the neural basis of adaptive behavior, we need to know how central pattern generators and motor neurons interact with sensory receptors to produce motor output that tracks changes in an animal's external environment as well as its internal state. Current theories suggest that sensory input acts directly on CPGs to change the frequency, amplitude, and phase of

motor patterns (Rossignol *et al.*, 1988). In theory, such changes result from the effects of neurotransmitters and neuromodulators on the membrane properties of CPG neurons (Harris-Warrick, 1988). Empirically, however, the mechanisms by which sensory input influences CPGs are not yet well understood, even in relatively well-studied systems such as lamprey swimming (Grillner *et al.*, 1988).

Comparative studies of the neural control of movement should be conducted in the context of the adaptive modification of CPG activity by incoming sensory input. Within this conceptual framework, we can investigate which sensory modalities are involved in modulating prey capture movements, how sensory information influences the pattern of motor activity produced by central pattern generators, and how sensory modalities interact to modulate movement. We can then proceed to ask whether species differ in these aspects of motor control.

There are several problems that frogs must overcome to capture prey successfully. These include detecting the prey, locating it in space, and analyzing its relative size, shape, and speed of movement. Once prey are detected and located, a frog must respond to it before it escapes, place its tongue accurately on the prey, apprehend it, and bring it back to the mouth. Apprehension requires planning and execution of precisely coordinated movements of the head, jaws and tongue (Nishikawa and Gans, 1996). Some of these problems will be discussed later. Other problems, such as locating prey in space (Ingle, 1983), are beyond the scope of this chapter.

In terms of neural control, prey capture in frogs is a goal-oriented movement that is similar to reaching in humans (Gottlieb *et al.*, 1989; Flanders *et al.*, 1992) or pecking in pigeons (Bermejo and Ziegler, 1989). Performance of these goal-oriented tasks requires sensory information about the target and sensory information about the animal's internal state, both of which are used to modulate the output of CPGs. Relevant information about the target is often obtained visually and includes target position in three dimensions (distance, azimuth, and elevation), size, shape, and velocity. Relevant information about the animal's internal state is obtained through a variety of proprioceptive sense organs distributed throughout the body and includes the length and mass of musculoskeletal elements, the force-velocity relationships 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.

Prey recognition has been studied extensively in amphibians (Ewert, 1987; Roth, 1987), and a review of these studies is beyond the scope of this chapter. To date, motor control of prey capture has been studied in

detail in only two anuran species, *R. pipiens* (family Ranidae) and *B. marinus* (family Bufonidae). Methods that have been used to study neural control of prey capture include behavioral studies, deafferentation experiments, electrophysiological recording, and neuro-anatomical tracing. These studies have focused on the modulatory effects of visual analysis of prey features (Anderson, 1993; Valdez and Nishikawa, 1997), of proprioceptive tongue afferents (Nishikawa and Gans, 1992; Nishikawa *et al.*, 1992; Anderson and Nishikawa, 1993, 1997), and of the interaction between vision and proprioception in controlling feeding movements (Anderson and Nishikawa, 1993, 1996). The modulatory effects of visual input on prey capture movements, the modulatory effects of tongue afferents on prey capture movements, and the interaction between vision and proprioception in controlling feeding movements are described in detail next.

A. Visual Analysis of Prey Features

Some anurans will snap in response to tactile stimulation (Comer and Grobstein, 1981). Some species also can locate prey on the basis of olfactory cues alone (Dole *et al.*, 1981; Shinn and Dole, 1978). Even auditory stimuli can be used to locate prey (Martof, 1962; Jaeger, 1976). However, vision appears to be the dominant sensory modality that most frogs use to detect prey. When vision is intact, frogs seldom lunge or snap at stationary prey (Lettvin *et al.*, 1959; Kaess and Kaess, 1960; Ewert, 1985; Satou and Shiraishi, 1991).

There have been numerous studies of the visual cues used in prey recognition by toads (reviewed in Ewert, 1987). These studies measured the rates of orientation and snapping elicited by artificial, two-dimensional, prey-like stimuli that differed in shape, size, and speed of movement. These studies showed that toads (*B. bufo*) exhibit higher orienting rates for rectangular objects which move in a direction that is parallel to their long axis (i.e., worm orientation) than for similar objects that move perpendicular to their long axis (i.e., anti-worm orientation).

Not only the tendency to respond, but also patterns of movement change in response to prey characteristics (Anderson, 1993; Anderson and Nishikawa, 1996; Valdez and Nishikawa, 1997). For example, *R. pipiens* (an inertial elongator, family Ranidae) exhibits different behavior patterns to capture small vs large prey (Anderson, 1993). Small prey are captured with the tongue and are transported to the esophagus without contacting the jaws (here termed "tongue prehension"), whereas large prey are first contacted with the tongue but the head rotates downward, the prey are captured in the closing jaws, and are transported into the oral cavity with the forelimbs (here termed "jaw

prehension"). During tongue prehension, the head remains more nearly level with respect to the horizon, the lunge distance is shorter, the tongue is protracted to a greater distance, and the mouth remains open for a longer time than during jaw prehension (Anderson, 1993).

