

The strike of the tiger salamander: quantitative electromyography and muscle function during prey capture

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Summary. 1. We provide a quantitative description of the motor pattern of 11 cranial muscles that control terrestrial prey capture behavior via tongue projection in the tiger salamander (*Ambystoma tigrinum*) and test the hypothesis that the cranial motor pattern does not differ between successful and unsuccessful strikes.

2. Simultaneous high-speed video images and electromyograms from cranial muscles were recorded during prey capture by 4 individuals. Neither the time to prey contact by the tongue nor gape cycle duration during the strike were significantly different between successful and unsuccessful strikes. In addition, 76 out of 77 parameters measured from 11 cranial muscle electromyograms during the strike showed no significant differences between successful and unsuccessful captures. We conclude that the strike of the tiger salamander shows little variability under these experimental conditions.

3. During the strike all head muscles have nearly synchronous onsets of electromyographical activity. The subarcualis rectus 1 muscle exhibits two bursts of activity: one during tongue projection and a second during tongue retraction. The genioglossus and interhyoideus muscles both show sharp single peaks of activity during the tongue projection phase. The depressor mandibulae muscle typically shows a second peak in activity coincident with the plateau phase of the gape cycle.

Key words: *Ambystoma tigrinum* – Feeding behavior – Motor pattern – Quantitative electromyography – Muscle function

Abbreviations: *AMe* adductor mandibulae externus muscle; *AMi* adductor mandibulae internus muscle; *bb* basibranchial element; *BURAR* total burst area; *BURDUR* burst duration; *DM* depressor mandibulae muscle; *EMG* electromyographic; *EP* epaxial muscle; *GG* genioglossus muscle; *GH* geniohyoideus muscle; *hql* hyoquadrate ligament; *IH* interhyoideus muscle; *IM* intermandibularis posterior muscle; *MAXAR* maximum area; *MAXSP* maximum number of spikes; *og* otoglossal cartilage; *ONSET* onset of EMG activity; *RCp* rectus cervicis profundus muscle; *RCs* rectus cervicis superficialis muscle; *SARI* subarcualis rectus 1 muscle; *TMAXAR* time to maximum area; *uh* urohyal

Introduction

The process of prey capture by amphibians has been used extensively as a model system for studying sensory physiology and the physiological basis of behavior (Ewert 1980; Roth 1986, 1987). Specifically, many neuroethologists interested in the central processing of sensory input and in the neuroanatomical basis of motor output in vertebrates have focused on amphibian feeding behavior, and considerable progress has been made especially in understanding how sensory input may evoke the feeding response (e.g., Comer and Grobstein 1978, 1981; Ewert 1970, 1984; Ingle 1968; Roth 1976, 1978, 1982; Tsai and Ewert 1987). However, there are relatively few analyses of the motor output itself and of the motor basis of prey capture behavior in amphibians (Bemis et al. 1983; Gans and Gorniak 1982a, b; Lauder and Reilly 1990; Lauder and Shaffer 1988; Thexton et al. 1977). In particular, there is no complete quantitative analysis of motor output during terrestrial prey capture in salamanders, comparable to the research now available on frogs (Gans and Gorniak 1982a, b; Matsushima et al. 1985), to provide a basis for interpreting analyses of sensory systems and neuroethological results (Roth et al. 1988). The paper of Lauder and Shaffer (1988) presented some data on motor patterns during terrestrial feeding, but focused primarily on the question of metamorphosis of the motor pattern in salamanders. This paper did not provide either a general summary of motor output or an interpretation of motor patterns in terms of feeding behavior and prey capture ability.

One additional issue that is of relevance for understanding amphibian feeding behavior is the question of variability. Analyses of motor patterns in aquatic salamanders have suggested that motor output during feeding is relatively invariant across metamorphosis and when different prey types are fed upon (Lauder and Shaffer 1988; Reilly and Lauder 1989a). However, no study to date has examined the effect of feeding success on the motor pattern and motor patterns during terrestrial feeding behavior have not been analyzed for vari-

ability. Do successful strikes in which the prey is captured involve different motor output than those in which the prey is not captured?

The goals of this paper are (1) to provide a quantitative description of the motor patterns in the jaw muscles used during terrestrial prey capture by the tiger salamander, *Ambystoma tigrinum*, (2) to test the hypothesis that feeding kinematics and motor output are stereotyped, and (3) to interpret the pattern of muscle activity during prey capture in terms of a previously proposed kinetic model of the feeding system.

Materials and methods

Simultaneous kinematic and electromyographic (EMG) patterns were obtained from 4 adult *Ambystoma tigrinum mavortium* (snout-vent lengths 110–125 mm) collected near Limon, Lincoln County, Colorado. A detailed analysis of strike and intraoral prey transport kinematics in these animals is presented elsewhere (Reilly and Lauder 1989b; in press), and the major focus of this paper is the analysis of muscle function during the strike.

Kinematic analysis. Animals were trained to feed under strobe lights and filmed at 200 frames/s using a NAC HSV-400 high-speed video system. Elapsed time in milliseconds and a 100 Hz signal synchronizing electromyographical recordings were recorded on each video frame during filming. Lateral views of tiger salamanders were filmed in an 8 l glass aquarium with a background marked with a grid of 1 cm squares. Strikes were elicited by offering the animals 3–6 cm long earthworm pieces (*Lumbricus*) presented directly in front of the jaws with forceps. Because tiger salamanders project the tongue from 3 to 6 mm past the jaws (Reilly and Lauder 1989b) worms were typically presented about 5 mm in front of the jaws (and between 1 and 3 cm off the ground), although sometimes (as in Fig. 2) the salamander approached the prey closely just before striking. In every strike the tongue successfully hit the worm and unsuccessful strikes resulted from failure of prey adhesion to the tongue during retraction. We explicitly attempted to get both successful and unsuccessful strikes from each individual. We chose this mode of prey presentation in order to maximize our ability to obtain clear lateral views of feeding and to specifically examine the effects of unsuccessful captures that did not result from a complete miss of the prey. It was not possible to obtain clear video footage when prey position is varied in three dimensions. This method of presenting the prey may reduce kinematic and EMG variability shown during prey capture as discussed below.

A total of 38 strikes (3–5 successful and 5–7 unsuccessful from each animal) were used in the kinematic analysis. Video frame sequences for each strike were analyzed frame by frame using a PC-based image analysis system and custom morphometric software to quantify strike kinematics and synchronize feeding kinematics with electromyographical patterns. For each feeding cycle, frame (time) zero was defined as the frame preceding the first frame in which the mouth began to open before a strike.

To examine statistically the extent of kinematic differences between successful and unsuccessful strikes two variables were digitized from each strike sequence. Time to prey contact was measured from the onset of mouth opening (time zero) until the tongue contacted the prey item. Time to prey contact occurs 0 to 5 ms before peak tongue projection. Gape cycle time was measured from mouth opening (time zero) until the mouth closed after the strike. Retraction time, therefore, is the time from prey contact to mouth closing. Each variable was analyzed using a two-way analysis of variance design with strike performance (successful vs. unsuccessful strikes) as a fixed effect and individuals ($n=4$) as a random effect. Thus, the interaction mean square was used as the denominator in computing the F-ratios for the strike performance effect (Sokal and Rohlf 1981).

