

Reprint

Publisher: S. Karger AG, Basel
Printed in Switzerland

Original Paper

Brain Behav Evol 1993;42:189-196

Curtis W. Anderson
Kiisa C. Nishikawa

Physiology and Functional Morphology
Group, Department of Biological Sciences,
Northern Arizona University,
Flagstaff, Ariz., USA

A Prey-Type Dependent Hypoglossal Feedback System in the Frog *Rana pipiens*

Key Words

Denervation
Motor control
Frogs
Feeding behavior
Rana pipiens
Sensory feedback
Hypoglossal nerve

Abstract

Nerve transection experiments combined with high-speed videography and electromyography were used to characterize a prey-type dependent hypoglossal feedback system which coordinates mouth opening and tongue protraction in the common leopard frog, *Rana pipiens*. When feeding on small prey, sensory feedback from the tongue through the hypoglossal nerve is necessary to trigger mouth opening. If sensory feedback is prevented from reaching the brain by transection of the hypoglossal nerve, then the mouth fails to open although the feeding behavior appears otherwise normal. However, when feeding on large prey, the mouth opens normally even after the hypoglossal nerve has been transected. Thus, peripheral feedback is not necessary to trigger mouth opening when feeding on large prey, and presumably a central coordination mechanism is used. In *Rana pipiens*, the evolution of a new tongue morphology and a new motor pattern for feeding on small prey has been accompanied by the evolution of a novel, peripheral mechanism for coordinating tongue protraction and mouth opening. However, the primitive motor pattern for feeding on large prey and the primitive coordinating mechanism have been retained. These results imply that the neural circuits producing the different motor patterns for large and small prey are anatomically distinct at some level in the central nervous system. If they are not anatomically distinct, then sensory feedback should be necessary to trigger mouth opening regardless of which motor pattern is being expressed. While the anatomy of these distinct pathways remains to be elucidated, these results suggest that novel neural circuits may in fact underlie different behaviors even when they seem, superficially, to be relatively similar.

Introduction

Previous researchers have shown that many properly sequenced, simple rhythmic behaviors are produced centrally and do not require feedback from peripheral sense organs [Delcomyn, 1980; Grillner, 1985]. Recently, numerous studies have shown that peripheral sensory feedback can

modify centrally controlled output [Andersson et al., 1981; Grillner and Wallen, 1982; Feldman and Grillner, 1983; Skorupski and Sillar, 1988]. These studies raise two interesting questions: (1) to what extent can a centrally controlled motor program be modified from the periphery; and (2) what happens to the primitive neural circuitry during the evolution of a novel, peripherally coordinated behavior?

Curtis Anderson
Department of Biological Sciences
Northern Arizona University
Flagstaff, AZ 86011-5640 (USA)

In amphibians, the evolution of motor patterns and the degree to which these motor patterns can be modified has been better understood by combining studies of comparative neuromuscular anatomy with studies of the kinematics of feeding behavior [Nishikawa and Roth, 1991; Deban and Nishikawa, 1992; Nishikawa et al., 1992]. By combining this approach with nerve transection experiments and electromyography, we hope to further understand the evolution and neural control of feeding behavior in amphibians. The goals of this paper are: (1) to determine the extent to which a motor pattern can be modified by sensory input; and (2) to elucidate what happens to the neural connections during the evolution of a novel behavior.

This hypothesis of the evolution of motor control can be tested in *Rana pipiens*, a frog which has been shown previously to exhibit both the plesiomorphic and the derived patterns of feeding behavior [Anderson, 1990, 1991, 1993]. When feeding on small prey, *R. pipiens* uses tongue protraction to catch prey, minimizing head and body movements. When feeding on large prey, it lunges forward with its body, flexes the head downward, and uses jaw prehension to capture the prey. These different behavior patterns correspond to differences in feeding behavior between derived and more primitive frogs. Archaeobatrachian frogs have short tongues which can be protracted only a few millimeters [Nishikawa and Cannatella, 1991; Nishikawa and Roth, 1991]. In contrast, most neobatrachians have long tongues which they project to catch small prey [Regal and Gans, 1976]. The similarity between the behavior that neobatrachians use to catch large prey and the movement patterns of archaeobatrachians suggests that *Rana pipiens* has retained the primitive archaeobatrachian motor pattern and uses it to catch large prey, while evolving a new motor pattern for catching small prey. Nishikawa and Gans [1990, 1992] identified a novel, peripheral feedback system in which sensory feedback from the hypoglossal nerve is necessary to coordinate mouth opening and tongue protraction in the marine toad, *Bufo marinus*. If the hypoglossal nerve is transected, the toad's feeding behavior appears normal except that the mouth does not open throughout the feeding bout. *Bufo marinus* is a neobatrachian anuran which feeds using a highly projectile tongue. The plesiomorphic condition for anurans is the lack of a projectile tongue and the concomitant lack of hypoglossal sensory control of mouth opening and tongue projection [Deban and Nishikawa, 1992; Nishikawa and Roth, 1991]. The plesiomorphic condition for the coordination of tongue protraction and mouth opening may be one of central control and the evolution of a projectile tongue has resulted in a peripheral mechanism coordinating the behavioral output.