Because they depend heavily on lingual adhesion to capture prey, it is not surprising that frogs with generalized diets use different strategies to capture prey of different sizes. Tongue prehension is more effective for capturing small prey than jaw prehension because the prey is transported to the esophagus in a single movement, which offers less chance for escape. However, tongue prehension is effective only if the mass of the prey is less than the adhesivity between tongue and prey. Thus, jaw prehension is more effective for capturing large prey (Anderson and Nishikawa, 1996; Valdez and Nishikawa, 1997).

It has been shown that the decision to use jaw vs tongue prehension is made on the basis of a visual analysis of prey size (Anderson and Nishikawa, 1996). When offered pieces of earthworm ranging in size from 1.5 to 4.5 cm, adult frogs (*R. pipiens*) always use tongue prehension to capture 1.5-cm prey and jaw prehension to capture 2.0-cm and larger prey (Figs. 5.13A and 5.13B). Not surprisingly, the distinction between "small" vs "large" prey is relative to the size of the frog. Larger frogs switch behavior patterns at larger prey sizes than smaller frogs.

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* (a mechanical puller, family Hylidae) (Valdez and Nishikawa, 1997). This study showed that these frogs modulate their feeding movements in response to features of prey in addition to size, especially shape and speed of movement. It also showed that the ability to use a visual analysis of prey characteristics to modulate feeding movements is widespread among frogs. Distantly related frogs with different tongue morphologies (i.e., *R. pipiens*, family Ranidae, and *C. novaehollandiae*, family Hylidae) use tongue prehension to capture small prey and jaw prehension to capture large prey. However, some frogs appear to have lost the ability to switch between tongue prehension and jaw prehension. For example, *B. marinus* uses tongue prehension to capture large prey as well as small prey, whereas *Leptopelis* uses jaw prehension to capture both small and large prey.

B. Role of Tongue Afferents

In both frogs (*R. pipiens*) and toads (*B. marinus*), mechanosensory afferents of the tongue, innervated by

the hypoglossal nerve, serve a variety of functions in feedforward (i.e., open loop, planned in advance) control of jaw and tongue movements during prey capture. One function is to modulate the phase of activity in the mouth opening and closing muscles (Nishikawa and Gans, 1992; Anderson and Nishikawa, 1993). In intact frogs and toads, the mouth opening muscles are active approximately 90 msec before the mouth closing muscles. After bilateral transection of the hypoglossal nerves, the mouth remains closed when *Rana* or *Bufo* attempt to feed because the M. levator mandibulae and the M. depressor mandibulae are activated simultaneously (Figs. 5.12E–5.12H and 5.13C). Thus, sensory input from the tongue coordinates jaw muscle activity by sending an afferent signal to the brain that delays activity of the jaw levators. This signal is produced

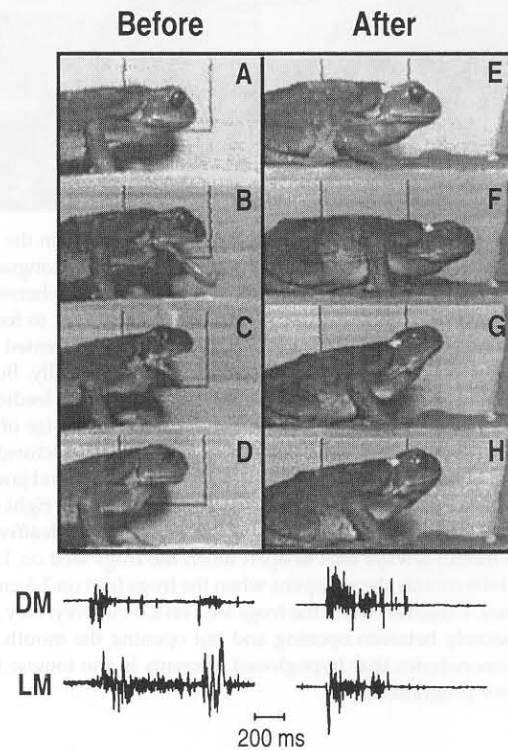


FIGURE 5.12. The function of hypoglossal afferents in the marine toad, *Bufo marinus*. (Left) Normal feeding in an intact toad before deafferentation, illustrating inertial elongation. (A) The toad orients toward the prey, (B) the mouth opens and the tongue is protracted, (C) the tongue is retracted, and (D) the mouth closes. (Right) After deafferentation, (E) toads orient normally, but (F–H) the mouth fails to open during the feeding attempt. Electromyographic traces on the left show activity in the jaw muscles depressor mandibulae (DM) and levator mandibulae (LM) in intact toads before deafferentation. DM reaches its peak activity approximately 90 msec before LM. Right traces show that DM and LM reach their peak activity simultaneously after deafferentation. These results demonstrate that hypoglossal afferents modulate the phase of activity in the jaw muscles during feeding.

