

# The Role of Hypoglossal Sensory Feedback During Feeding in the Marine Toad, *Bufo marinus*

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**ABSTRACT** Behavioral observations demonstrate that bilateral deafferentation of the hypoglossal nerves in the marine toad (*Bufo marinus*) prevents mouth opening during feeding. In the present study, we used high-speed videography, electromyography (EMG), deafferentation, muscle stimulation, and extracellular recordings from the trigeminal nerve to investigate the mechanism by which sensory feedback from the tongue controls the jaw muscles of toads. Our results show that sensory feedback from the tongue enters the brain through the hypoglossal nerve during normal feeding. This feedback appears to inhibit both tonic and phasic activity of the jaw levators. Hypoglossal feedback apparently functions to coordinate tongue protraction and mouth opening during feeding. Among anurans, the primitive condition is the absence of a highly protrusible tongue and the absence of a hypoglossal sensory feedback system. The hypoglossal feedback system evolved in parallel with the acquisition of a highly protrusible tongue in toads and their relatives. © 1992 Wiley-Liss, Inc.

The functional morphology and neurobiology of feeding behavior in anurans have been studied extensively, especially in toads of the genus *Bufo* (Emerson, '77; Gans and Gorniak, '82a,b; Ewert, '87; Matsushima et al., '85, '86, '87, '88, '89). During feeding, toads first orient toward the prey, then fixate the prey in their gaze (reviewed in Ewert, '87). Prey capture begins as the toads rotate forward on their forelimbs, open the mouth and protract the tongue, raise the cranium, and then retract the eyes and close the mouth. Electromyographic studies of feeding in toads suggest that muscles of the tongue (i.e., m. hyoglossus) and hyoid (i.e., m. geniohyoideus) are active before the onset of mouth opening, and may be involved in positioning the tongue within the oral cavity (Gans and Gorniak, '82a,b; Matsushima et al., '85).

The currently accepted model of feeding biomechanics was developed for toads by Gans and Gorniak ('82a,b). In this model, the anteriorly attached, stiffened tongue is rotated forward and flipped over the depressed mandibular symphysis by a muscular wedge-and-lever system. The function and innervation of muscles involved in feeding are listed in Table 1.

As part of an ongoing series of experiments on the biomechanics and neuromuscular control of prey capture in frogs (Nishikawa and Cannatella, '91; Nishikawa and Roth, '91; Deban and Nishikawa, '92), we conducted a series of cranial nerve tran-

section experiments in the marine toad *Bufo marinus* (Nishikawa and Gans, '90). To our great surprise, we discovered that bilateral transection of the hypoglossal nerve prevented mouth opening during feeding (Nishikawa and Gans, '90). Because the hypoglossal nerve does not innervate the muscles of the jaw (Gaupp, 1896; Stuesse et al., '83), the implication of this observation is that sensory feedback entering the brain through the hypoglossal or some other nerve is necessary for normal mouth opening.

Although previous studies have shown that the hypoglossal nerve of frogs contains both sensory and motor fibers (Stuesse et al., '83), we know of no previous studies that have investigated the function of this hypoglossal sensory pathway. We designed a series of experiments using electromyography (EMG), deafferentation, muscle and nerve stimulation, and extracellular recordings from the trigeminal nerve to investigate the mechanism by which sensory feedback from the tongue controls the jaw muscles of *Bufo marinus* during feeding behavior.

## MATERIALS AND METHODS

### *Nerve transection*

Adult *Bufo marinus* were obtained from animal suppliers. The toads were videotaped while feed-

Received October 30, 1991; revision accepted June 2, 1992.