In *Rana pipiens*, is the feeding behavior based on small prey and the large prey type feeding behavior regulated by the same hypoglossal sensory feedback mechanism? Results presented here support the hypothesis that the two behaviors are under independent control. We tested this by transection of the ramus hypoglossus in *R. pipiens*. If, after transection of the ramus hypoglossus, both feeding behaviors appear to be subject to the same mechanism which coordinates mouth opening and tongue protraction, then we can postulate that peripheral control of feeding is a plesiomorphic condition and that motor control is highly conservative. Alternatively, if the two behaviors are not both controlled by hypoglossal sensory feedback, this may suggest that the primitive behavior is retained, and there is the addition of a novel behavior which accompanies the new tongue morphology.

Materials and Methods

For the nerve transection experiments, adult *Rana pipiens* (62–67 mm snout-vent length) were obtained from animal suppliers. The effects of nerve transection were quantified by using a high-speed video motion analysis of the feeding behavior to analyze the kinematics of feeding behavior on differing prey types. In addition, electromyographic techniques were used to measure the timing of activation of selected muscles involved in feeding behavior. For the kinematic analysis of feeding behavior, earthworms (*Lumbricus* sp.) and waxworms (*Galleria* sp.) were used to provide variation in prey size, shape, weight, and mobility. All frogs were filmed before and after surgical transection of the hypoglossal nerve while feeding on both prey types. The original research reported herein was approved and performed under guidelines established by the Northern Arizona University Institutional Animal Care and Use Committee.

Kinematic Analysis

Kinematic data were obtained using a Display Integration Technologies™ model DIT 660 high-speed, multi-framing video camera. The frogs were placed on a flat stage covered with a damp paper towel and allowed to feed unrestrained. The feeding sequences were videotaped at 120 fields/sec with synchronized strobe illumination. Filming was done at room temperature (approximately 21–23 °C).

Five feeding sequences per prey type per individual both before and after surgery were obtained from 4 frogs, for a total of 40 waxworm feeding sequences and 40 earthworm sequences. The feeding sequences were analyzed using Peak 2D™ motion analysis software on an IBM compatible computer. For each frame of the feeding sequence, the X, Y coordinates of the prey item, a non-moving reference point, and 10 points on the frog were digitized from the video monitor (fig. 1). Feeding sequences typically consisted of 12–16 frames (96–128 milliseconds).

For the kinematic analysis, the following variables were measured in milliseconds:

(1) Onset of forward head movement: the video field in which first movement toward the prey was observed.

(2) Onset of mouth opening: the field in which the mouth first appeared to open, which is the zero time from which the other variables were measured.

(3) Onset of tongue protraction: the field in which the tongue pad first became visible.

(4) Time of minimum mandible angle: the field in which the angle subtended by the lower jaw tip, midpoint of the lower jaw, and the jaw joint was minimal.

(5) Time of prey contact: the field in which the tongue makes contact with the prey.

(6) Completion of tongue protraction: the field in which the tongue is protracted maximally.

(7) Onset of tongue retraction: the field in which the tongue first began to be retracted.

(8) Time of maximum gape: the field in which the mouth is maximally open.

(9) Completion of tongue retraction: the field in which the tongue has become fully retracted.

(10) Time to maximum displacement of upper jaw tip: the field in which maximum forward movement of the upper jaw tip is reached during the lunge.

(11) Onset of mouth closing: the field in which the mouth begins to close.

(12) Completion of mouth closing: the field in which the mouth closed.

(13) Duration of mouth opening (8-2): the time from the onset of mouth opening to the time of maximum gape.

(14) Duration of tongue protraction (6-3): the time from the onset of tongue protraction to the completion of tongue protraction.

(15) Duration of tongue at target (7-5): the time from prey contact to the onset of tongue retraction.

(16) Duration of tongue retraction (9-7): the time from the onset of tongue retraction to the completion of tongue retraction.

(17) Duration of mouth closing (12-8): the time from maximum gape until the mouth is closed.

(18) Total time mouth is open (12-2): the time from onset of mouth opening to the completion of mouth closing.

In addition, the following variables were calculated from the digitized points: (1) maximum gape angle, the maximum angle subtended by the upper and lower jaw tips with the jaw joint at the vertex; (2) minimum mandible angle, the angle subtended by the jaw joint, the midpoint of the mandible, and the tip of the mandible; (3) maximum head flexion, the angle to which the head is ventroflexed; (4) maximum tongue reach, the distance from the tip of the protracted tongue to the line connecting the upper and lower jaw tips; (5) tongue angle, the angle subtended by the tip of the tongue, the lower jaw tip, and the jaw joint; and (6) absolute gape (cm), the distance between the upper and lower jaw tips at maximum gape.

Nerve Transection

For nerve transection, the frog was placed in a glass dish containing approximately 50 milliliters of 2% tricaine methanesulfonate (MS222). The frog was immersed in MS222 until breathing stopped, usually between 7 and 15 min. The frog was then removed from the dish, rinsed in tap water, and wrapped in damp paper towels. The frog was placed ventral side up on the stage of a dissecting microscope and moistened throughout surgery to prevent desiccation.