Electromyography. Muscle activity patterns (motor patterns) of the head and hyobranchial musculature were quantified by recording electrical activity patterns (EMGs) produced by 11 muscles during the strike. A total of 51 strikes were analyzed from 4 individuals, including 18 successful (4–5 per individual) and 33 unsuccessful (5–13 per individual). Electromyographical recordings were made simultaneously in 5 muscles from each of the 4 individuals by implanting bipolar stainless steel electrodes into each muscle as in previous research (Lauder and Shaffer 1988; Reilly and Lauder 1989a; Jayne et al. 1990a; Wainwright et al. 1989). All electrode implantations were done while the animals were under anaesthesia, induced by placing the animals in a solution of tricaine methane sulphonate (1 g/l) for 15 min. The bared metal tips of each electrode were 0.5 mm long and the insulated portions were glued together proximal to the bared ends with a cyanoacrylate adhesive to prevent tip displacement within the muscle (Jayne 1988). Electrodes were implanted percutaneously directly into the belly of each muscle. Individual electrodes were glued to the skin to prevent movement of the electrode and to minimize movement artifacts during feeding. The 5 pairs of electrodes were then glued together and fixed to the back of the animal using tissue tape and glue. In addition, a ground electrode and a copper-constantine thermocouple were implanted subcutaneously into the dorsal musculature. Body temperature at the thermocouple was monitored with a Tegam model 821 microprocessor thermometer. Animals recovered from anaesthesia within one hour and fed vigorously. All synchronized EMG and kinematic data were recorded within 1/2 to 2 h postanaesthesia and the body temperatures ranged from 20–22 °C. Immediately following each experiment the animals were sacrificed by overdose of anaesthetic and preserved in 10% formalin. Electrode position was then confirmed by dissection.

EMG signals were amplified 10 000 times using Grass AC P511J preamplifiers with a bandpass of 100 to 3000 Hz (and a 60 Hz notch filter), and recorded on a Bell and Howell 4020A multichannel FM tape recorder along with a synchronization pulse simultaneously recorded on the video frames. The 6 analog signals (5 EMGs plus synchronization pulse) for each feeding by each individual were converted to a digital data file with a Keithley analog-to-digital converter and an IBM AT microcomputer. The effective sample rate for each of the 6 channels was 8084 Hz at 12 bit resolution. This sample rate was chosen because of the results of a separate study which showed that 8 kHz allowed the faithful reproduction of rapid spikes present in the EMGs from terrestrial salamander muscles (Jayne et al. 1990b).

The digital data file for each feeding was then analyzed using a Tektronix 4107 graphics terminal (to determine EMG bin to video frame synchronization points) and custom software that counted spikes (using the algorithm of Beach et al. 1982; also see Jayne et al. 1990a, b) and calculated other measures of activity (described below) for each 5 ms bin of the signal for each muscle. Our aim was to characterize the motor pattern relatively completely (with many variables) in order to detect any differences between successful and unsuccessful strikes and to quantitatively describe the muscle activity patterns (motor patterns) during the strike. Peaks in EMG voltage were counted as spikes only when they exceeded a threshold voltage of +12 μ V in the unamplified signal, the level at which baseline noise was eliminated. Files containing the bin-wise measures of EMG activity for each feeding were aligned to the onset of mouth opening (video time zero) for that feeding using the synchronization pulse. Thus, several measures of muscle activity were calculated for each 5 ms bin or time period corresponding to synchronized high speed video frames during the strike.

To compare successful and unsuccessful strikes, seven variables describing the numbers, timing, and amplitudes of EMG spikes, rectified integrated areas and relative onsets of EMG activity were measured from each muscle. These variables are: 1) BURAR = total burst area or sum of bin-wise rectified integrated EMG areas for the burst; 2) BURDUR = burst duration in ms; 3) MAXSP = maximum number of spikes per 5 ms bin found in the burst; 4) TMAXSP = time in ms to the bin with the maximum number of spikes; 5) MAXAR = maximum area per 5 ms bin found in

the burst; 6) TMAXAR = time to the bin with maximum area; 7) ONSET = onset of EMG activity relative to the beginning of mouth opening (video time zero).

Analysis of variance in these variables (ANOVA) was used to test the extent of stereotypy by comparing successful vs. unsuccessful strikes. EMG patterns of 5 of the 11 muscles (see Table 2) were recorded from each of 2–3 individuals and thus a two-way analysis of variance design was used with individuals as a random effect and strike performance as a fixed effect (Sokal and Rohlf 1981). EMG patterns of the 6 remaining muscles (see Table 3) were recorded from single individuals; therefore one-way analysis of variance was used with strike performance (successful vs. unsuccessful strikes) as the main effect. Because of problems that arise in interpreting significance levels when many univariate analyses of variance are conducted, a Bonferroni adjusted significance level of 0.007 ($P < 0.05/7$ variables) was used for each muscle. Another possible Bonferroni correction would be to divide each P -value by 77 (the total number of tests). We chose not to do this in order not to bias our tests severely toward acceptance of the stereotypy hypothesis (dividing by 77 would produce an extremely conservative test making it almost impossible given our degrees of freedom to detect a difference in motor pattern between behaviors). In addition, we conducted several multivariate analyses. The large number of variables, relatively small number of observations for each behavior (4 to 10), and the fact that only 4 or 5 of 11 muscles were studied in any individual precluded a direct a priori multivariate analysis of variance (MANOVA) on all variables simultaneously. Instead, we ran MANOVAs on subsets of the variables by individuals and across individuals to alleviate problems caused by making multiple statistical comparisons.

To quantitatively describe motor patterns during the strike, bin-wise EMG area values, synchronized to mouth opening (video time zero), for many strikes were averaged for each 5 ms bin to produce profiles of EMG activity for each muscle during the strike (e.g., Fig. 3). Because our statistical analyses indicated no kinematic or EMG difference in successful vs. unsuccessful strikes but did reveal significant individual variation, we pooled all strikes (successful and unsuccessful) per individual to construct EMG area profiles for each muscle. Therefore, each illustration of muscle activity pattern (see Figs. 3, 4) is based on the average of 9 to 18 synchronized strikes per individual.

To examine patterns of muscle synergism bivariate plots of the bin-wise rectified integrated area during the strike were constructed for several pairs of muscles. The absolute levels of muscle activity were plotted for each 5 ms bin, and each point was coded for tongue projection and retraction phases to interpret the relative contribution of each muscle during different kinematic phases of the strike (e.g., Fig. 5).

Muscle contractile properties. In order to provide an indication of some of the basic physiological properties for a few of the jaw muscles from which EMGs were recorded, 3 additional animals were heavily anaesthetized (and subsequently overdosed) in a solution of tricaine methane sulphonate (1 g/l). The adductor mandibulae internus muscle (AMi) from the left side was dissected free with small portions of lower jaw and parietal bone still attached and placed in a dish of amphibian Ringer's solution (in mM: 120 NaCl, 2 KCl, 1.8 CaCl₂, 4 HEPES, 2 g/l glucose, pH 7.6 at 23°C). The AMi was attached to the motor arm of a Cambridge Technology 300II servo-controlled muscle ergometer by a stainless-steel chain tied to the coronoid tendon. The parietal bone was tied to a stationary steel hook. The muscle was suspended vertically in a chamber between two platinum plate electrodes placed on opposite sides of the muscle. The muscle was continuously bathed in recirculating oxygenated amphibian Ringer's solution at 21–22 °C. Muscle length was adjusted to give maximal isometric twitch response.

Force output from the transducer was analyzed using a Nicolet 3091 digital storage oscilloscope and simultaneously recorded on FM tape. A Grass S48 stimulator was used to produce 1 ms pulses of 140–150 V. The contraction time (TPT; from first mechanical response to maximal twitch tension) and maximal twitch tension

(Pt) were determined on single twitches. Next, a series of 10 tetani at 2 min intervals were elicited with 0.3 s pulse trains at 25–30 Hz to determine maximal tetanic tension (Po), time to 90% of peak tetanic tension (TPo), and half relaxation time (RT1/2, time from last stimulus to one half of maximal tetanic tension). In addition, from one animal the pair of geniohyoideus muscles was removed intact from the lower jaw to the urohyal and treated similarly. After each stimulation regime the transducer was calibrated by hanging weights from it. The entire procedure took at most 2 h for each muscle; procedures generally followed those of John-Alder and Bennett (1987) and Marsh and Bennett (1985).

Myology. The 11 muscles chosen for analysis (Fig. 1) include all of the major head muscles involved in tongue projection and retraction during salamander feeding. Detailed anatomical descriptions of these muscles are available elsewhere in the literature (Druner 1902, 1904; Francis 1934; Hilton 1957; Lauder and Shaffer 1988; Reilly and Lauder 1989b) and only a brief summary of muscle morphology (together with a schematic figure, Fig. 1) is provided here as an aid to understanding motor patterns. Interpretations of muscle functions are based on muscle stimulations (Druner 1902, 1904; Reilly and Lauder 1989b), functional analyses of homologous muscles in larval tiger salamanders (Lauder and Shaffer 1985, 1988), and anatomical data such as muscle lines of action. To some extent these proposed functions will remain unproven until direct experimental tests are done on each muscle individually.