TABLE 1. Function and innervation of muscles<sup>1</sup>

Muscle	Function	Innervation
Depressor mandibulae	Opens mouth	Facial nerve
Levator mandibulae	Closes mouth	Trigeminal nerve
Submentalis	Bends mandible	Trigeminal nerve
Intermandibularis posterior	Raises floor of mouth	Trigeminal nerve
Genioglossus medialis	Protracts tongue	Hypoglossal nerve
Genioglossus basalis	Protracts tongue	Hypoglossal nerve
Geniohyoideus	Protracts hyoid	Hypoglossal nerve

<sup>1</sup>See text discussion.

ing before and after unilateral (N = 2) or bilateral (N = 3) transection of the hypoglossal nerve. In addition, five toads received control treatments, in which anesthesia was identical, but different cranial nerves (i.e., trigeminal, N = 4 or glossopharyngeal, N = 1) were transected. A Display Integration Technologies model DIT 660 high-speed, multiframing video camera was used to film the toads at 120 fields/s with synchronized stroboscopic illumination. Feeding behavior was filmed at room temperature (approximately 21–25°C) before and after surgery. Waxworms (*Galleria* sp.) and crickets (*Gryllus* sp.) were used as prey.

In order to study the peripheral anatomy of the cranial nerves of the head, several individuals of *B. marinus* were cleared, and the peripheral nerves were stained with Sudan black B (Fig. 1A,B) following the methods of Nishikawa ('87). For nerve transection, the toads were anesthetized by immersion in 10% ethanol or 1% tricaine methanesulfonate (MS222) for 30–60 min. The ramus hypoglossus was transected surgically in the lower jaw region, distal to the branch that innervates the geniohyoideus muscle (Fig. 1A). A 2-mm length of the nerve was excised to retard regeneration. Following recovery from anesthesia (1–2 h after surgery), the first 5–10 feeding attempts of each toad were videotaped as above. Most postsurgical observations of feeding behavior were recorded within 48 h of surgical treatment. The time course of recovery from hypoglossal nerve transection was followed in one toad, which was observed every day while attempting to feed until it had recovered the ability to open its mouth during feeding.

### Electromyography

Electromyography alone, or synchronized with video, was used to compare the activity of the mouth opening muscles (depressors mandibulae) and the mouth closing muscles (levators mandibulae) before and after surgery. EMG recordings of muscle activity were obtained using bipolar, Teflon- or enamel-coated, stainless steel electrodes (bared tip length

= 1 mm). Electrodes were implanted percutaneously into the muscles of anesthetized toads using 23- to 25-gauge hypodermic needles. Electrodes were implanted in the belly of the m. depressor mandibulae, about 5 mm posterior to the tympanum and at the level of the center of the tympanum. Electrodes were implanted in the belly of the m. levator mandibulae anterior longus (m. pterygoideus of Gaupp, 1896) about halfway between the orbit and the tympanum, at the same dorsoventral level as the m. depressor mandibulae electrode.

The external ends of the electrodes were soldered to a harness of earphone wire. After recovery from anesthesia (1–2 h after surgery), toads were offered crickets or waxworms. EMG signals were amplified through 23A2 Tektronix preamplifiers and Honeywell 117 DC amplifiers and were stored on a Honeywell 5600 medium bandpass 1-inch tape recorder. Recordings of muscle activity were obtained from feeding attempts of toads both before (N = 4) and after (N = 3) hypoglossal transection. We obtained EMG recordings and videotapes of at least four feeding attempts before and four feeding attempts after hypoglossal transection for each toad. The onset of activity (time of first spike above threshold) and time of peak activity (time of largest spike) in the jaw levators and depressors were measured from chart records at a time scale of 50 mm/s.

### Nerve transection and muscle stimulation experiments

Simultaneous nerve transection and muscle stimulation experiments (Table 2) were conducted on spinal-pithed toads to determine the source of the sensory feedback signal and to investigate the inhibitory effects of hypoglossal sensory feedback on tonic jaw levator activity. These experiments were inspired by an earlier report (Emerson, '77), which showed that stimulation of the geniohyoideus and/or sternohyoideus muscles, but not the mandibular depressors, produced mouth opening in spinal-pithed toads. The results of this experiment are puzzling, because the mandibular depressors,