The ramus hypoglossus leaves the brain with the second spinal nerve, crosses the vagus nerve, runs between the sternohyoid and petrohyoid muscles, and then is directed anteriorly to the root of the

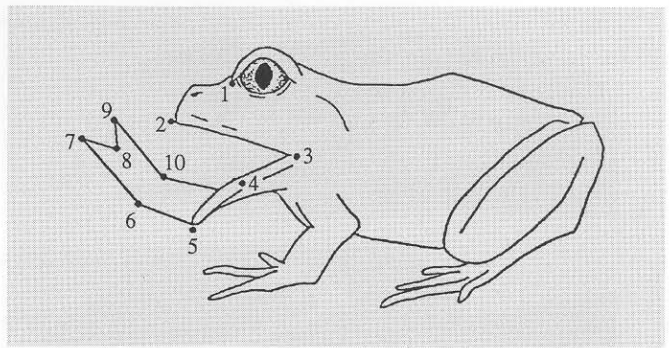


Fig. 1. Schematic diagram illustrating the points used in the kinematic analysis of feeding behavior. (1) Anterior corner of the eye, (2) upper jaw tip, (3) jaw angle, (4) midpoint of lower jaw, (5) lower jaw tip, (6) anterior tip of tongue, (7) left tongue tip, (8) mid tongue tip, (9) right tongue tip, (10) interior tongue.

tongue [Stuesse et al., 1983]. There, it provides motor innervation to the mm. genioglossus medialis and genioglossus basalis, both of which are involved in tongue protraction [Gans and Gorniak, 1982a, b]. Under anaesthesia, the hypoglossal nerve was dissected free and a 2-mm piece was removed just distal to the branch that innervates the geniohyoideous muscle but proximal to the innervation of the mm. genioglossus medialis and genioglossus basalis. The incision was then rinsed with tap water and closed with Nexaband™ surgical cement.

Each frog ($n=4$) was filmed both before and after surgery feeding on both prey types. The frogs were filmed as soon as possible after surgery to minimize learned adjustments to the surgical treatment. After the feeding sequences had been filmed, the frogs were sacrificed and the surgeries were verified by dissection.

Electromyography

Electromyographic recordings of muscle activity were obtained using bipolar, enamel or teflon-coated, stainless steel electrodes with a bared tip of approximately 1 mm [Nishikawa and Gans, 1992]. Electrodes were implanted percutaneously using 26.5 to 27.5 gauge hypodermic needles. The external ends were connected to Grass HIP511E high-impedance probes and the EMG signal was amplified with Grass P511 H/K pre-amplifiers and recorded on an A.R. Vetter 8-channel tape recorder. The video images were synchronized with EMG traces using an LED light source and a Peak Performance Technologies™ sync pulse generator.

Statistical Analysis

Some of the variables could not be measured after surgery when feeding on waxworms because the mouth does not open. A three way factorial analysis of variance with a mixed model could only be utilized for those variables that were measured in all treatments. Minimum mandible angle, maximum head flexion, and lunge length were analyzed for the following three factors: (A) individual (random); (B) prey type (fixed); and (C) surgery (fixed). Paired t-tests were used to test the significance of differences between individual means for two prey types before surgery, and for before vs. after surgery for earthworm feedings ($\alpha=0.05$, two-tailed). All statistics were run using SuperAnova™ statistical software on a MacIntosh IICI computer.

