

# Prey Transport in the Tiger Salamander: Quantitative Electromyography and Muscle Function in Tetrapods

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**ABSTRACT** A quantitative analysis of the muscle activity patterns (motor patterns) used by tiger salamanders (*Ambystoma tigrinum*) during terrestrial feeding is presented to provide comparative data on motor output during prey transport in amphibians, compare prey transport motor patterns to those used during initial prey capture, and test the generality of previously proposed models of the feeding cycle in tetrapods.

Simultaneous electromyographic and kinematic recordings during prey transport reveal four phases in the prey transport cycle. The Preparatory phase precedes prey transport with activity found mainly in muscles of the buccal floor (genioglossus, geniohyoideus, interhyoideus, and intermandibularis), but with all muscles silent at the end of this phase. Prey transport occurs during the Fast Opening and Closing phases. The Fast Opening phase begins with near simultaneous onset of activity in all jaw and hyoid muscles, including anatomical antagonists such as the depressor mandibulae and adductor mandibulae. The subarcualis rectus one muscle is active during the Fast Opening and Closing phases of transport despite the lack of accompanying tongue projection and may function to stabilize the hyobranchial apparatus. The motor pattern of terrestrial prey transport differs considerably from that of initial prey capture, but appears to be similar to the motor pattern used during aquatic prey capture and hydraulic prey transport. We hypothesize that post-metamorphic tiger salamanders accomplish terrestrial prey transport by retaining the larval motor pattern employed during suction feeding. The motor pattern and kinematics of prey transport in *Ambystoma tigrinum* differ in nearly all aspects from previous models of the generalized tetrapod feeding cycle.

The ability to feed on land is one of the key features of tetrapod vertebrates. Paleontological evidence indicates that the transition from water to land in vertebrate evolution involved many modifications to skull bones and architecture (Carroll, '88; Jarvik, '80; Romer, '45; Schmalhausen, '68), and comparative anatomical data provide evidence that the ability to process and swallow prey captured on land is associated with many modifications in the jaw and hyoid musculature and soft tissues (Bramble and Wake, '85; Carroll and Holmes, '80; Edgeworth, '35; Lauder, '85).

In contrast to aquatic vertebrate life where the process of prey capture involves use of water currents (Bemis, '87; Bemis and Lauder, '86; Lauder, '85, Lauder and Shaffer, '86), a critical feature of the feeding mechanism in tetrapods is the use of the tongue to transport prey from the mouth to the esophagus. Tongue-based intraoral prey transport is used in virtually all clades of tetrapods and contrasts with the hydraulic mechanism used by major clades of fishes (Lauder, '80a,b, '85;

Lauder and Shaffer, '85; Liem, '70; Reilly and Lauder, '90b).

To date, virtually all studies of the mechanics of terrestrial prey transport have been conducted on amniotes, and the majority of comparative data has been obtained from lizards and mammals (e.g., Bels, '89; Byrd et al., '78; Cleuren et al., '89; Crompton et al., '77; Crompton, '89; Franks et al., '84; Gans et al., '78; Gorniak and Gans, '80, '82; Greet and De Vree, '84; Herring, '85; Hiiemae and Crompton, '85; Hiiemae et al., '79; Hylander et al., '87; Schwenk and Throckmorton, '89; Smith, '82, '84, '86, '88; Throckmorton, '80; Weijs,

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Abbreviations used: AMe, adductor mandibulae externus muscle; AMi, adductor mandibulae internus muscle; bb, basibranchial element; C, Closing phase; DM, depressor mandibulae muscle; EP, epaxial muscle; FO, Fast Opening phase; GG, genioglossus muscle; GH, geniohyoideus muscle; hql, hyoquadrate ligament; IH, interhyoideus muscle; IM, intermandibularis muscle; ms, milliseconds; mv, millivolts; og, otoglossal cartilage; P, Preparatory phase; R, Recovery phase; RCp, rectus cervicis profundus muscle; RCs, rectus cervicis superficialis muscle; SAR, subarcualis rectus 1 muscle; SE, standard error; SO, Slow Opening phase; uh, urohyal.

'75; Weijs and Dantuma, '81). Patterns of muscle activity (motor patterns) and jaw movements measured during these studies have provided the basis for recent analyses of the evolution of feeding mechanisms in tetrapods (Bramble and Wake, '85; Schwenk and Throckmorton, '89).

Despite the range of comparative data now available on terrestrial feeding in amniotes, comparative data from anamniote tetrapods are lacking and no paper has quantitatively compared the motor patterns used during initial prey capture (the strike) with those used during prey transport. Data from anamniotes are critical for comparisons to the process of prey manipulation in fishes, especially since many amphibians will capture and process prey both on land and in the water, and for examining the generality of models for tetrapods based on amniote data. If current models of tetrapod prey transport and intraoral manipulation do not apply to anamniote tetrapods, then the ability of these models to explain transitions from aquatic to terrestrial feeding systems will be severely limited.