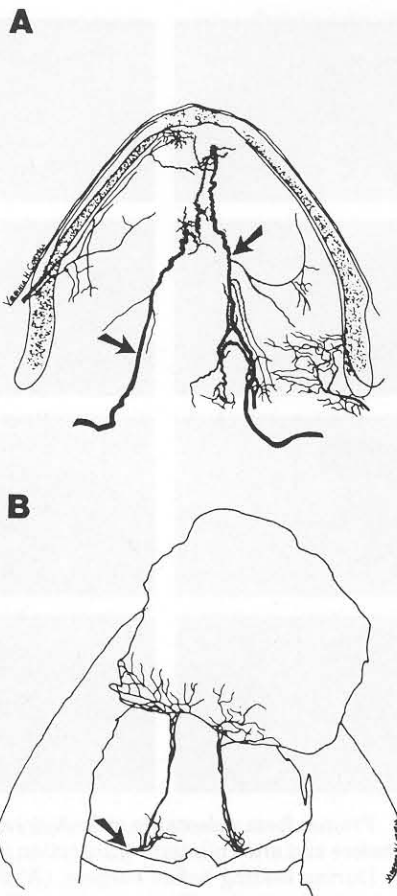


Fig. 1. Camera lucida drawings of the peripheral nerves in the lower and upper jaw of *Bufo marinus* (jaw width = 36 mm). **A:** Lower jaw. The trigeminal and glossopharyngeal nerves are figured on the left side, and the facial and hypoglossal nerves are figured on the right side. Sites of transection of the ramus lingualis (left) and the ramus hypoglossus (right) are indicated by arrows. **B:** Upper jaw (with mucosa reflected). The ramus palatinus, which provides sensory innervation of the maxilla, is figured on both sides. Arrow indicates the site of transection of the ramus palatinus.

not the geniohyoideus muscles, are considered to be the major mouth opening muscles of frogs (Gans and Gorniak, '82a,b). Because the hypoglossal nerve runs through the belly of the geniohyoideus muscle, we hypothesized that mouth opening occurred in Emerson's experiments not only because contraction of the geniohyoideus muscle opens the mouth, but also because stimulation of the hypoglossal nerve (via the geniohyoideus muscle) inhibits the mandibular levators and permits the mouth to open, whereas stimulation of the depressor mandibulae does not.

The hypoglossal nerve carries both sensory signals coming toward the brain and motor signals going out to the genioglossus medialis and geno-

TABLE 2. Results of simultaneous nerve transection and muscle stimulation experiments in nonfeeding, spinal-pithed toads

Nerve transected	Muscle stimulated	Mouth opening?
Ramus maxillaris	Depressor mandibulae	Yes
Ramus maxillaris	Geniohyoideus	Yes
None	Depressor mandibulae	No
None	Geniohyoideus	Yes
Ramus hypoglossus	Depressor mandibulae	No
Ramus hypoglossus	Geniohyoideus	No
Ramus palatinus	Depressor mandibulae	No
Ramus palatinus	Geniohyoideus	Yes
Ramus lingualis	Depressor mandibulae	No
Ramus lingualis	Geniohyoideus	Yes

glossus basalis muscles in the tongue (Gaupp, 1896; Stuesse et al., '83). Thus, it is uncertain whether the effects of hypoglossal transection on mouth opening during feeding are due to the elimination of sensory or motor activity. The sensory signal could enter the brain through the hypoglossal nerve itself, or it could be a result of contraction of the tongue muscles innervated by the hypoglossal nerve, entering the brain through another cranial nerve. Only two nerves ramify in the region of the genioglossus medialis and genioglossus basalis muscles: (1) the ramus palatinus of the trigeminal and facial nerves (Fig. 1B) innervates the maxilla, against which the tongue may be pushed when these muscles contract; and (2) the ramus lingualis of the glossopharyngeal nerve (Fig. 1A) ramifies within the tongue. These nerves, as well as the hypoglossal nerve, were transected in spinal-pithed toads to determine which nerves, if any, carry sensory signals that inhibit the activity of the m. levator mandibulae.