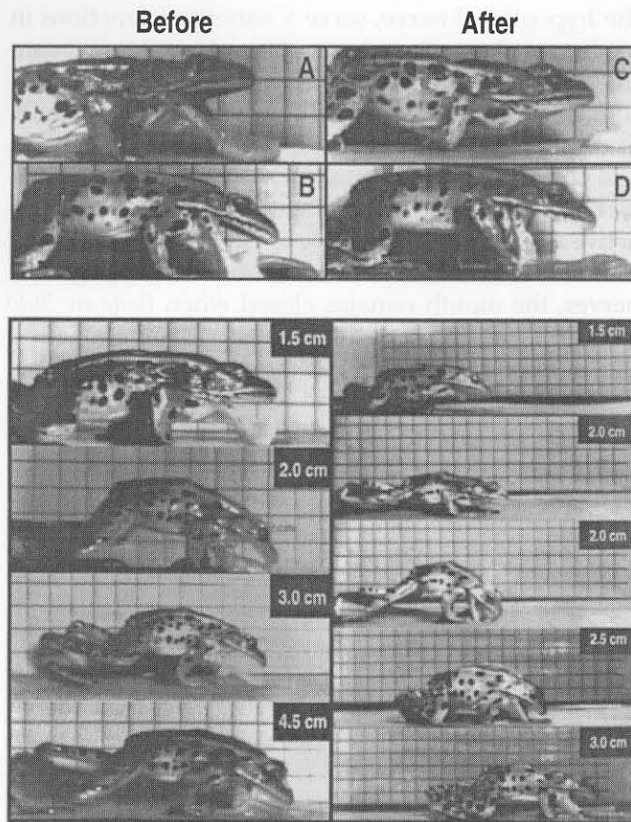


FIGURE 5.13. The function of hypoglossal afferents in the leopard frog, *Rana pipiens*. Top portion: (A) intact frogs use tongue prehension to capture small prey, (B) intact frogs use jaw prehension to capture large prey, (C) when deafferented frogs attempt to feed on small prey, the mouth fails to open; but (D) when deafferented frogs attempt to feed on large prey, the mouth opens normally. Bottom portion: The four panels on the left show intact frogs feeding on earthworm pieces that vary in size from 1.5 to 4.5 cm (size of prey is indicated by numbers in upper right corner of each picture). The frogs always exhibit tongue prehension for 1.5-cm prey and jaw prehension for 2.0-cm and larger prey. The five panels on the right show deafferented frogs feeding on earthworm pieces. After deafferentation, the mouth always fails to open when the frogs feed on 1.5-cm prey and the mouth always opens when the frogs feed on 2.5-cm and larger prey. However, when the frogs feed on 2.0-cm prey, they alternate randomly between opening and not opening the mouth. This result demonstrates that hypoglossal afferents in the tongue influence motor program choice.

before the onset of mouth opening and may result from stimulation of tongue mechanoreceptors by retraction of the hyoid during the preparatory stage of feeding. In intact frogs and toads, we hypothesize that 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 and Gans, 1996). If this hypothesis is correct, then we would expect that these afferents

would be absent, or would have a different function, in mechanical pullers and hydrostatic elongators because these frogs lack synchronous acceleration of tongue and jaws, as well as a straight trajectory of the tongue tip from mouth to prey (Table 5.1). Studies on the evolution of hypoglossal afferents are described in more detail later (Section V,C).

C. Interactions between Tongue Afferents and Visual Input

It is somewhat surprising that afferent input from the tongue interacts with visual input in controlling prey capture movements. In *R. pipiens*, the modulatory effect of tongue afferents depends on attributes of the visual stimulus that is presented to elicit feeding (Anderson and Nishikawa, 1993). When presented with small prey, deafferented frogs attempt to use tongue prehension to capture the prey and the mouth remains closed, as noted earlier. However, when the same deafferented frogs are presented with large prey, they use jaw prehension to capture the prey and their mouths open normally (Fig. 5.13; Anderson and Nishikawa, 1993). These results demonstrate that the modulatory effect of hypoglossal afferents on feeding movements is itself modulated by visual input, and they suggest that visual input has a gating effect on the hypoglossal afferents.

Hypoglossal afferents also interact with visual input during motor program choice in *R. pipiens* (Anderson and Nishikawa, 1996). As mentioned previously, 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 hypoglossal deafferentation experiments described earlier, 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 inactivated, the mouth never opens for 1.5-cm prey and always opens for 2.5-cm and larger prey, as expected. However, the frogs alternate randomly between tongue prehension and jaw prehension when 2.0-cm prey are offered (Fig. 5.13). Thus, the ability to choose between motor programs for tongue prehension and jaw prehension is impaired by hypoglossal transection. In *R. pipiens*, hypoglossal afferents not only subservise typical motor control functions, such as modulating motor output, but also have become involved in behavioral decision making. Neural network modeling is being used in conjunction with neuroanatomical tracing studies to understand the premotor circuits that underlie interactions between vision and proprioception in the control of feeding movements (Corbacho *et al.*, 1996).