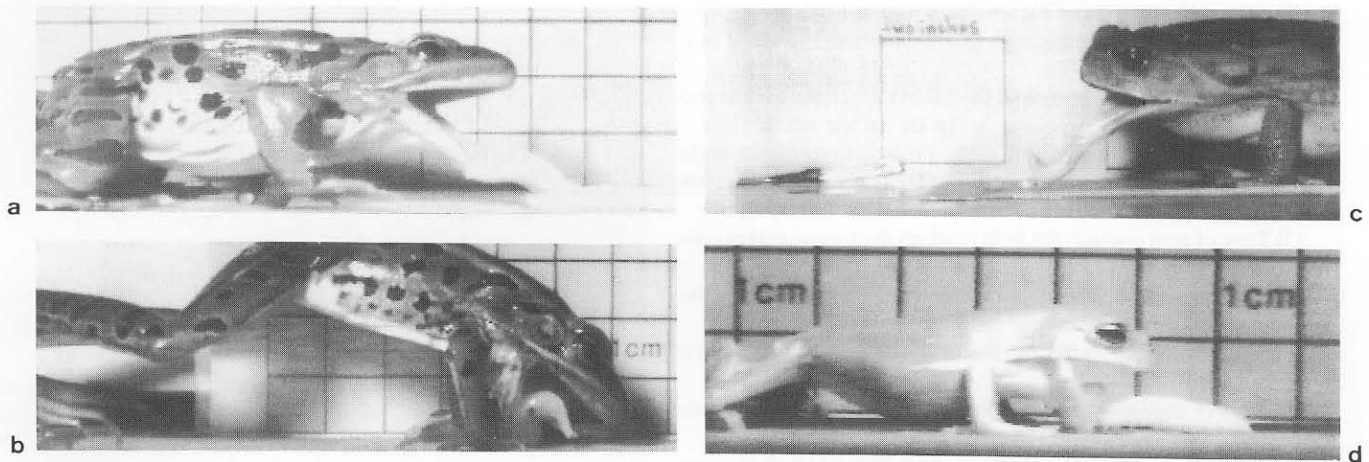


Fig. 2. Variation found in anuran feeding behavior. The upper right hand corner illustrates *Bufo marinus* feeding on a small waxworm. Note the long, protrusible tongue. The bottom right hand photograph is taken from *Hyla cinerea*. This non-protrusible tongue is considered the plesiomorphic condition. The upper left hand photo is from *Rana pipiens* feeding on waxworms. This prey item elicits a feeding behavior similar to *Bufo marinus* in which the prey is captured with a protrusible tongue. The bottom left photo is also from *Rana pipiens*, but when feeding on an earthworm. This feeding behavior is characteristic of the primitive condition, in which a protrusible tongue is not used to capture the prey.

Table 1. Means (N=40), standard errors and results from a paired t-test to determine the differences in the means of kinematics variables, before surgery, between waxworm and earthworm feedings

	Earthworm \bar{X} (SE)	Waxworm \bar{X} (SE)	t-value	p-value
Duration of mouth opening	43.2 (5.0)	52.8 (4.2)	-0.740	0.5127
Duration of tongue protraction	21.6 (2.1)	18.0 (1.1)	1.800	0.1697
Duration of tongue at target	10.4 (3.0)	8.8 (0.6)	0.440	0.6897
Duration of tongue retraction	44.8 (3.9)	91.2 (12.3)	-1.708	0.1862
Duration of mouth closing	60.0 (4.1)	120.4 (12.0)	-5.057	0.0149
Maximum gape angle (degrees)	59.7 (2.5)	56.8 (2.0)	0.677	0.5470
Tongue angle (degrees)	93.8 (6.4)	121.9 (3.5)	-1.689	0.1897
Absolute gape (cm)	1.9 (0.1)	1.9 (0.1)	-0.123	0.9097
Maximum tongue reach (cm)	1.2 (0.1)	1.5 (0.2)	-1.570	0.2144

Results

Rana pipiens modulates its patterns of feeding behavior depending upon prey type. When feeding on waxworms, the body remains relatively stationary throughout the feeding bout, with the exception of the forward movement due to the lunge. The head is moved forward as the body rotates over the front limbs, but remains level during the feeding bout (mean head flexion = $23.7^\circ \pm 1.8$ SE). The tongue contacts the prey (mean maximum tongue reach = 1.5 ± 0.2 SE; mean tongue angle = 121.9 ± 3.5 SE), which adheres to the sticky tongue, and the prey item is returned to the mouth (fig.2A, table 1).

When feeding on earthworms, the body arches forward, the head is ventroflexed, and the tongue is protracted less (mean maximum tongue reach = 1.2 ± 0.1 SE) than when feeding on waxworms (fig.2B). Because the body is arched and the head is ventroflexed downward to a greater degree (mean head flexion = 53.5 ± 2.1 SE; $f = 5.740$, $p = 0.0195$), the gape angle is directed downward, and the tongue angle is smaller (mean tongue angle = 93.8 ± 6.4 SE), although not significantly so.

Following transection of the ramus hypoglossus, when feeding on waxworms, the head remains relatively stationary as the frog rotates forward. There is little ventroflexion of the head, and the mouth never opens throughout the