Four major pairs of cranial muscles have been proposed to mediate mouth opening and closing (Fig. 1). The depressor mandibulae muscle (DM), originating on the cranium dorsolaterally and inserting on the rear of the mandible posterior to the jaw articulation point, depresses the lower jaw. Two large cranial muscles lying side by side function to close the mouth by adducting the mandible against the upper jaw. While both originate on the dorsolateral aspect of the cranium the adductor mandibulae externus muscle (AMe) inserts broadly on the posterior third of the mandible while the adductor mandibulae internus muscle (AMi) has a narrow tendinous insertion on the dorsally projecting coronoid process of the mandible. The anterior epaxial muscles (EP) extending from the vertebrae to the dorsal aspect of the cranium, elevate the skull on the vertebral column during feeding and contribute to mouth opening.

Two thin transverse ventral muscles spanning the mandibles elevate the entire buccal area (Fig. 1). The intermandibularis posterior muscle (IM) spans the anterior half of the mandible and the interhyoideus muscle (IH) spans the posterior half of the mandible and the throat region behind the jaws.

Four pairs of muscles attach to the hyobranchial apparatus and serve to advance and retract the hyobranchial apparatus and tongue. Two anterior extensions of the ventral hypaxial muscles extend forward to insert on the hyobranchial apparatus and retract the apparatus and tongue. The rectus cervicis superficialis muscle (RCs) inserts medially on the posterior free floating urohyal element of the hyobranchial apparatus (uh, Fig. 1) while the rectus cervicis profundus muscle (RCp) extends to the root of the tongue, inserting on the medial basibranchial element (bb) of the hyobranchial apparatus and dorsally onto the intrinsic muscles and otoglossal cartilage of the tongue (og, Fig. 1). The geniohyoideus muscle (GH) acts to advance the hyoid apparatus and to elevate the floor of the buccal cavity. It extends superficially from the mental symphysis to a weak fascial connection to the bb and posteriorly to insert on the urohyal cartilage. The deeper genioglossus muscle (GG) also extends from the mental symphysis to insert on the bb, but a large portion of the fibers of this muscle extend above the hyobranchial apparatus to the glandular ventral surface of the tongue forming the bulk of the muscular part of the tongue pad. Contraction of the jaw-to-basibranchial portion advances the tongue toward the lower jaw while contraction of the tongue pad portion of the GG flips the tongue forward relative to the hyobranchial apparatus and lower jaw.

The last muscle, the subarcualis rectus one (SAR), is an intrinsic hyobranchial muscle that protracts the hyobranchial apparatus

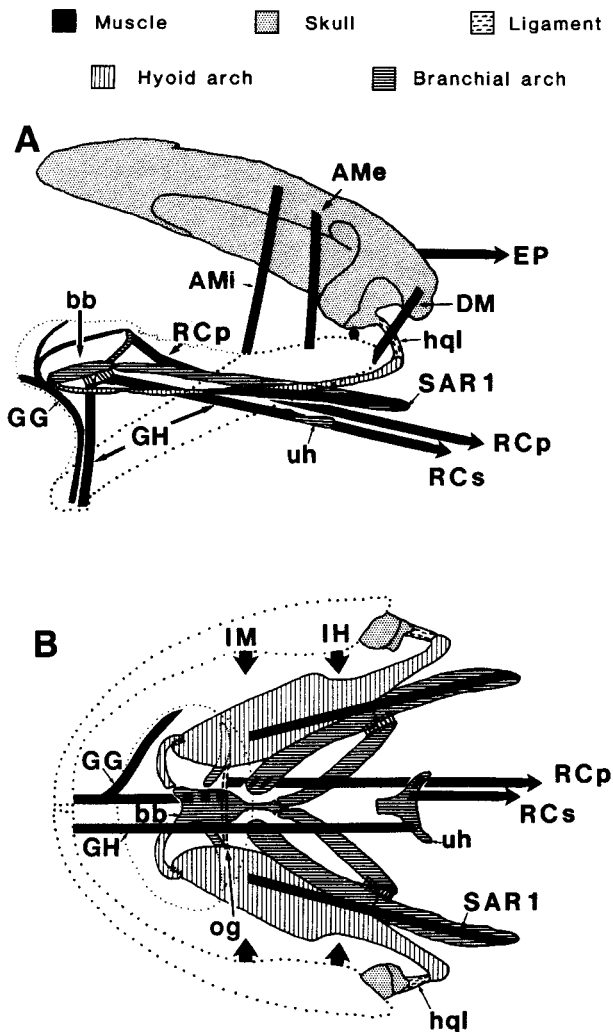


Fig. 1A–B. Schematic diagrams of the major morphological components of the tongue projection mechanism in *Ambystoma tigrinum* shown (A) in left lateral view during tongue projection with the hyobranchial apparatus elevated and protracted and the tongue not flipped (as in Fig. 2, 25 ms), and (B) at rest in ventral view (as in Fig. 2, 0 ms). Dotted lines indicate extent of lower jaw (large dots) and the tongue surface (small dots). Large arrows associated with the IM and IH muscles indicate that these muscles span the mandibular rami ventrally; they were not drawn to allow a clear view of the underlying muscles. Modified from Reilly and Lauder (1989b). *Abbreviations:* AMe adductor mandibulae externus; AMi adductor mandibulae internus muscle; bb basibranchial element; DM depressor mandibulae muscle; EP epaxial muscles; GG genio-glossus muscle; GH geniohyoideus muscle; hql, hyoquadrate ligament; IM, intermandibularis posterior muscle; IH interhyoideus muscle; og, otoglossal cartilage; RCp, rectus cervicis profundus muscle; RCs, rectus cervicis superficialis muscle; SAR1, subarcualis rectus one muscle; uh, urohyal element

and tongue by advancing the first branchial arch anteriorly relative to the hyoid arch which is attached to the skull by the hyoquadrate ligament (hql, Fig. 1). This critical muscle is the hypothesized primary protractor of the hyobranchial apparatus but can apparently only produce hyobranchial protraction with a complex synergistic interaction with the other hyobranchial muscles that contribute to the elevation and advancement of the hyobranchial apparatus during tongue projection (Reilly and Lauder 1989b).

Results

Tongue projection kinematics

Kinematic frames depicting tongue projection behavior in the tiger salamander with synchronized EMG activity patterns are illustrated in Fig. 2. Tongue projection involves a projection phase when the mouth opens rapidly as the tongue is projected to contact the prey item (Fig. 2, time 0–35 ms). The hyobranchial apparatus is protracted anterodorsally into the oral cavity as a platform from which the fleshy tongue pad flips forward to contact the prey. The end of the projection phase does not always correspond exactly to peak gape. Tongue projection is followed by a retraction phase when the tongue is retracted with the prey item stuck to it and the mouth closes rapidly upon the prey (Fig. 2 time 35–90 ms). Retraction and ventral rotation of the hyobranchial apparatus pulls the tongue and prey posteroventrally deep into the buccal cavity as the jaws close. There is a plateau in the gape as the mouth remains maximally opened during the time that the tongue is out of the mouth (time 25–55 ms). The time to prey contact averages 36.5 ms while the entire gape cycle from opening to closing averages 113 ms (Table 1).

Successful vs unsuccessful strikes

Based on the time to prey contact and gape cycle time, the kinematics of strikes resulting in prey capture are statistically indistinguishable from unsuccessful strikes (Table 1). Although there are significant differences among individuals in strike kinematics, the means for these two kinematic variables for all 4 salamanders are nearly identical. Likewise the duration of mouth opening (gape cycle time) encompassing both tongue projection and retraction does not vary with feeding success.