V. EVOLUTION OF THE FEEDING APPARATUS

A major goal of comparative and functional morphology is to understand the evolution of complex functional systems. This goal can be achieved using cladistic analysis, in which a phylogeny is obtained for the group, data are collected on characters of interest, and the distribution of these characters is mapped onto the phylogeny. A cladistic analysis permits identification of the ancestral condition for the character(s) of interest, which represents the starting point for evolutionary diversification. This type of analysis also locates transitions in character state on the phylogeny that indicate when and how the condition has changed. Studies in my laboratory have used a cladistic approach to study the evolution of mechanisms of tongue protraction and neural control of feeding behavior in anurans, and the results of these studies are described next.

A. Evolutionary Transitions in Mechanisms of Tongue Protraction

A phylogenetic analysis (Fig. 5.14) of feeding behavior in 148 species of frogs representing 75 of approximately 330 described genera (23%) and 20 of 27 families (74%) was conducted by mapping characters derived from high-speed video motion analysis (Nishikawa *et al.*, 1992) onto the most recent hypothesis of frog phylogeny (Ford and Cannatella, 1993). The results of this analysis show that all archaeobatrachian frogs that have been studied (*Ascaphus*, Ascaphidae; *Leiopelma*, Leiopelmatidae; *Bombina*, Bombinatoridae; and *Discoglossus*, Discoglossidae) possess mechanical pulling tongues that shorten during protraction (Fig. 5.14). Some members of the clades Mesobatrachia (e.g., *Pelobates*) and Neobatrachia (e.g., hyline hylids) also possess short tongues (Fig. 5.14). The most parsimonious interpretation of the observed character distribution across taxa is that anurans ancestrally possess tongues that shorten during protraction and therefore can be protracted only a few millimeters beyond the tips of the mandibles. Other ancestral characteristics include (1) downward bending of the lower jaw during mouth opening and (2) use of the whole body as a projectile, which brings the short tongue into contact with the prey (Nishikawa *et al.*, 1992).

Tongues that elongate during protraction have evolved many times independently from mechanical pulling tongues that shorten during protraction (Fig. 5.14). It is difficult to estimate the exact number of independent evolutionary events due to the lack of resolution of family relationships (Cannatella *et al.*, 1992).

However, at least seven lineages possess elongating tongues (Fig. 5.14). Among mesobatrachians, the most parsimonious hypothesis is that mechanical pulling is ancestral and inertial elongation has evolved once in the common ancestor of *Megophrys montana* and *Leptobranchium*. *Megophrys* is the only known genus in which the constituent species differ in tongue length, with *M. aceras* using mechanical pulling and *M. montana* using inertial elongation to protract the tongue (Fig. 5.14).

Among neobatrachians, mechanical pulling also appears to be the ancestral method of tongue protraction based on parsimony analysis. The most parsimonious hypothesis is that mechanical pulling is ancestral for the group and that elongating tongues evolved independently in as many as six different lineages: (1) *Ceratophrys* and *Chacophrys*, (2) *Physalaemus* and *Pleurodema*, (3) *Eleutherodactylus* and *Syrrophus*, (4) the phyllomedusine hylids, (5) the bufonids, and (6) the ranoids (Nishikawa *et al.*, 1992). The most variable families are the Leptodactylidae (which is probably not monophyletic; Ford and Cannatella, 1993) and Hylidae, both of which possess species with both long and short tongues.

Most frogs with elongating tongues share many derived behavior patterns, particularly a reduction in lunge length (Nishikawa *et al.*, 1992). The phyllomedusine hylids are exceptional in retaining a long lunge despite possessing a long tongue (Gray and Nishikawa, 1995). However, there are many differences among long-tongued lineages as well. Long tongues appear to have evolved to enhance crypsis in *Bufo* (Gray, 1997), for catching rapidly moving prey in the phyllomedusines (Gray and Nishikawa, 1995), for capturing large prey in *Megophrys* (Emerson, 1985; Gans *et al.*, 1991), and for capturing prey accurately in *H. marmoratum* (Ritter and Nishikawa, 1995).

Among species with elongating tongues, all use inertial elongation to protract the tongue, except members of the families Microhylidae and Hemisotidae, all species of which use hydrostatic elongation. Given the phylogeny of Ford and Cannatella (1993), it appears that mechanical pulling is the ancestral tongue protraction mechanism, that inertial elongation evolved up to seven times independently from mechanical pulling, and that hydrostatic elongation evolved once or maybe twice from inertial elongation within the ranoid clade (Fig. 5.14). This hypothesis is somewhat counterintuitive, however, because hydrostatic elongation is the slowest mechanism of tongue protraction whereas inertial elongation is the fastest (Table 5.1). However, these tongue types appear to represent a morphocline in terms of the amount of connective tissue in the tongue that would restrict elongation (see next section; Webster, 1996).