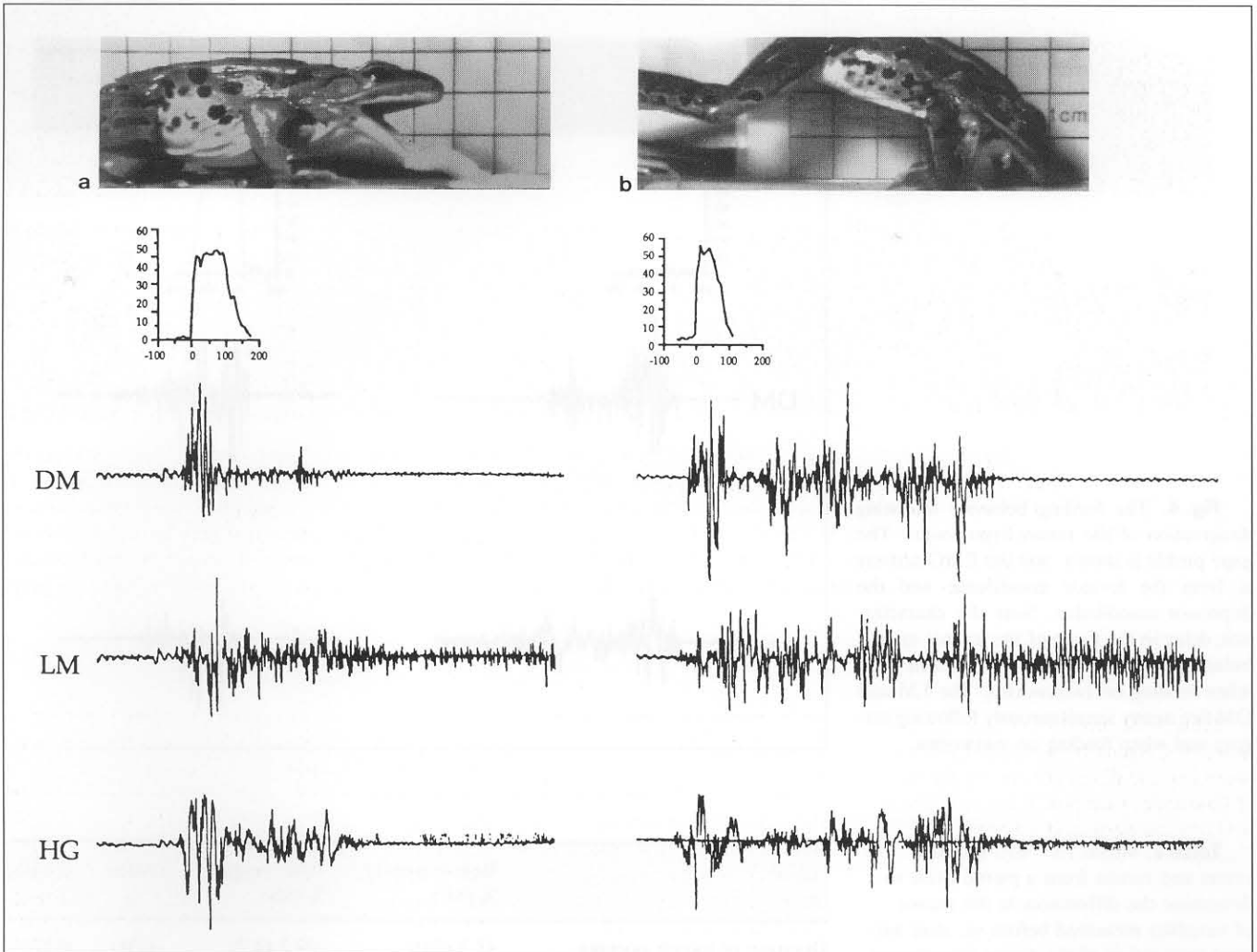


Fig. 3. The feeding behavior before surgical denervation of the ramus hypoglossus. The graph shows the gape profile throughout the feeding bout. LM is the levator mandibulae, DM is the depressor mandibulae. Note the delay of firing in the LM after the DM has reached its period of peak activity.

feeding bout (fig. 4, table 2). Because the mouth never opens, most of the variables could not be measured. However, minimum mandible angle (mean = 170.1 ± 0.5 ; $f = 42.448$, $p < 0.0001$), maximum head flexion (mean = 40.5 ± 18.3 ; $f = 5.740$, $p = 0.0195$), and lunge length (mean = 2.6 ± 0.2 ; $f = 6.965$, $p = 0.0104$) were all significantly different between waxworm and earthworm feedings following surgery. When feeding on earthworms after hypoglossal transection, the frog arches the body, exhibits a large degree of ventroflexion of the head (mean = 54.4 ± 2.2 SE), opens the mouth and captures the prey using jaw prehension (fig. 4, table 2). The minimum mandible angle (mean = 154.0 ± 1.5 SE) was significantly less

when feeding on earthworms than on waxworms, and lunge length (mean = 1.5 ± 0.2 SE) was significantly less. Lunge length ($f = 2.788$, $p = 0.0476$) was significantly different among individuals.

Among waxworm feedings, for those variables which could be recorded, the minimum mandible angle was significantly larger following surgery ($f = 167.571$, $p < 0.0001$), and the lunge length was significantly longer ($f = 8.537$, $p = 0.0048$). Maximum head flexion did not differ significantly following surgery when feeding on waxworms. When comparing before vs. after hypoglossal transection for earthworm feedings, the duration of tongue protraction ($f = 4.200$, $p = 0.0246$), the tongue angle ($f = 5.089$,