Analysis of variance in the EMG patterns for the cranial, hyobranchial and tongue muscles used in tongue projection revealed no difference in the motor patterns for successful vs. unsuccessful strikes (Tables 2 and 3). Of the seven variables used to characterize the EMG patterns in each of 11 muscles during strikes, only one variable (MAXAR) for one muscle (interhyoideus) was statistically different (Table 3). Examination of the means for this measure indicate that the maximum area per 5 ms bin for the IH was significantly greater in strikes resulting in prey capture. Of the remaining 76 comparisons only 3 approached significance (Tables 2 and 3) and the relatively large F-values for these 3 variables may indicate a significant effect that was not detected due to the low degrees of freedom. MANOVA tests on muscle activity patterns within each individual showed that the individuals differed in the extent of variation among behaviors. On average, variation among behaviors was low.

Significant differences among individuals were found in 32 out of 35 muscle activity pattern variables (Table 2) and individual salamanders thus showed significant dif-

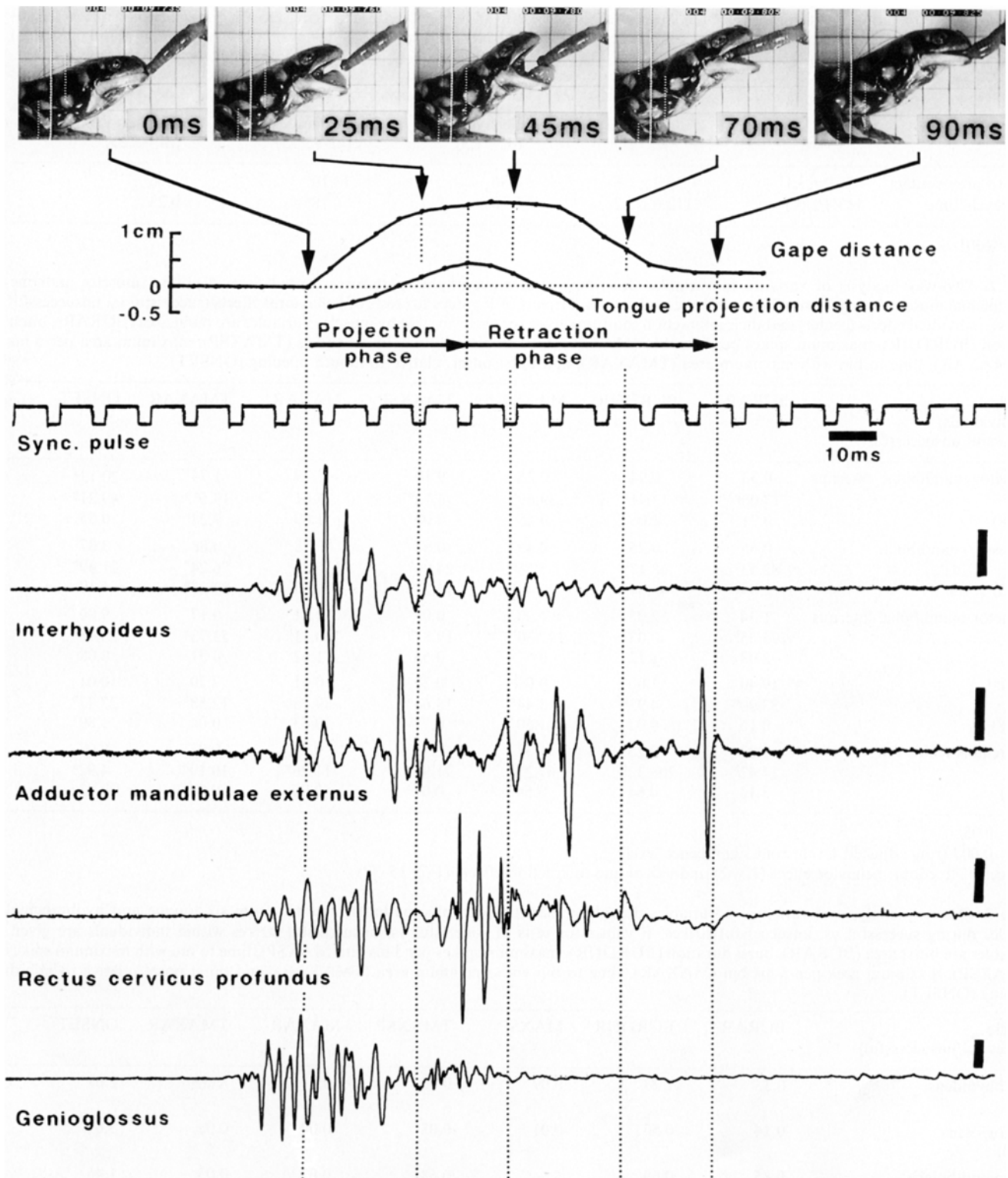


Fig. 2. Synchronized kinematic and EMG patterns during a successful strike. Video frames at the top depict tongue and head movements relative to digitized gape and tongue projection distances and digitized EMG bursts for 4 muscles from a single strike. 0 ms) The frame before the mouth begins to open. 25 ms) The mouth is opening rapidly and the hyobranchial apparatus is protracted into the oral cavity as the tongue begins to flip forward. 45 ms) Early tongue retraction 10 ms after peak tongue projection. 70 ms) Late tongue retraction as the mouth closes. 90 ms) Tongue retracted and

the mouth closes on prey. Scene and time codes are present in the upper right corner of each video frame. The time of peak tongue projection distance separates the tongue projection phase from the retraction phase. Note the typical plateau in gape distance from about 25 to 55 ms. The synchronization pulse was used to align kinematic (video) and EMG recordings and is visible on the left in the video frames as a series of white dots. EMG amplitude scales are indicated by the vertical scale bars representing 0.1 mV

Table 1. Analysis of variance of tongue projection kinematics for successful and unsuccessful strikes in four *A. tigrinum*. Pooled means (\pm SE) for gape cycle time and time to prey contact (peak projection) on the left. ANOVA results for behavioral (misses vs. captures) and individual effects presented as F values on the right

Variable	Successful strikes	Unsuccessful strikes	Analysis of Variance		
			Behavior (df = 1,3)	Individual (df = 3,25)	Interaction (df = 3,25)
Time to prey contact	36.9 \pm 3.1	36.2 \pm 1.8	0.96	13.19 ^a	1.66
Gape cycle time	113.4 \pm 6.3	112.6 \pm 7.2	0.70	6.18 ^a	0.23

^a $P < 0.001$ **Table 2.** Two-way analysis of variance in variables describing electromyographic patterns recorded from 4 cranial muscles and one hyobranchial muscle during successful vs. unsuccessful strikes. Triplets of F values for tests of behavioral effects (successful vs. unsuccessful strikes), individual effects (center) and their interaction (bottom) given for each variable by muscle. Variables are burst area (BURAR), burst duration (BURDUR), maximum spikes per 5 ms bin (MAXSP), time to bin with maximum spikes (TMAXSP), maximum area per 5 ms bin (MAXAR), time to bin with maximum area (TMAXAR), and burst onset relative to mouth opening (ONSET)

Muscle (# individuals) (successful/unsuccessful)	BURAR	BURDUR	MAXSP	TMAXSP	MAXAR	TMAXAR	ONSET
Adductor mandibulae externus (3)	0.33	0.94	0.25	9.10	3.79	1.74	20.13 ^a
(13/28)	17.00 ^b	13.41 ^b	39.69 ^b	6.73 ^b	27.61 ^b	19.51 ^b	49.21 ^b
	0.71	1.03	0.45	0.06	1.09	7.28 ^b	0.85
Depressor mandibulae (3)	0.55	0.25	0.49	0.67	0.78	0.88	3.87
(14/23)	82.53 ^b	68.17 ^b	5.56 ^a	24.00 ^b	135.26 ^b	76.24 ^b	21.49 ^b
	2.84	46.54 ^b	26.49 ^b	15.27 ^b	0.83	32.27 ^b	1.10
Adductor mandibulae internus (2)	1.34	2.95	1.00	0.07	0.21	0.17	9.00
(9/10)	295.55 ^b	40.03 ^b	127.30 ^b	19.87 ^b	230.11 ^b	53.73 ^b	23.18 ^b
	2.03	1.12	0.67	0.65	1.62	4.31	0.08
Epaxial (2)	19.40	1.00	0.01	0.35	0.01	7.70	0.01
(10/18)	33.00 ^b	4.93 ^a	13.44 ^b	18.66 ^b	89.25 ^b	12.58 ^b	27.77 ^b
	0.16	0.02	1.50	0.77	0.63	0.04	1.89
Subarcualis rectus one (2)	1.03	0.25	1.33	2.25	0.71	0.07	0.08
(9/18)	14.42 ^b	206.33 ^b	67.23 ^b	21.94 ^b	11.26 ^b	10.19 ^b	4.92 ^a
	3.13	0.64	0.54	0.01	2.90	0.06	2.83