Spinal-pithed toads were used in these experiments for two reasons: (1) to repeat Emerson's ('77) experimental protocol; and (2) to immobilize the toads during muscle stimulation experiments. Anesthesia was not used to immobilize the toads because it reduces tonic contractions of the m. levator mandibulae, and the presence of this activity was essential for interpretation of the experimental results.

Toads (N = 7) were deeply anesthetized by immersion in 10% ethanol for 30–60 min, after which the spinal cord was severed from the brain at the foramen magnum, and the spinal cord was destroyed with a dissecting needle following the method outlined by Emerson ('77). The geniohyoideus and

sternohyoideus muscles and the hypoglossal nerve were exposed in the lower jaw. Electrical stimuli (2–5 V) were applied with bipolar, steel electrodes at a frequency of 10 pps and a duration of 10 ms using a Grass S88 stimulator. We also recorded spontaneous activity from the trigeminal nerve in the levator mandibulae muscle of one spinal-pithed toad using bipolar, silver hook electrodes.

After the experiments were completed, the effects of spinal pithing were confirmed by dissection. The spinal cord of toads is greatly foreshortened. A cauda equina is present, in which most spinal nerves exit the cord at mid-cervical levels, and the posterior spinal cord is composed of an attenuate filum terminale. The hypoglossal nerve enters the brain several millimeters anterior to the foramen magnum and exits from the vertebral canal at the anterior end of the foramen magnum. Thus in these experiments, the hypoglossal nerve and motor nucleus, and thus the entire sensory feedback pathway, remained intact after spinal pithing.

The nonfeeding, spinal-pithed preparation was used to test the following hypotheses: (1) the m. levator mandibulae exhibits tonic activity, which keeps the mouth closed when the toads are not feeding; (2) stimulation of the geniohyoideus muscle results in mouth opening, as observed by Emerson ('77); and (3) transection of the ramus hypoglossus, but not the r. lingualis or the r. palatinus, should eliminate mouth opening when the geniohyoideus muscle is stimulated, because sensory feedback is prevented from inhibiting the mandibular levators.

## RESULTS

### *Behavioral observations*

During normal feeding before hypoglossal transection, toads rotate forward on the forelimbs, open the mouth, protract the tongue, raise the cranium and retract the eyes, then retract the tongue and close the mouth (Fig. 2A). After bilateral hypoglossal transection, they rotate forward on the forelimbs, retract the eyes, and raise the cranium normally, but the mouth fails to open (Fig. 2B). An inability to open the mouth during feeding persists for about 4 weeks, after which the mouth opens normally during feeding, presumably because the sensory fibers have regenerated.

In all our surgical treatments, the toads always opened their mouths normally during feeding, unless the hypoglossal nerves were transected bilaterally. These results indicate that failure of mouth opening is not an artifact of anesthesia or surgery. Unlike bilateral hypoglossal transection, the mouth opens normally after unilateral hypoglossal tran-