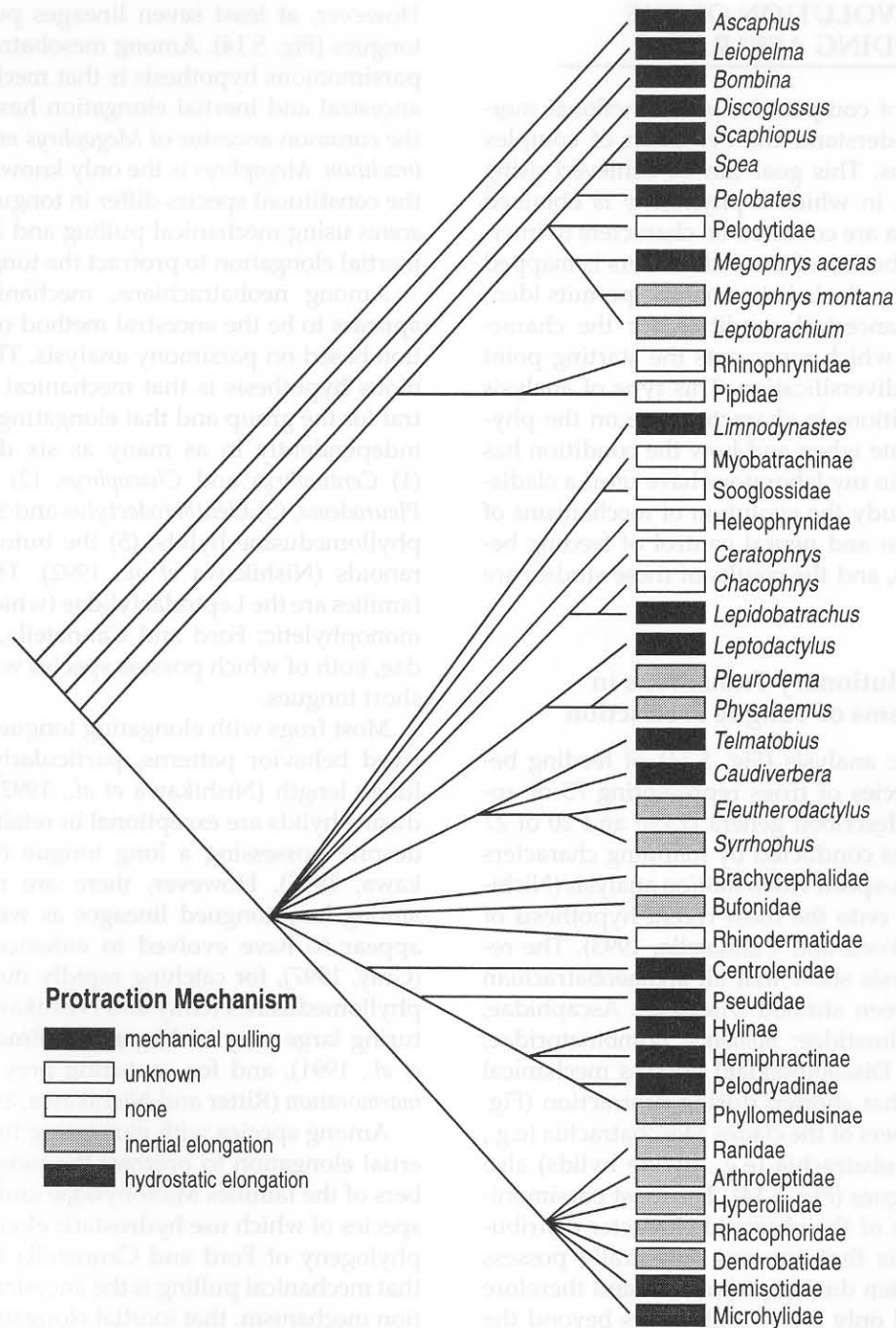


FIGURE 5.14. Cladogram illustrating the evolution of tongue protraction mechanisms among frogs. For mechanisms of tongue protraction, mechanical pulling is the ancestral condition. Inertial and hydrostatic elongation are derived conditions that evolved several times independently among frogs.

B. Morphological Correlates of Tongue Protraction Mechanisms

It is interesting to ask what morphological changes are responsible for the profound functional changes in

the biomechanics of the feeding apparatus that have occurred during anuran evolution (Table 5.1). Comparative studies have demonstrated considerable diversity in the feeding behavior of frogs (compare Figs. 5.8, 5.9 and 5.10; Table 5.1). Anuran species vary

considerably in the length of the fully protracted tongue, which ranges from less than 10% of jaw length in semiaquatic species such as *Lepidobatrachus llanensis* (unpublished observation) to nearly 300% of jaw length in *H. marmoratum* (Ritter and Nishikawa, 1995). Even among frogs with relatively long tongues, species vary in the speed of tongue protraction from 24 cm/sec in the slowest hydrostatic elongators to 270 cm/sec in the fastest inertial elongators (Table 5.1). In anurans, these functional changes appear to have involved relatively small quantitative and qualitative changes in the anatomy and physiology of the muscles of the feeding apparatus.