^a $P < 0.05$ ^b $P < 0.007$ (row adjusted Bonferroni significance level)

Degrees of freedom: behavior effect (1,1–2), individual and interaction effects (1–2, 15–32)

Table 3. One-way analysis of variance in variables describing electromyographic patterns recorded from six tongue and hyobranchial muscles during successful vs. unsuccessful strikes. F values for tests of successful vs. unsuccessful strikes within individuals are given. Variables are burst area (BURAR), burst duration (BURDUR), maximum spikes per 5 ms bin (MAXSP), time to bin with maximum spikes (TMAXSP), maximum area per 5 ms bin (MAXAR), time to bin with maximum area (TMAXAR), and burst onset relative to mouth opening (ONSET)

Muscle (successful/unsuccessful)	BURAR	BURDUR	MAXSP	TMAXSP	MAXAR	TMAXAR	ONSET
Geniohyoideus (4/5)	0.35	1.23	0.09	0.00	0.37	5.66 ^a	2.07
Genioglossus (4/10)	0.14	0.50	0.01	0.03	0.04	0.08	3.61
Intermandibularis (5/7)	0.85	0.69	5.56 ^a	0.68	0.02	0.03	1.46
Interhyoideus (4/10)	2.29	3.38	0.41	0.64	16.16 ^b	0.00	3.65
Rectus cervicis superficialis (5/13)	0.12	1.35	0.59	0.17	0.06	0.48	0.64
Rectus cervicis profundus (4/10)	0.70	0.07	0.26	0.00	0.04	0.79	1.64

^a $P < 0.05$ ^b $P < 0.007$ (row adjusted Bonferroni significance level)

Degrees of freedom (1,7–13)

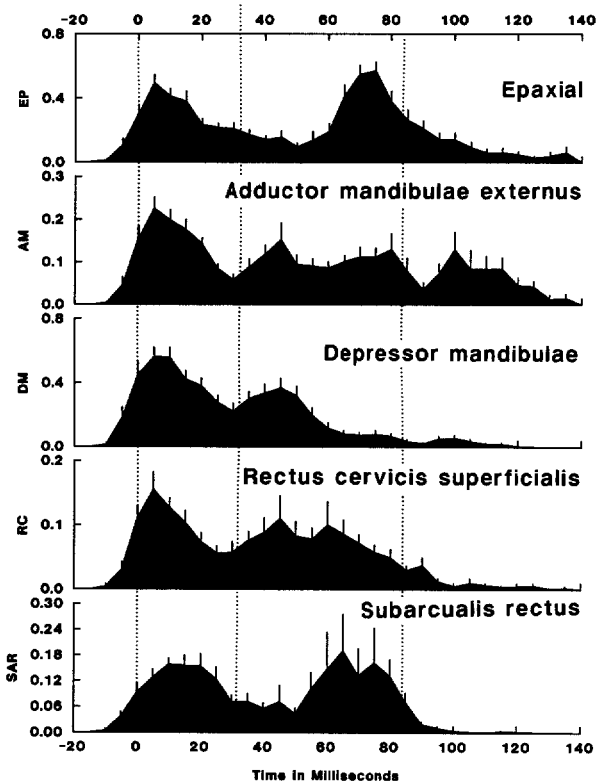


Fig. 3. Mean muscle activity patterns for 5 muscles during the strike for one individual. Levels of muscle activity plotted as mean rectified integrated EMG area (in units of $\text{mV} \cdot \text{ms} \pm \text{SE}$, $n = 18$ strikes) for each 5 ms bin corresponding to synchronized video frames. Kinematic events indicated by vertical lines for mouth opening (time 0), mean time to peak tongue projection (32 ms), and mean time to mouth closing (84 ms)

ferences from each other in muscle activity pattern despite a lack of difference between successful vs. unsuccessful strikes.

Muscle activity patterns

The activity patterns of the cranial muscles during the strike relative to the beginning of mouth opening (time 0), peak tongue projection at prey contact and mouth closing are presented in Figs. 3 and 4. The primary cranial muscles controlling jaw opening (EP, DM) become active prior to mouth opening (-10 to -5 ms) and peak in activity during mouth opening ($+5$ to 10 ms). These muscles remain moderately active until the gape begins to close ($+55$ ms) during the retraction phase. As the mouth closes the DM becomes silent while a second peak in activity occurs in the epaxial muscles.

The two jaw adductor muscles also become active prior to jaw opening but their patterns during mouth opening and the retraction phase differ. The AMe (Fig. 3) has a peak during the time that the mouth rapidly opens and then remains moderately active throughout the retraction phase until jaw closing. Activity in the AMi (Fig. 4) is low as the mouth is held open early in tongue retraction and then there is a large burst of activity when the jaws close.

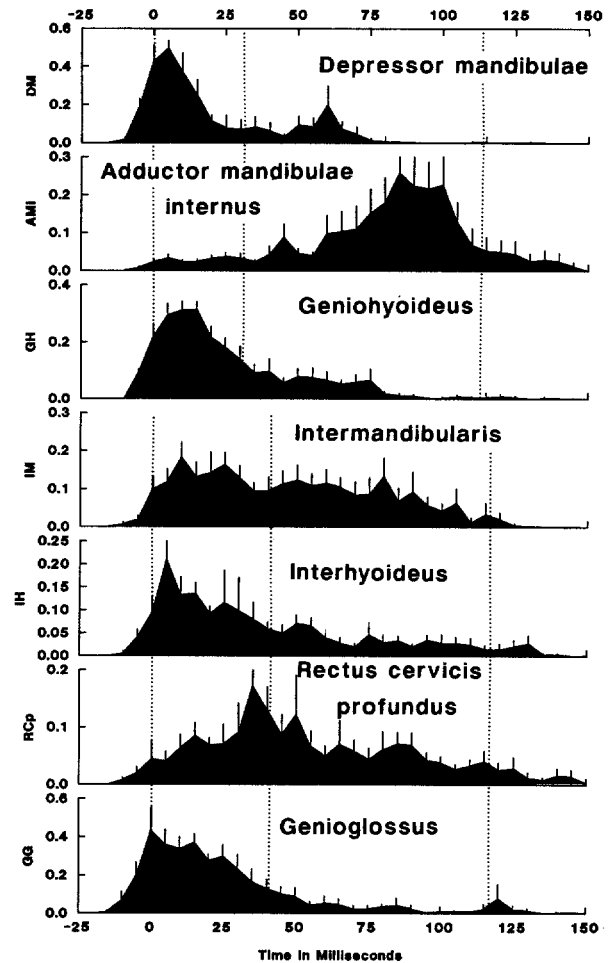


Fig. 4. Mean muscle activity patterns ($n = 9$ to 14) for 7 muscles during the strike summarized from 3 individuals. Levels of muscle activity plotted as mean rectified integrated EMG area (in units of $\text{mV} \cdot \text{ms} \pm \text{SE}$) for each 5 ms bin corresponding to synchronized video frames. Kinematic events for each individual indicated by vertical lines for mouth opening (time 0), mean time to peak tongue projection, and mean time to mouth closing. Upper 3 plots from one individual, plot for IM muscle from another individual, and bottom 3 plots from a third individual

Two of the buccal muscles, the GH and IM (Fig. 4: GH, IM), become active before the onset of mouth opening. Both muscles peak in activity early in mouth opening and then activity tapers off by the end of the retraction phase in the GH. The third buccal muscle, the IH, has a large peak in activity during mouth opening and becomes nearly silent when the mouth closes during the second half of the retraction phase.