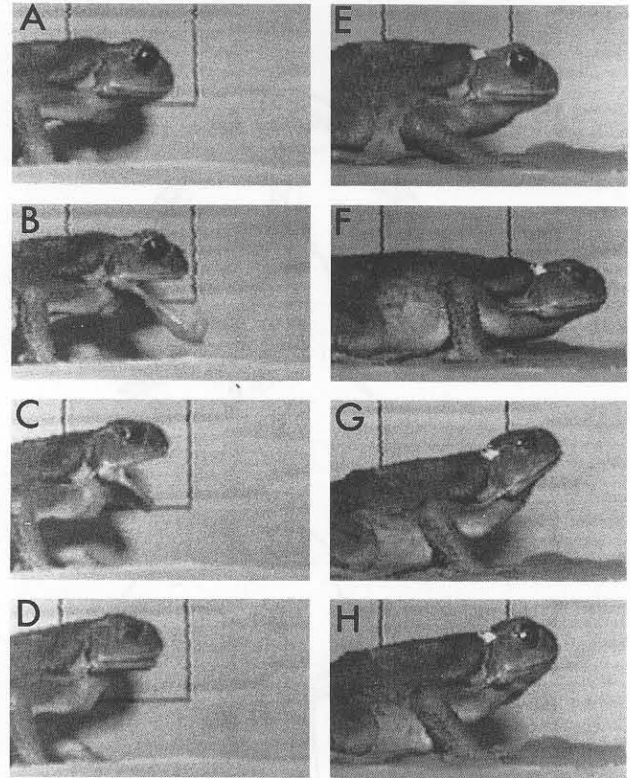


Fig. 2. Frames from videotapes of feeding behavior in *Bufo marinus* before and after bilateral transection of the hypoglossal nerve. During feeding before surgery, (A) the toad moves forward over the forelimbs, (B) opens its mouth and protracts its tongue, (C) retracts the tongue and raises the cranium, and (D) retracts its eyes and closes its mouth. After bilateral transection of the ramus hypoglossus, (E–F) the toad moves forward over the forelimbs, (G) retracts the eyes and raises the cranium, and (H) recovers its original position, but the mouth does not open.

section, showing that sensory feedback from one side of the tongue is sufficient to cause the mouth to open.

### *Electromyography*

The results of EMG show that the onset of activity in the mandibular depressors and levators is nearly simultaneous ( $\pm 10$  ms) both before and after hypoglossal transection (Fig. 3A,B). However, the relative timing of peak activity in the jaw levators and depressors is affected by hypoglossal transection. Before hypoglossal transection, the mandibular depressors reach their peak activity 86.2 ms earlier, on average, than the mandibular levators (Fig. 3A). After hypoglossal transection, the two muscles show nearly synchronous ( $\pm 10$  ms) peak activity (Fig. 3B). After hypoglossal transection, the activity of other feeding muscles, including the mm. submentalis, intermandibularis posterior, and geniohyoideus (see Table 1 for muscle function and