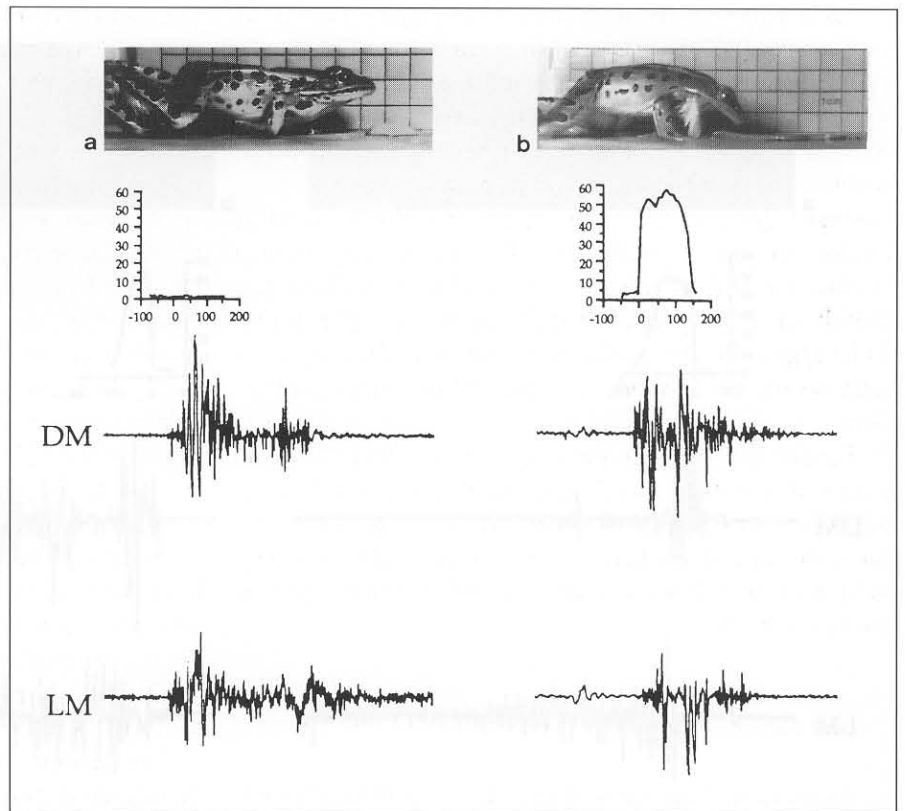


Fig. 4. The feeding behavior following denervation of the ramus hypoglossus. The gape profile is shown, and the EMG activity is from the levator mandibulae and the depressor mandibulae. Note the characteristic delay in the firing of the levator mandibulae seen before surgery is present only when feeding on earthworms. The LM and DM fire nearly simultaneously following surgery and when feeding on waxworms.

Table 2. Means (N=40), standard errors and results from a paired t-test to determine the differences in the means of variables measured before vs. after surgical transection of the ramus hypoglossus in *Rana pipiens*. All measurements were taken from earthworm feeding sequences

	Before surgery X̄ (SE)	After surgery X̄ (SE)	t-value	p-value
Duration of mouth opening	43.2 (5.0)	33.2 (4.2)	1.341	0.2725
Duration of tongue protraction	21.6 (2.1)	13.2 (2.2)	4.200	0.0246
Duration of tongue at target	10.4 (3.0)	-19.2 (7.5)	1.982	0.1417
Duration of tongue retraction	44.8 (3.9)	40.0 (4.5)	0.555	0.6173
Duration of mouth closing	60.0 (4.1)	68.8 (3.5)	-1.677	0.1920
Maximum gape angle (degrees)	59.7 (2.5)	68.6 (1.9)	-3.917	0.0296
Tongue angle (degrees)	93.8 (6.4)	50.1 (4.2)	5.089	0.0147
Absolute gape (cm)	1.9 (0.1)	2.2 (0.1)	-7.635	0.0047
Maximum tongue reach (cm)	1.2 (0.1)	0.1 (0.1)	5.092	0.0146

$p=0.0147$), and the maximum tongue reach ($f=5.092$, $p=0.0146$) were all significantly less following surgery (table 2). The maximum gape angle ($f=-3.917$, $p=0.0296$) and the absolute gape ($f=-7.635$, $p=0.0047$) were significantly larger following transection of the hypoglossal nerve.

Electromyographic recordings ($n=2$ individuals, $N=6$ trials) obtained before surgical denervation of the hypoglossal nerve illustrate the patterns of activation in the man-

dibular depressors (mouth opening muscles), mandibular levators (mouth closing muscles), and m. hypoglossus (tongue retractor muscle) (fig. 3). During normal feeding on both waxworms and earthworms, the mandibular levators reach their maximum activity an average of 111.0 milliseconds after the period of peak activity of the mandibular depressors (waxworms = 108.3 ± 10.4 SE; earthworms = 113.7 ± 5.4 SE).

Electromyographic data from *Rana pipiens* feeding on waxworms following hypoglossal transection show the nearly simultaneous firing of both the mandibular depressors and the mandibular levators (mean = -3.7 ± 17.3 SE ms delay; fig. 3). After surgery, when feeding on earthworms, the electromyographic data show that the characteristic delay in the firing of the mandibular levators before surgery is still present after surgery (mean = 104.7 ± 0.8 SE ms delay; fig. 4). As figure 4B illustrates, mouth opening occurs, but the tongue is not protracted. This suggests that the genioglossus basalis and genioglossus medialis did not contract, thus preventing tongue protraction.

Earthworm feedings provide a good control for the effects of surgery on mouth opening. Because mouth opening occurs after surgery when feeding on earthworms, but not in the same frog when feeding on waxworms, the ability to open the mouth was not simply an effect of the surgery or the anaesthesia.