Among the hyobranchial and tongue muscles there are two that are primarily responsible for tongue projection and a pair of retractor muscles. The primary hyobranchial protractor muscle, the SAR, and the major muscle to advance and flip the tongue, the GG, both peak in activity during tongue projection phase with an earlier peak in the GG (Fig. 4). The GG becomes silent early in the retraction phase but the SAR has an unexpected second peak in activity during the retraction phase (Fig. 3).

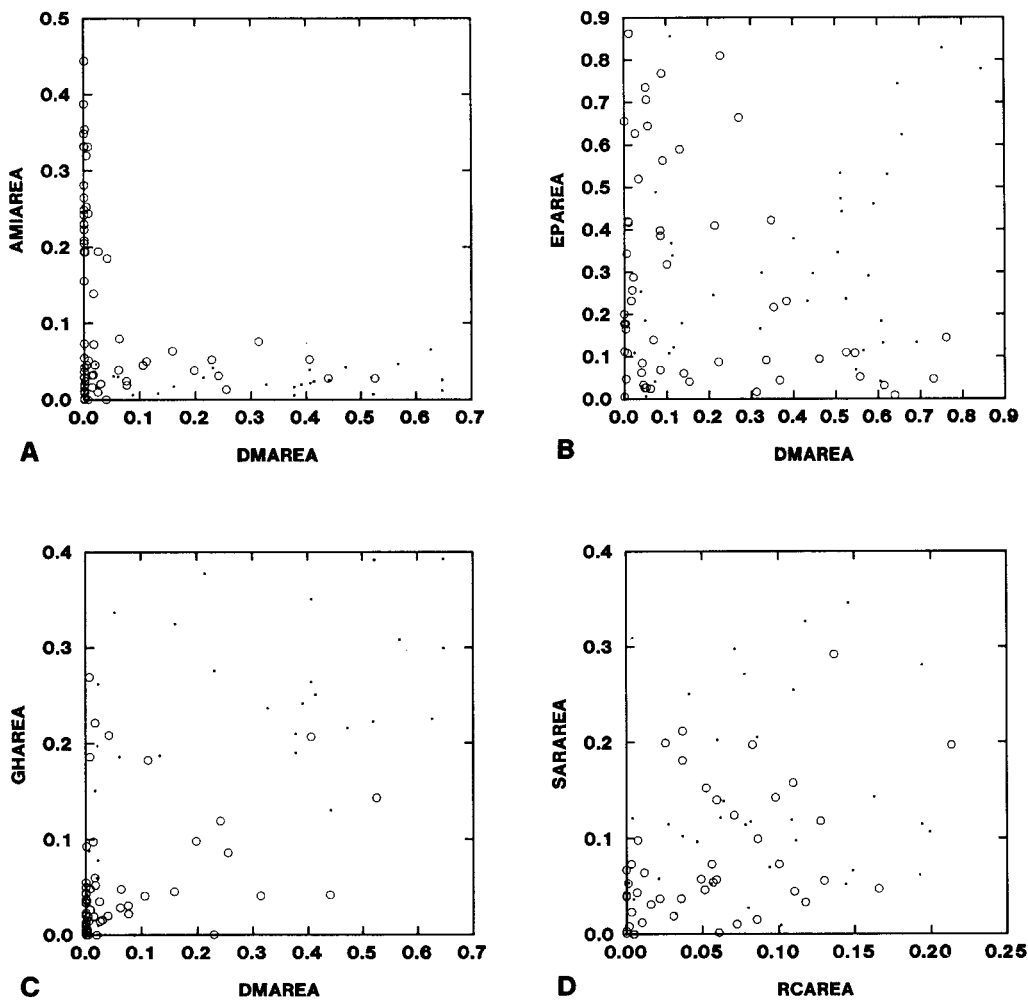


Fig. 5A–D. Patterns of synergistic muscle activity during the strike from one individual. Muscle activity plotted as rectified integrated EMG area for each 5 ms bin (in units of $mV \cdot ms$) during the projection (*dots*) and retraction (*circles*) phases of successful strikes ($n=4-5$) from single individuals. A–C, Activity of the jaw depressor

(DMAREA) plotted relative to (A) a jaw adductor (AMIAREA), (B) cranial elevator (EPAREA), and (C) the geniohyoideus muscle (GHAREA). D, Hyobranchial protractor (SAR muscle, SARAREA) vs. rectus cervicis superficialis (RCAREA)

The two hypaxial hyobranchial muscles exhibit somewhat different patterns of activity. The RCs (attached to the free floating urohyal of the hyobranchial apparatus, Fig. 1) has a sharp peak in activity during mouth opening early in the projection phase and then has a long burst of activity during the retraction phase which ends abruptly at mouth closing (Fig. 3). Activity in the RCp (which attaches to the bb and tongue itself), increases to a sharp peak at the time retraction begins and then remains moderately active until after mouth closing.

Patterns of muscle synergism

Representative patterns of bin-wise intensity of muscle activity (EMG area) for several muscle pairs during projection (dots) and retraction (circles) are presented in Fig. 5. When compared to the overall patterns of muscle activity (Figs. 3 and 4) these plots indicate the relative functional synergism occurring within muscle pairs

during the two phases of tongue projection. The jaw opening (DM) and closing (AMi) muscles exhibit an antagonistic (L-shaped) pattern of activity during the gape cycle. As expected, early in the projection phase (dots, Fig. 5A) the high levels of DM activity are associated with low levels of AMi activity. This pattern continues through the projection phase and into the retraction phase (circles along DM axis, Fig. 5A) as the mouth is held open during the plateau in gape distance. Once the mouth begins to close, high levels of activity in the AMi appear and the DM becomes silent (circles along AMi axis, Fig. 5A).

Comparison of EP and DM activity indicates the relative contribution of each muscle to jaw opening during the gape cycle (Fig. 5B). During the projection phase activity in the EP and DM is highly correlated as they both contribute to jaw opening (dots, Fig. 5B). Early in the retraction phase when the mouth is held open, high DM activity and low EP activity (circles along DM axis, Fig. 5B) indicate that the DM alone is main-

taining the maximal gape plateau during excursion of the tongue. As the jaws close, DM activity drops off and EP activity peaks.

Activity patterns in the DM and GH (which elevates and advances the hyobranchial apparatus) reveal similar patterns in these muscles during the gape cycle. Both have high levels of activity during the projection phase (dots, Fig. 5C) when the hyobranchial apparatus is protracted and the jaws open, and generally low levels during the retraction phase (circles). Moderate DM activity during gape plateau associated with low levels in the GH (circles along DM axis, Fig. 5C), is followed by low activity in both muscles as the mouth begins to close. Then activity in the GH peaks again at mouth closing as maximum retraction is reached and the hyobranchial apparatus is elevated again.

Interesting similarities were found in the patterns of activity of the presumed anatomical antagonists controlling hyobranchial protraction and retraction, the SAR and RCs. Both muscles have virtually the same patterns with moderate to high levels of activity during the projection phase (dots, Fig. 5D) and low to moderate activity during the retraction phase (circles).

Contractile properties

The AMi muscle had a mean twitch contraction time (TPT) of 61.3 ms, a mean time to 90% tetanic tension (TPo) of 89.3 ms, and a mean half relaxation time (RT1/2) of 70.3 ms. Maximal tetanic tension generated by this muscle was 94.02 kN/m².

The GH muscle had a mean TPT of 54.8 ms, a mean (TPo) of 220.0 ms, and a (RT1/2) of 182.6 ms. Maximal tetanic tension generated by this muscle was 48.7 kN/m².