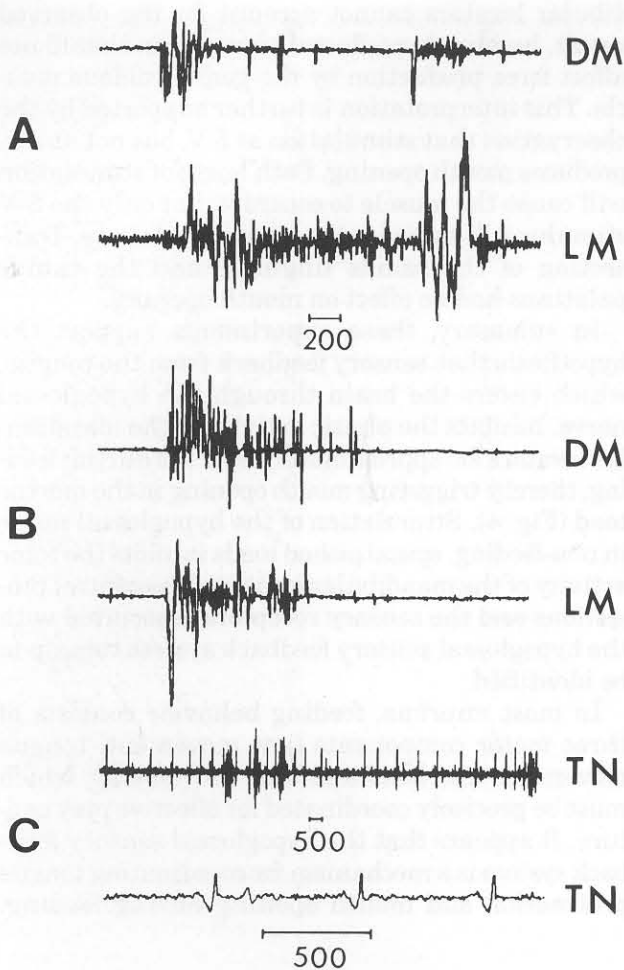


Fig. 3. Electromyographic activity of the mandibular depressors (DM) and levators (LM) during feeding before and after bilateral transection of the ramus hypoglossus. Scale bar = 200 ms. The onset of activity is nearly simultaneous both before and after surgery. **A:** Before transection, the depressors reach their peak activity on average 86.7 ms earlier than the levators. **B:** After transection, peak activity of the levators occurs nearly simultaneously with the peak activity of the depressors. **C:** Tonic activity recorded extracellularly from the trigeminal nerve (TN) in the jaw levator muscle of a spinal-pithed toad at two time scales (scale bars = 500 ms). In the upper trace (lower temporal resolution), the high-frequency activity is associated with buccal pumping and the frequency of the tonic activity is approximately 1 spike/s. The lower trace shows the tonic activity at higher temporal resolution.

innervation) is normal. Thus, only the activity of the m. levator mandibulae appears to be affected by hypoglossal transection.

#### *Nerve transection and muscle stimulation experiments*

In the spinal-pithed toad, extracellular recording from the trigeminal nerve in the m. levator mandibulae shows that the motor neurons that

innervate the mandibular levators exhibit tonic activity (Fig. 3C). This pattern of tonic activity remains stable for more than 2 h, and thus is unlikely to be due to nerve damage. This interpretation is supported by the observation that positive pressure is exerted on a finger inserted into the mouth of a lightly anesthetized toad.

Because of this tonic activity of the m. levator mandibulae, either the force generated by the tonic activity must be overcome or the tonic activity must be inhibited in order for the toad's mouth to open. Transection of the ramus maxillaris of the trigeminal nerve denervates the mandibular levators (Table 1), thus preventing their tonic contraction. After denervation of the mandibular levators, stimulation of either the geniohyoideus or the depressor mandibulae muscles causes the mouth to open (Table 2).

In the spinal-pithed toad before nerve transection, stimulation of the geniohyoideus, but not the depressor mandibulae, results in mouth opening, as was observed by Emerson ('77) (Table 2). As predicted, hypoglossal transection eliminates mouth opening during stimulation of the m. geniohyoideus (Table 2). We also used the spinal-pithed preparation to test whether sensory feedback controlling the mandibular levators enters the brain through the ramus palatinus or the ramus lingualis. If either of these nerves carries sensory feedback that controls the mandibular levators, their transection should eliminate mouth opening during stimulation of the genioglossus muscle. However, transection of neither ramus abolishes mouth opening when the geniohyoideus muscle was stimulated (Table 2).

#### DISCUSSION

The behavioral observations reported here demonstrate that hypoglossal transection prevents mouth opening during feeding in the toad *Bufo marinus*. If jaw muscle activity were coordinated centrally, as predicted by current theories of motor control (Delcomyn, '83; Grillner, '85), hypoglossal transection (which denervates only the tongue protractor muscles genioglossus medialis and genioglossus basalis) should not affect mouth opening, because the hypoglossal nerve does not innervate the jaw muscles. Failure of mouth opening after hypoglossal transection must be caused by the interruption of a sensory feedback signal, which enters the brain through either the hypoglossal nerve itself or the ramus lingualis or the ramus palatinus, both of which ramify in the vicinity of denervated muscles.

Electromyographic recordings support the hypothesis that hypoglossal transection changes the timing of activity of the mandibular levators relative to the activity of the mandibular depressors. Before hypoglossal transection, the mm. levator mandibulae become active approximately 86.7 ms after the peak activity of the mm. depressor mandibulae. After hypoglossal transection, the mandibular levators and depressors reach their peak activity nearly simultaneously ( $\pm 10$  ms). Thus, hypoglossal transection delays the peak in mandibular levator activity by approximately 90 ms, which is just slightly shorter than the time normally required for mouth opening (Gans and Gorniak, '82a,b; Matsushima et al., '85). This result suggests that hypoglossal sensory feedback inhibits phasic activity of the mandibular levators for approximately 90 ms during normal feeding. We hypothesize that the mouth fails to open after hypoglossal transection because the m. levator mandibulae fails to be inhibited, which causes the mouth opening and closing muscles to reach their peak activity nearly simultaneously.