Discussion

As previously reported, *Rana pipiens* modifies its feeding behavior in response to prey type [Anderson, 1993]. When feeding on waxworms, there is very little movement of the body, the head remains level, and tongue prehension is used to capture prey. However, when feeding on earthworms, *Rana* exhibits increased body movement and ventroflexion of the head. The tongue plays a smaller role in prey capture. Instead, jaw prehension is used to capture prey. During earthworm feedings, the head is ventroflexed to a significantly larger degree and the tongue angle and maximum tongue reach are smaller.

When feeding on small pieces of earthworms, *R. pipiens* feeds using its highly protrusible tongue in the same way as when feeding on waxworms [unpubl. observ.]. This suggests that *Rana* coordinates these differing behaviors through a visual analysis of prey size, and not through another sensory modality such as olfaction. The idea of visual prey discrimination is supported by Ewert [1974, 1980, 1981], who found that when offered visual prey 'dummies', the key stimuli producing prey capture responses depended upon (1) the overall movement of the dummy, and (2) the shape of the dummy relative to the direction it was moving.

Rana pipiens coordinates mouth opening and tongue protraction through peripheral hypoglossal feedback when feeding on small prey items. If the ramus hypoglossus is transected, the frog rotates forward over its front limbs, the

head and body remain relatively stationary, but the mouth never opens throughout the feeding bout. When feeding on earthworms after hypoglossal transection, the mouth opens normally.

The mechanism coordinating mouth opening and tongue protraction can be hypothesized from the EMG data. Before surgery, the mandibular levators reach peak activity an average of 111.0 milliseconds after the peak activity of the mandibular depressors. This delay is sufficient to allow the frog to open its mouth. After surgery, the mouth does not open and the levators and depressors fire nearly simultaneously when feeding on waxworms. These findings correspond with the results obtained by Nishikawa and Gans [1992] from *Bufo marinus* that the inability of *B. marinus* to open its mouth was caused by the simultaneous activation of the mandibular depressors and the mandibular levators. One hypothesis to explain why mouth opening in *R. pipiens* occurs before surgery is that the mandibular levators are inhibited from firing until the mandibular depressors reach maximum activity [Nishikawa and Gans, 1992]. The characteristic delay of firing observed before surgery is still present when feeding on earthworms.

Transection of the hypoglossal nerve apparently disrupts sensory feedback returning to the brain. This feedback appears to inhibit the activity of the mandibular levators during mouth opening [Nishikawa and Gans, 1992]. The result is the simultaneous activation of both the mouth opening and mouth closing muscles. Because this delay is not eliminated by hypoglossal nerve transection when feeding on earthworms, it appears that peripheral feedback from the hypoglossal nerve is not necessary for mouth opening in *Rana pipiens* when feeding on earthworms. These data do not conclusively show that sensory activity returns to the brain through the ramus hypoglossus. The pathway for sensory feedback could be through one of two other nerves: the ramus palatinus of the trigeminal nerve, which carries mechanosensory afferents from the maxilla; or the ramus lingualis of the glossopharyngeal nerve which carries tongue afferents. However, Nishikawa and Gans [1990, 1992] were able to eliminate both of these possibilities. Following denervation of either the ramus palatinus or the ramus lingualis, they found no effect on mouth opening.

It has been suggested previously that the two modes of feeding found in *Rana pipiens* are two distinctly different behaviors, one representing the primitive, or plesiomorphic behavior and one a derived behavior [Anderson, 1993]. The plesiomorphic condition for anurans is to possess a non-projectile tongue, such as that found in *Ascapus* [Nishikawa and Cannatella, 1991], *Discoglossus*

[Nishikawa and Roth, 1991], or *Hyla* [Deban and Nishikawa, 1992] (fig. 2). When *Rana* feeds on earthworms, its feeding behavior is similar to the primitive behavioral pattern. When feeding on waxworms it uses a derived behavior, similar to that found in *Bufo* [Gans and Gorniak, 1982a, b]. It also has been shown that the plesiomorphic condition for anurans is the concomitant lack of hypoglossal sensory coordination of mouth opening and tongue projection [Nishikawa and Roth, 1991; Deban and Nishikawa, 1992; Nishikawa and Gans, 1992]. The plesiomorphic condition for the coordination of tongue protraction and mouth opening may be one of central control and the evolution of a projectile tongue has resulted in a peripheral mechanism coordinating the motor output.

Previous authors have suggested that the evolution of neural circuitry differs from that of other morphological structures. Morphological structures tend to be plastic, but neural circuits tend to be highly conservative because the neural pathways are often multifunctional [Roth and Wake, 1989; Kavanau, 1990]. Therefore, an infrequently

used pathway may not be selected against, but rather it may cease to be accessed [Dumont and Robertson, 1986]. The results from *Rana pipiens* suggest that during the evolution of a projectile tongue, a novel, peripheral mechanism for coordinating mouth opening and tongue protraction has evolved. Thus, the primitive neuronal pathway was not selected against. Instead, the ancestral behavioral condition has been retained and is accessed when feeding on large prey items.