Discussion

Feeding variability

The results of this study suggest that terrestrial prey capture during head-on strikes in the tiger salamander shows low variability. Under our experimental conditions the motor pattern and the associated kinematics do not vary with success or failure of the feeding strike. This does not preclude the fact that different individuals may have significantly different motor patterns or that strikes in different directions or those that do not hit the prey may be different. We would expect that strikes directed toward prey in different locations such as on the ground or to the left may show differences in EMG patterns. Virtually by definition some kinematic differences would be found since the head must be moved toward the prey at each location. However, statistical analysis of the kinematics of the gape and tongue cycles in unsuccessful vs. successful strikes showed significant variation among individuals but no significant difference in the kinematics within each individual when prey are presented in front of the salamander. Thus, movements of the jaws and tongue are not modulated during tongue

projection in response to sensory feedback indicating that the prey is not being pulled back into the mouth. In addition, the lack of prey attachment to the tongue does not modify the duration of tongue retraction. There appears to be no effect of the prey on the motor pattern of cranial muscles used during retraction and thus no evidence of sensory modulation of this phase of feeding. In addition we point out that the method of prey presentation, while it might have reduced the range of feeding variability, did not mask the detection of considerable inter-individual variation in feeding motor patterns.

Analysis of EMG patterns of muscles used during feeding produces further evidence for a lack of within individual variation in feeding behavior. Of 77 measures of muscle activity patterns in 11 muscles used during feeding (Tables 2 and 3) only one measure for one muscle (IH MAXAR, Table 3) was significantly different in successful vs. unsuccessful strikes, and MANOVA results further indicate the lack of difference in EMG patterns between these two types of strikes. There is no indication of modulation of the motor pattern driving feeding behavior to adjust for unsuccessful retraction of the prey into the mouth. Failure of the strike appears to be related to loss of prey adhesion during tongue retraction and not to a shortened tongue projection distance or to missing of the prey entirely. During unsuccessful strikes the prey was always hit by the tongue.

The kinematic and EMG stereotypy demonstrated here for terrestrial feeding adds to data from other quantitative studies demonstrating the stereotyped nature of rapid feeding behaviors in salamanders. Larval salamanders do not modulate motor patterns driving aquatic suction feeding in response to more elusive prey types (Reilly and Lauder 1989a). Despite morphological changes at metamorphosis, the motor patterns of 5 cranial muscles used in aquatic suction feeding do not change significantly at metamorphosis (Lauder and Shaffer 1988). Finally, the kinematics of intraoral transport of prey after capture by tongue projection do not vary significantly with prey type or consistency (Reilly and Lauder, in press).

Muscle function during feeding

The cycle of mouth opening that encompasses tongue projection is controlled largely by the jaw depressor (DM), the jaw adductors (AMi and AMe), and the epaxial muscles (EP). A key finding is that these muscles become activated nearly synchronously (within 5 ms of each other on average) and that even anatomically antagonistic muscles have synchronous onset times. This result is comparable to that obtained in a study of aquatic feeding in salamanders (Lauder and Shaffer 1985). However, it must be emphasized that the ability to partition patterns of muscle activity into 5 ms bins each of which is the average of many feedings shows clearly that each muscle has a characteristic activity profile that is not revealed by simple indications of onset and offset times. For example the jaw adductor muscles, while possessing

similar onset times, show different activity profiles during the strike. The relatively low variation in these activity profiles suggests that each muscle has a preprogrammed characteristic activity pattern with low variation within any set of feedings by one individual.

The gape profile exhibits a plateau phase during maximal tongue projection which may be maintained by the second peak of activity in the DM because the EP is quiet at this time. During mouth closing the DM becomes silent while the EP exhibits a second peak in activity. Because the head depresses during closing (Reilly and Lauder 1989b), mouth closing must involve a lengthening contraction in the EP that may be opposing the retraction of the hyobranchial apparatus.

The two adductor mandibulae muscles appear to have complex roles in effecting mouth closing. Both muscles have peaks in activity during mouth opening, then maintain moderate activity into the retraction phase. The AMe maintains this level of activity until mouth closing while the AMi quickly becomes silent at the end of the gape plateau and then has a large burst of activity in the second half of the retraction phase when the mouth closes.

An additional finding from the analysis of synchronous kinematic and electromyographic data is that most of the muscles involved in the strike undergo significant lengthening contractions at some point during the prey capture event. For example, as the mouth begins to open, activity is found in the jaw closing muscles (Figs. 1, 2, 3) indicating that both the AMe and AMi are being stretched as their motor units are activated by the nervous system. The EMG data suggest that the jaw depressor and adductor muscles are being stimulated at tetanic frequencies during prey capture because of the relatively high frequency components present in the EMG data (Jayne et al. 1990b) and the large number of counted spikes within each burst. Lengthening contractions may act to greatly decrease the time to peak force development in the jaw muscles, as the twitch and tetanic times measured under unstretched conditions are too slow to explain the rapidity of bone movements during the actual strike. As discussed by Hill (1970), a muscle that is electrically activated while being lengthened may generate up to 15% more force in one-fifth the time of the same muscle contracting isotonicly. The lengthening contractions of jaw muscles during prey capture by salamanders may help explain how the feeding behavior may be so rapid (jaw closing in 55 ms) when the time to 90% peak isometric tetanic tensions may range from 90 to 220 ms. However, these data are only suggestive and do not address several key questions concerning physiological function of the head muscles during feeding. For example, there are no data on rates of muscle shortening and on the lengths at which each feeding muscle shows a maximal rate of shortening. In addition, passive elastic properties of the jaw muscles may vary and contribute to differential rates of shortening in jaw muscles.

Comparisons to other amphibians

Limited data on other amphibian taxa are currently available for comparison with these data on *Ambystoma*

tigrinum. However, the data that are available for one salamander and two toads show remarkably similar patterns in the gape cycle and EMG patterns for several muscles. Our finding that the SAR1 and RCs have nearly synchronous onsets and nearly identical motor patterns during tongue projection is similar to data reported for *Bolitoglossa occidentalis* during ballistic tongue projection. Thexton et al. (1977) found that the onset of EMG activity in the SAR1 and rectus cervicis tended to be synchronous and patterns for these two muscles in sample EMG traces look similar to our data (Fig. 3, Thexton et al. 1977). The gape cycle and the activity patterns of several muscles of *Ambystoma tigrinum* also show some similarities to patterns reported in toads. Matsushima et al. (1985) illustrate several gape profiles for *Bufo japonicus* that are similar to the gape cycle pattern during tongue projection in the tiger salamander; the mouth opens rapidly, plateaus during tongue projection, and then gradually closes during retraction. Quantitative EMG patterns during tongue projection in the DM, GH, IM, RCp, and GG muscles of *Bufo marinus* (Figs. 7 and 8 in Gans and Gorniak 1982) are also similar in several respects to our data for the tiger salamander. Four jaw muscles in *Bufo* have synchronous onsets just before the mouth begins to open. The onset of activity of the toad DM occurs about 50 ms before mouth opening (which is earlier than in *Ambystoma*) but the DM does show a double burst pattern which is very similar to DM activity in *Ambystoma*. These comparative data suggest the hypothesis that the double-burst pattern in the DM may be related to maintaining a gape plateau while the tongue is projected and retracted in both frogs and salamanders. In both the toad and the salamander the GH and IM have a large burst of activity during tongue projection and then go silent during retraction while the GG has a large peak in activity when the tongue is flipped during projection. The toad tongue retractor (RC) and the tiger salamander RCp both increase in activity during tongue projection to reach a peak during tongue retraction.