Extracellular recordings of spontaneous activity in axons of trigeminal motoneurons that innervate the mandibular levators show that the mandibular levators of toads are tonically active in spinal-pithed toads. Tonic activity prevents the mouth from opening when the animal is not feeding. This interpretation is supported by the fact that stimulation of the depressor mandibulae muscles, which are the major mouth opening muscles, results in mouth opening only after denervation of the mandibular levators.

Simultaneous nerve transection and muscle stimulation experiments support the hypothesis that hypoglossal stimulation inhibits the tonic activity of the mandibular levators in the nonfeeding, spinal-pithed toad. In the spinal-pithed toad before hypoglossal transection, stimulation of the geniohyoideus muscle, but not the depressor mandibulae, causes the mouth to open. This observation confirms Emerson's ('77) earlier report. However, hypoglossal transection abolishes mouth opening when the geniohyoideus muscle is stimulated. This result demonstrates that stimulation of the geniohyoideus muscle itself does not cause mouth opening, as reported by Emerson ('77). Instead, stimulation of the hypoglossal nerve, which runs through the geniohyoideus muscle, permits the mouth to open, most probably by inhibiting the tonic activity of the mandibular levators. The alternative hypothesis that the mouth opens because the geniohyoideus muscle overcomes the force of the uninhibited man-

dibular levators cannot account for the observed result, because hypoglossal transection should not affect force production by the geniohyoideus muscle. This interpretation is further supported by the observation that stimulation at 5 V, but not at 2 V, produces mouth opening. Both levels of stimulation will cause the muscle to contract, but only the 5-V stimulus will spread to the hypoglossal nerve. Transection of the ramus lingualis and the ramus palatinus had no effect on mouth opening.

In summary, these experiments support the hypothesis that sensory feedback from the tongue, which enters the brain through the hypoglossal nerve, inhibits the phasic activity of the mandibular levators for approximately 86.7 ms during feeding, thereby triggering mouth opening in the marine toad (Fig. 4). Stimulation of the hypoglossal nerve in non-feeding, spinal pithed toads inhibits the tonic activity of the mandibular levators. The central projections and the sensory receptors associated with the hypoglossal sensory feedback system remain to be identified.

In most anurans, feeding behavior consists of three motor components (jaw movement, tongue movement, and head and body movement), which must be precisely coordinated for effective prey capture. It appears that the hypoglossal sensory feedback system is a mechanism for coordinating tongue protraction and mouth opening during feeding.

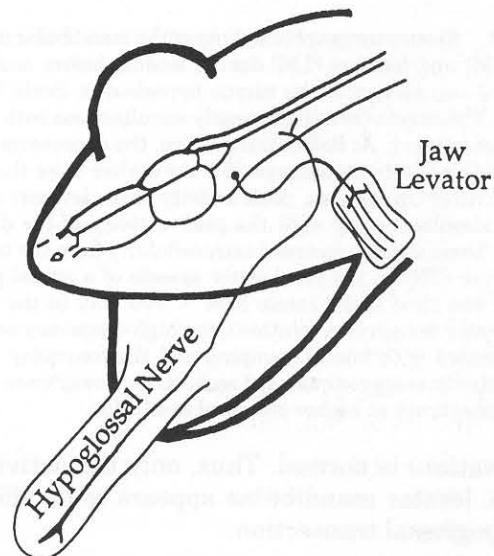


Fig. 4. Schematic diagram of the hypoglossal sensory feedback system in *Bufo marinus*. Sensory receptors in the tongue send a signal to the brain via the hypoglossal nerve, which inhibits the jaw levators and thus triggers mouth opening during feeding.

There are at least three nonexclusive hypotheses for the functional advantage of such a system:

1. The tongue is protracted before the mouth opens, and mouth opening releases the "pre-loaded" tongue (the principle upon which the "jack-in-the-box" is designed).
2. The tongue rests on the lower jaw, which is an unstable platform because it moves through a downward trajectory during feeding. Thus, aiming of the tongue may require precise coordination of tongue protraction with jaw movement.
3. In toads, the tongue can be protracted to a distance that is greater than the gape. Jaw-tongue coordination may ensure that the tongue is protracted without hitting the upper jaw.