Acknowledgments

We would like to thank Dr. Paul Hansen, Dr. Stan Lindstedt, Dr. David Prior, Mr. James C. O'Reilly, Ms. Erika Wiltenmuth, and Mr. Dale Ritter for technical help and critical reading of the manuscript. This research was supported in part by NSF grant No. BNS 8909937 to K. Nishikawa, a Northern Arizona University Organized Research grant to K. Nishikawa, and a Grant-in-Aid-of-Research from Sigma Xi to C. Anderson.

References

- Anderson, C. (1990) The effect of prey size on feeding kinematics in two species of ranid frogs. *Amer. Zool.*, 30: 140A.
- Anderson, C. (1991) The modulation of feeding behavior in response to visual stimuli in *Rana pipiens*. *Arizona-Nevada Academy of Science*, 26: 14.
- Anderson, C. (1993) The modulation of feeding behavior in response to prey type in the frog, *Rana pipiens*. *J. Exp. Biol.*, in press.
- Andersson, O., H. Forsberg, S. Grillner, and P. Wallen (1981) Peripheral feedback mechanisms acting on the central pattern generators for locomotion in fish and cat. *Can. J. Physiol. Pharmacol.*, 59: 713-726.
- Deban, S.M., and K.C. Nishikawa (1992) The kinematics of prey capture and the mechanism of tongue protraction in the green tree frog, *Hyla cinerea*. *J. Exp. Biol.*, 170: 235-256.
- Delcomyn, F. (1980) Neural basis of rhythmic behavior in animals. *Science*, 210: 492-498.
- Dumont, J.P.C., and R.M. Robertson (1986) Neuronal circuits: An evolutionary perspective. *Science*, 233: 849-853.
- Emerson, S.B. (1985) Skull shape in frogs - correlations with diet. *Herpetologica*, 41: 177-188.
- Ewert, J.-P. (1974) The neural basis of visually guided behavior. *Sci. Amer.*, 230: 34-42.
- Ewert, J.-P. (1980) Neuroethology. An Introduction to the Fundamentals of Behavior. Springer-Verlag, Berlin.
- Ewert, J.-P. (1981) Neural coding of 'worms' and 'antiworms' in the brain of toads: The question of hardwired and softwired systems. In *Brain Mechanisms of Behavior in Lower Vertebrates* (ed. by P.R. Laming), Cambridge University Press, Cambridge, pp. 137-168.
- Feldman, J.L., and S. Grillner (1983) Control of vertebrate respiration and locomotion: A brief account. *Physiologist*, 26: 310-316.
- Gans, C., and G.C. Gorniak (1982a) How does the toad flip its tongue? Test of two hypotheses. *Science*, 216: 1335-1337.
- Gans, C., and G.C. Gorniak (1982b) Functional morphology of lingual protrusion in marine toads (*Bufo marinus*). *Amer. J. Anat.*, 163: 195-222.
- Grillner, S. (1985) Neurological bases of rhythmic motor acts in vertebrates. *Science*, 228: 143-149.
- Grillner, S., and P. Wallen (1982) On peripheral control mechanisms acting on the central pattern generators for swimming in the dogfish. *J. Exp. Biol.*, 98: 1-22.
- Kavanau, J.L. (1990) Conservative behavioural evolution, the neural substrate. *Anim. Behav.*, 39: 758-767.
- Nishikawa, K.C., and D.C. Cannatella (1991) Kinematics of prey capture in the tailed frog *Ascaphus truei* (Anura: Ascaphidae). *Zool. J. Linn. Soc.*, 103: 289-307.
- Nishikawa, K.C., and C. Gans (1990) Neuromuscular control of prey capture in the marine toad, *Bufo marinus*. *Amer. Zool.*, 30: 141A.
- Nishikawa, K.C., and C. Gans (1992) Peripheral control of mouth opening during feeding behavior in the toad *Bufo marinus*. *J. Exp. Zool.*, in press.
- Nishikawa, K.C., and G. Roth (1991) The mechanism of tongue protraction during prey capture in the frog *Discoglossus pictus*. *J. Exp. Biol.*, 159: 217-234.
- Nishikawa, K.C., C.W. Anderson, S. Deban, and J.C. O'Reilly (1992) The evolution of neural circuits controlling feeding behavior in frogs. *Brain, Behav. Evol.*, 40: 125-140.
- Regal, J.R., and C. Gans (1976) Functional aspects of the evolution of frog tongues. *Evolution*, 30: 718-734.
- Roth, G., and D.B. Wake (1989) Conservatism and innovation in the evolution of feeding in vertebrates. In *Complex Organismal Functions: Integration and Evolution in Vertebrates* (ed. by G. Roth and D.B. Wake), Wiley, New York, pp. 7-21.
- Skorupski, P., and K.T. Sillar (1988) Central synaptic coupling of walking leg motor neurons in the crayfish: Implications for sensorimotor integration. *J. Exp. Biol.*, 140: 355-379.
- Stuesse, S.L., W.L.R. Cruce, and K.S. Powell (1983) Afferent and efferent components of the hypoglossal nerve in the grass frog, *Rana pipiens*. *J. Comp. Neurol.*, 217: 432-439.