The transition from mechanical pulling to inertial elongation appears to have involved (1) a decrease in relative tongue mass; (2) an increase in the relative length of muscle fibers in both the *M. genioglossus* and *M. hyoglossus*; (3) a change in insertion of the *M. hyoglossus* from the anterior to the posterior part of the tongue pad (Horton, 1982); (4) a decrease in the amount of connective tissue (as measured subjectively from scanning electron micrography of muscles digested with NaOH), which appears to restrict tongue elongation in mechanical pullers (Webster, 1996); and (5) an increase in contraction velocity compared to mechanical pullers (Peters and Nishikawa, 1999).

The transition from inertial to hydrostatic elongation involved only (1) the addition of a new dorsoventral compartment in the *M. genioglossus*, which elongates the tongue when it contracts; and (2) a further decrease in the amount of connective tissue in the tongue.

Peters and Nishikawa (1999) completed a study of the contractile properties of the tongue protractor and retractor muscles of mechanical pullers, inertial elongators, and hydrostatic elongators. The studies show that although there are some differences (e.g., in contraction and half relaxation time of the muscles), the contractile properties of the muscles alone cannot account for differences in function (i.e., differences in length or velocity of tongue protraction).

A major difference among frog tongues is in the amount of connective tissue they contain, as well as the orientation of collagen fibers within the tongue (Webster, 1996). Mechanical pullers have the most connective tissue, inertial elongators are intermediate, and hydrostatic elongators have the least. Furthermore, the orientation of collagen fibers also differs among taxa. Mechanical pullers have the largest proportion of fibers with low orientation angles ($<55^\circ$) relative to the long axis of the tongue, inertial elongators are intermediate, and hydrostatic elongators have the most fibers with high orientation angles ($>55^\circ$). In mechanical pullers, these parallel connective tissue fibers would

actively resist elongation of the tongue. In *H. marmoratum*, most of the collagen fibers are oriented nearly perpendicular to the long axis of the tongue (modal angle = 80°), where they do not resist tongue elongation but instead resist increases in tongue diameter (Nishikawa *et al.*, 1999).

The differences in tongue morphology among mechanical pullers, inertial elongators, and hydrostatic elongators are so small and subtle that it has not proved possible to predict differences in function on the basis of anatomical differences. Ironically, the functions of most of the larger and less subtle anatomical differences that have been described among anuran species remain obscure. Based on the preliminary data described earlier, it seems quite likely that relatively small quantitative differences in the amount and orientation of connective tissue in the tongue, via their effects on passive properties, may have a greater effect on tongue function than anatomical and physiological differences in tongue muscles among anurans.

C. Evolution of Tongue Afferents

We next conducted a cladistic analysis of the evolution of hypoglossal afferents among anurans (Nishikawa *et al.*, 1993). For the cladistic analysis, 57 species of anurans representing 39 genera and 15 families were filmed while feeding before and after bilateral transection of the hypoglossal nerves (Fig. 5.15). Results of this analysis show that hypoglossal afferents that modulate the phase of activity in the jaw muscles are absent in all mechanical pullers and all hydrostatic elongators (Fig. 5.15). Some but not 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: (1) in the leptodactyline leptodactylids *Pleurodema* and *Physalaemus*; (2) in the phyllomedusine hylids; (3) in the bufonids; and (4) in ranoids except for hemisotids and microhylids, in which hypoglossal afferents appear to have been lost (Fig. 5.15).

Although the function of these afferents is very similar across species at the behavioral level, both cladistic analyses and comparative neuroanatomical studies show that the circuits are convergent rather than homologous in the different anuran lineages (Nishikawa *et al.*, 1993; Anderson and Nishikawa, 1997). Frogs ancestrally lack afferents in the hypoglossal nerve, as do most vertebrates (Ariens-Kappers *et al.*, 1936). In toads of the family Bufonidae, sensory fibers from the glossopharyngeal nerve have invaded the tongue via the hypoglossal nerve and these fibers ascend to higher brain centers in the tractus solitarius (Nishikawa *et al.*, 1993). In frogs of the family Ranidae, large myelinated