Previous studies of the effects of hypoglossal transection in other anuran species provide insight into the evolution of the hypoglossal sensory feedback system. Frogs from basal lineages (Cannatella, '85) appear to exhibit the primitive condition of tongue morphology (i.e., the condition possessed by the common ancestor of all anurans). Species including *Ascaphus truei* (Nishikawa and Cannatella, '91), *Bombina orientalis* (unpubl. data), *Discoglossus pictus* (Nishikawa and Roth, '91), and *Hyla cinerea* (Deban and Nishikawa, '90, '92) possess weakly protrusible tongues, which cannot be protracted more than 2–3 mm beyond the jaws. These species also appear to lack hypoglossal coordination of jaw and tongue movements. In *Discoglossus*, *Bombina*, and *Hyla*, transection of the hypoglossal nerve has no effect on mouth opening, and coordination of tongue and jaw movements apparently is achieved by a central mechanism (Nishikawa and Roth, '91; Deban and Nishikawa, '92). Frogs with weakly protrusible tongues may not need a peripheral jaw-tongue coordination mechanism, because their tongues cannot be protracted more than 2–3 mm.

During their phylogenesis, several frog lineages, including phyllomedusine hylids (Deban and Nishikawa, '92), bufonids (Nishikawa and Gans, '90), and ranids (Anderson, '90), have evolved independently from a primitive (or ancestral) state characterized by short tongues of limited protrusibility to a new, derived state (i.e., not possessed by the common ancestor of all frogs), characterized by an elongate, highly projectile tongue (Magimel-Pelonnier, '24; Regal and Gans, '76; Gans and Gorniak, '82a,b; Horton, '82). Among anurans, the neural circuits controlling feeding behavior have evolved from a state in which they lack hypoglossal control of

mouth opening, to a new state in which hypoglossal feedback is necessary for mouth opening. The change in motor control appears to have occurred in parallel with the acquisition of a projectile tongue.

How neural circuits evolve to produce behavioral diversity is a fundamental question of comparative neurobiology. While there are numerous studies of the way in which sensory systems evolve (Bullock et al., '83; Northcutt, '84; Ryan, '86), relatively few studies (Cohen, '88; Lauder, '83) have investigated the evolution of motor systems. EMG studies (Goslow, '85; Lauder and Shaffer, '88) have reported that motor patterns evolve conservatively among tetrapods, even across major behavioral transitions. If we had examined the motor control of toad feeding behavior using only EMG, we also would have concluded that motor control has evolved conservatively, when in fact toads have evolved a new mechanism of motor control during the acquisition of their projectile tongues. It is probable that motor systems have generally evolved during behavioral and morphological transitions, to meet the new functional demands of the organisms that possess them. However, an experimental approach involving deafferentation and other neurological techniques may be necessary to reveal the evolutionary diversity of motor control mechanisms. More comparative studies of motor systems will be necessary before conclusions can be reached about whether peripheral control is generally a derived feature of motor systems.

#### ACKNOWLEDGMENTS

This research was supported by NSF grant BNS 8909937 and by Organized Research grants from Northern Arizona University to K.C.N. Travel funds were provided by the NAU Department of Biological Sciences, and the Lee Leeser Foundation. We thank Sharon Emerson, Joseph Fetcho, Stan Lindstedt, James O'Reilly, Cathy Propper, and Philip Service for providing helpful comments on earlier versions of the manuscript, David Cannatella for help with stimulation and nerve transection experiments, and David Prior for help with extracellular recordings from the trigeminal nerve.

#### NOTE ADDED IN PROOF

Weerasuriya (in *Visuomotor Coordination: Amphibians, Comparisons, Models and Robots*, ed. by J.-P. Ewert and M.A. Arbib, 1989, pp. 589–614) noted that the mouth also fails to open after bilateral hypoglossal transection in the toad, *Bufo bufo*.

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