Mechanistic basis of tongue projection

Tongue projection is the salient feature of terrestrial prey capture in salamanders (Duellman and Trueb 1986; Lauder and Reilly (in press); Lombard and Wake 1976, 1977; Regal 1966; Reilly and Lauder 1989b; Severtsov 1972; Wake 1982; Wake et al. 1983). Reilly and Lauder (1989b) presented a kinetic model for tongue projection in *Ambystoma tigrinum* based on kinematics and the observed lines of action of individual muscle pairs and combinations of muscles (but not on recordings of muscle activity patterns). This model involves the coordinated protraction of the hyobranchial apparatus and simultaneous flipping of the tongue pad. They proposed that hyobranchial protraction results from the combined effects of several muscles bearing on the bb or root of the tongue that elevate and advance (protract) the hyobranchial apparatus into the oral cavity (Fig. 6A). The net anterior protraction of the hyobranchial apparatus (and tongue) is hypothesized to result from the combination of 3 force vectors; a lift vector, a SAR vector, and a

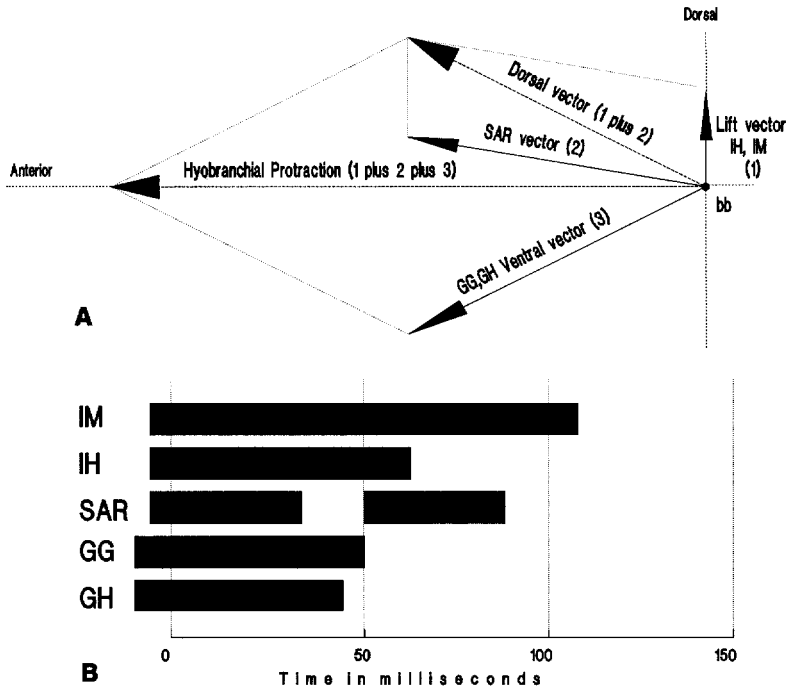


Fig. 6A. Schematic vector diagram of muscular forces involved in protraction of the hyobranchial apparatus during tongue projection (modified) from Reilly and Lauder 1989b). The dorsal vector (the resultant of vectors 1 and 2) is the force on the basibranchial (bb) produced by the SAR muscle (vector 2) once the hyobranchial apparatus has been elevated by the combined vertical forces of the IH and IM muscles (vector 1). The ventral vector (GG, GH) is the force on the bb produced primarily by the GG once the tongue has been elevated and the lower jaw is depressed. The resultant of these two vectors on the bb causes the anterior protraction of the hyobranchial apparatus (= tongue platform) from which simultaneous flipping of the tongue pad by the GG and other intrinsic tongue muscles projects the tongue out of the mouth. **B.** Schematic diagram of the pattern of electrical activity for muscles in the vector diagram above based on data in this paper. Black bars indicate roughly time during which the 5 muscles involved in tongue projection are active. Bars for the SAR muscle reflect the two major peaks of activity in Fig. 3

ventral force vector. The EMG analyses of cranial and hyobranchial muscles during tongue projection (Figs. 2 and 3) provide the basis for comparing muscle activity patterns to the major vectorial components of the proposed model (Fig. 6). The mechanistic basis of tongue projection will be discussed in terms of these vectors.

The lift force vector. Each of the 3 muscles proposed to elevate the hyobranchial apparatus during projection (Fig. 4: GH, IM, IH) exhibits a peak in activity early in the projection phase and then decreases in activity during the retraction phase. The first of these muscles to become active during feeding are the GH and IH which become active 15 to 20 ms before the mouth begins to open and reach high levels of activity by the beginning of mouth opening.

The third muscle affecting buccal elevation, the interhyoideus (IH), quickly peaks in activity during mouth opening and then grows silent around the end of the gape cycle. The net effect of these 3 ventral buccal muscles is to elevate the hyobranchial apparatus so that it can slide anteriorly over the lower jaw during tongue projection (Fig. 6A, lift vector).

The SAR vector. Contraction of the SAR advances the first branchial arch and the tongue forward and dorsally relative to the hyoid arch (Fig. 1). During the strike the SAR peaks in activity in the middle of the projection phase and then activity falls off during peak projection (Fig. 3). The combination of the lift force (Fig. 6, lift vector) of the buccal muscles with the anterodorsal force of the SAR (Fig. 6, SAR vector), produces a strong dorsal vector that pushes the hyobranchial apparatus anterodorsally into the oral cavity (Fig. 6, dorsal vector).

The ventral vector. A net anterior movement of the tongue (hyobranchial protraction) is attained by the

addition of a ventral force vector to the resultant dorsal vector (Fig. 6). This is accomplished predominantly by the action of the GG and GH muscles attaching anteriorly to the lower jaw. The large GG contracting between the lower jaw symphysis and tongue mass (Fig. 6, ventral vector) has a large, rapidly peaking and sustained burst of activity during the tongue projection phase and then grows silent.

Tongue flipping. Underlying the complete projection of the tongue is the coordinated flipping of the tongue pad from the protracted platform formed by the hyobranchial apparatus. Flipping of the tongue pad after hyobranchial protraction can be seen in Fig. 2 by comparing the shape of the tongue at times 25 and 45 ms. Activity of the GG rapidly peaks and is sustained as the tongue pad flips during the tongue projection phase and then activity quickly falls off at peak protraction (Fig. 4).

In addition, hyobranchial protraction imparts considerable force and momentum on the tongue pad, bulging it anteriorly and protruding it to the plane of the gape (Fig. 2, 25 ms). Therefore, it is likely that contraction of the bulk of the GG, that makes up the tongue mass, flips the tongue pad forward at the time when maximum momentum has been imparted on the tongue pad by hyobranchial protraction (Fig. 6, tongue protraction vector). Flipping of the tongue pad occurs simultaneously with hyobranchial protraction, resulting in complete projection of the tongue with the glandular surface of the tongue facing anteroventrally (Fig. 2: 45 ms).

Tongue retraction. The primary muscle directly involved with tongue retraction is the RCp. It extends from the hypaxials to the tongue pad, og, and bb and its contraction can retract both the flipped portion of the tongue pad and the hyobranchial apparatus. Activity in the RCp builds to a peak just before maximum tongue projection

and continues through the retraction phase, and thus is undergoing lengthening contraction during tongue projection. The other anterior extension of the hypaxial muscles, the RCs, inserts on the urohyal bone which is linked to the bb and lower jaw by the GH muscle. Thus, the function of the RCs depends on the position of the bb and the state of contraction of the GH.

In the kinetic model of Reilly and Lauder (1989b), the GH was implicated in pulling the hyobranchial apparatus anteroventrally through its weak connection to the bb. This action is dependent on the forward displacement of the urohyal and relaxation of the RCs to allow contraction of the anterior part of the GH to move the tongue anteroventrally through its attachment to the bb. Equally important is the insertion of the GH on the symphysis, which rapidly moves ventrally with lower jaw depression during protraction (Fig. 2). Depending on the position of the symphysis, the GH could elevate the hyobranchial apparatus, then pull the tongue anteriorly and, finally, it could pull the bb anteroventrally along with the GG. The rapid depression of the lower jaw, which occurs only early during protraction, allows the tongue to be pulled ventrally and is the key movement controlling the direction of the ventral vector (Reilly and Lauder 1989b). Due to the strong attachment of the GG to the lower jaw and bb, and the EMG patterns during the strike (Figs. 2, 4) we propose that the GG is the major muscle producing the ventral vector and that it acts in concert with the GH.

We further propose that the GH-urohyal-RCs linkage may function primarily as a buccal elevator and only secondarily in retraction. The activity pattern of the GH is nearly identical to that of the other major buccal elevator, the IH. Both have a burst of activity before and early in the projection phase as the buccal area is elevated, and then are quiet until the end of the retraction phase when the buccal area is again elevated after maximum retraction. The RCs also has a peak in activity early in the protraction phase that may contribute to buccal elevation. During the retraction phase when the GH is relaxing, the RCs has a secondary peak in activity that may contribute to urohyal retraction.

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