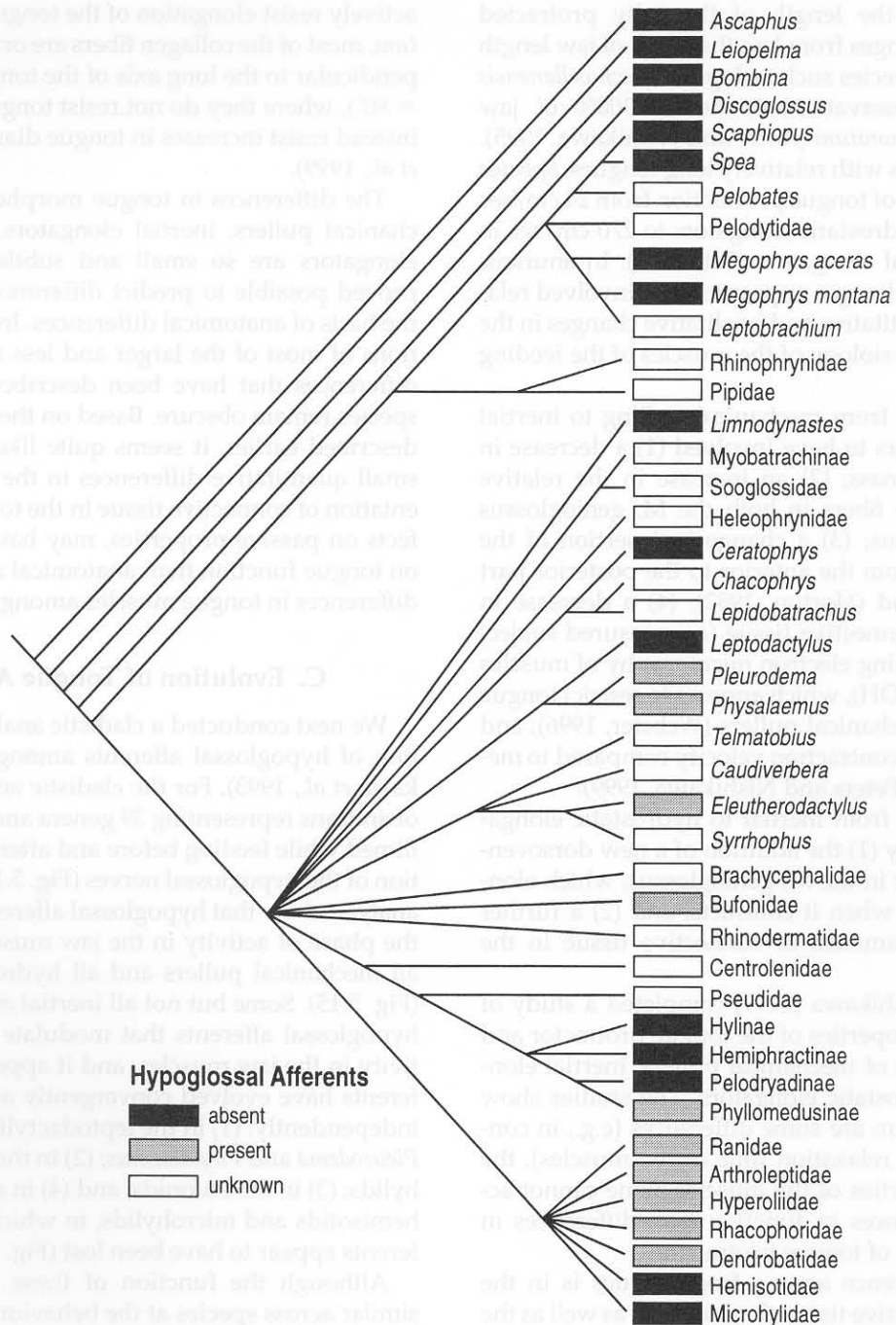


FIGURE 5.15. Cladogram illustrating the evolution of hypoglossal afferents among frogs. Hypoglossal afferents are ancestrally absent among frogs. These afferents have evolved several times independently, but only in frogs that use inertial elongation to protract the tongue. These afferents appear to have been lost in hydrostatic elongators (families Hemisotidae and Microhylidae).

afferents of the most anterior cervical spinal nerve have invaded the tongue via the hypoglossal nerve (Anderson and Nishikawa, 1997). These fibers ascend and descend in the dorsomedial funiculus and project to the granular layer of the cerebellum and the medial reticu-

lar formation. The source of hypoglossal afferents remains unknown in leptodactylids and hylids. During invasions of new territory in *Rana* and *Bufo*, sensory fibers have changed their peripheral pathways as well as 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. Current studies are exploring how these convergent neural circuits differ physiologically.

D. Evolutionary Transitions in Mechanisms of Neural Control

An important question that remains largely unanswered concerning the function and evolution of tetrapod feeding systems is whether evolution of the morphology and mechanics of the feeding apparatus affect mechanisms of neural control. A related question simply asks whether there is variation in the neural control of the feeding apparatus among tetrapods and, if so, what is the nature and significance of the variation. Because anuran species exhibit variation in the morphology and mechanics of the feeding apparatus, they offer a unique opportunity to investigate these questions.

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 feedforward, 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 and Gans, 1996). In contrast, mechanical pullers and hydrostatic elongators can rely on both feedforward and feedback control of tongue movements because there is no inertial stage of tongue elongation (Table 5.1).

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. Precise coordination is not necessary in mechanical pullers because the movement of the short tongue pad relative to the lower jaw is restricted to a few millimeters so that the tongue pad will always end up in nearly the same location as the tips of the mandibles. Precise coordination is unnecessary in hydrostatic elongators because the tongue is moved slowly and can be moved independently in three dimensions relative to the head. In inertial elongators, tongue afferents that are innervated by the hypoglossal nerve have evolved convergently in at least four independent lineages for the precise coordination of tongue and jaw movements. Small changes in the central and peripheral connections of cranial (Bufonidae) or spinal (Ranidae) mechanosensory afferents have led to the emergence of novel functions in coordinating feeding behavior in inertial elongators, including modulating the phase of activity in jaw muscles and influencing motor program choice during feeding.

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.

VI. CONCLUSIONS

In summary, the feeding behavior of anurans has proved to be an interesting model system for understanding the process of functional diversification during evolution. Comparative studies have demonstrated that frogs exhibit at least three different mechanisms for protracting their tongues. These are mechanical pulling, inertial elongation, and hydrostatic elongation. These mechanisms differ in the extent of tongue movement relative to the head, in the velocity, acceleration, and trajectories of tongue movements, in aiming ability, and in the accuracy of prey capture (Table 5.1).

Morphologically, the feeding apparatus of frogs is rather homogeneous. All species possess similar sets of muscles and bones, although there is variation in the presence of compartments within muscles, for example, the dorsoventral compartment of the *M. genio-glossus* in hydrostatic elongators, which has a major effect on tongue function. There are also differences among species in the contractile properties of tongue muscles as well as in the connective tissue that is responsible for transmitting the forces produced by the tongue muscles during feeding. In general, numerous small qualitative and quantitative morphological differences among species appear to be responsible for the rather large differences in the biomechanics of tongue protraction across anuran species.

Species that differ in the biomechanics of tongue protraction also differ in mechanisms of neural control. Species differ in the relative importance of feedforward vs feedback control, in the requirement for precise coordination of multijoint movements, in the afferents that are used to coordinate these movements, and finally in aiming ability and accuracy of prey capture. There has been considerable rewiring of cranial or cervical spinal afferents in inertial elongators to provide a mechanism for precise coordination of tongue and jaw movements.

In summary, these studies show that small changes in the anatomy of the feeding apparatus may lead to large changes in biomechanics and that small changes in neuroanatomy may lead to large changes in sensorimotor coordination. Potential precursors for novel sensory pathways appear to be prevalent and may change readily in response to natural selection. In anurans, high levels of neural and behavioral evolution

are found, even among closely related species and in parts of the brain usually thought to be evolutionarily conservative. A major implication of these studies on the evolution of frog tongues is that, for any given species, the neural networks that subserve sensorimotor coordination are fine-tuned to its particular morphology and environment (Nishikawa, 1997).

VII. CURRENT AND FUTURE DIRECTIONS

Numerous questions remain to be studied concerning the biomechanics and neural control of prey capture in anurans. In terms of biomechanics, a few differences in morphology and biomechanics of the feeding apparatus have been quantified in just a few species, and for many anatomical differences, their functional significance remains to be studied.

Current research in my laboratory is focused on using biomechanical modeling to investigate the diversification of function in frog tongues (Nishikawa *et al.*, 1997). With Eric Mallett and Gary Yamaguchi at Arizona State University, we have developed a planar, forward dynamic, multijoint, rigid body model of the anuran tongue to study the dynamics of tongue protraction and retraction during prey capture. The model contains four degrees of freedom, including the lower jaw (fixed length) and three segments of variable length in the tongue. In the model, the *M. genioglossus* and *M. hyoglossus* are used to actuate the tongue, while impulsive joint torques are applied at the jaw joint to open or close the mouth. Joint torques are obtained from a muscle model that incorporates nonlinear springs and dampers to simulate the force-length-velocity characteristics of the tongue muscles. The model takes anatomical data on the size and shape of the feeding apparatus, as well as contractile properties of the tongue muscles, as input. Simulations involve varying the pattern of muscle activation to find the optimal pattern for each mechanism of tongue protraction. This model is being used to explore the following questions: (1) how much complexity must be incorporated into the model in order for it to predict movement trajectories accurately? (i.e., is a four degree of freedom model sufficient, or are more segments necessary? is the mentomeckelian joint needed? is a movable hyoid needed?) (2) how will differences in size and shape affect movement kinematics? (3) do changes in musculoskeletal design represent suites that together may enhance a particular aspect of kinematics? (4) can the same pattern of muscle activation be used for all species? and (5) how much can morphology change before a different muscle activation strategy becomes desirable?

In terms of neural control, differences in the neuroanatomy of proprioceptive pathways have been described in only two anuran species, and the neurophysiology of convergent afferent pathways remains to be explored. The anatomy and physiology of hypoglossal mechanosensory receptors also require further study. Finally, hypoglossal afferents are only one of many proprioceptive pathways that coordinate feeding movements, and the modulatory effects of additional afferent systems on feeding behavior, such as the lingual withdrawal reflex (Matsushima *et al.*, 1986, 1987, 1988), remain to be described.

Our studies of the neural control of prey capture in anurans have barely scratched the surface of understanding the evolutionary relationships among morphology, biomechanics, and neural control of movement. It is hoped that our attempts to understand the evolution of prey capture in frogs will stimulate functional morphologists to undertake similar studies in other groups of animals.

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