The goals of this paper are to provide a quantitative description of patterns of cranial muscle activity (motor patterns) during prey transport in the tiger salamander, *Ambystoma tigrinum*, to contrast the motor patterns used during the strike with those used during prey transport, and to use these data to examine the generality of previous models of tetrapod intraoral prey transport based on data from amniotes.

## MATERIALS AND METHODS

Synchronized records of kinematic and electromyographic (EMG) patterns during feeding were obtained from four transformed adult *Ambystoma tigrinum mavortium* (snout-vent lengths 110–125 mm) collected from near Limon, Lincoln County, Colorado. Animals were trained to feed under lights and filmed at 200 fields per second using a NAC HSV-400 high-speed video system with two synchronized strobes. A 100 Hz pulse-coded signal was used to synchronize the electromyographical recordings with the video fields during filming. Tiger salamanders were filmed in lateral view in 8 liter glass aquaria with a background grid of 1 cm squares. The animals were offered 3–6 cm long earthworm pieces (*Lumbricus*) presented in front of the jaws with a pair of forceps. After the prey had been captured, the worms were moved to the pharynx by a series of transport cycles. A total of 35 transport cycles (7–10 from each animal) were used in the analysis. Video sequences

for each set of transport cycles were analyzed field by field using a PC-based image analysis system and custom digitizing software to quantify transport kinematics and to synchronize jaw bone movements with electromyographical patterns. For each cycle, field (time) zero was defined as the field preceding the first field in which the mouth began to open before the start of prey transport.

### Electromyography

Motor patterns in eleven major head and hyobranchial muscles used in feeding were quantified by recording electrical activity extracellularly. Electromyographical (EMG) recordings were made from groups of five muscles from each of the four individuals by implanting bipolar stainless steel electrodes (0.051 mm diameter) into each muscle as in previous research (Jayne et al., '90; Reilly and Lauder, '89a). Electrode implantations were done while the animals were anesthetized in a solution of tricaine methane sulphate (1 g/liter) for 15 minutes. The bared metal tips of each electrode were about 0.5 mm long, and the insulated portions were glued together proximal to the bared ends with a cyanoacrylate adhesive to prevent tip displacement as in previous research (Jayne, '88). Each electrode pair was implanted through the skin directly into the belly of each muscle, and was glued to the skin to prevent movement of the electrode and to minimize movement artifacts during feeding. The five pairs of electrodes were then glued together and attached to the back using glue and tissue tape. A ground electrode and a thermocouple (for body temperature measurement) were implanted subcutaneously into the back. Animals recovered from the anaesthesia within one hour and fed well immediately thereafter. All measurements were conducted within 1/2 to 2 hours postanaesthesia and body temperatures ranged from 20–22°C. After each experiment the animals were sacrificed by overdose of anaesthetic and preserved in 10% formalin, and electrode position was subsequently confirmed by dissection.

EMG signals were amplified 10,000 times using Grass AC P511J preamplifiers with a 60 Hz notch filter and a bandpass of 100 to 3000 Hz. Data were recorded on a Bell and Howell 4020A multichannel FM tape recorder with a synchronization pulse to correlate EMG signals with the video fields. The analog signals from each transport cycle 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 six channels was 8084 Hz with 12 bit resolution.

Because many of the head muscles studied with electromyography are located within several centimeters of each other, the possibility for cross-talk exists in which the signal from one muscle is picked up by electrodes located in an adjacent muscle. We examined the EMG traces for evidence of cross-correlation following the suggestions of Loeb and Gans ('86). We found no evidence that any muscle signals were contaminating adjacent muscle recordings. The spike patterns of nearby muscles were not similar and averaging of muscle activity patterns revealed distinct profiles (Figs. 2, 3, 5-9). Muscles that during one behavior might show some similarity in spike pattern showed a very different pattern of activity later during a second (equally rapid) behavior. For example, the activity profiles of the epaxial and adductor mandibulae externus muscles are similar in Figure 5, but examination of Figure 2 shows extensive subsequent activity in the adductor mandibulae externus not accompanied by signals in the epaxial muscles. Thus, we do not believe that cross-talk influenced the activity patterns reported below.

The digital data file for each feeding was analyzed using a Tektronix 4107 graphics terminal and custom software that counted EMG spikes (using the algorithm of Beach et al., '82; Jayne et al., '90) and calculated other measures of activity (described below) for each 5 ms bin of the signal from each muscle. Peaks in EMG voltage were counted as spikes only when they exceeded a threshold voltage of 12  $\mu$ V in the unamplified signal. Files containing the bin-wise measures of EMG activity for each feeding were aligned to the onset of mouth opening during transport (video time zero) for the feeding using the synchronization pulse.

#### *Statistics and data analysis*

To test for differences between strike and transport motor patterns, bin-wise EMG area values, synchronized to mouth opening (video time zero) for strikes and transports were averaged for each 5 ms bin to produce profiles of EMG activity for each muscle during feeding. Because a priori statistical analysis (Reilly and Lauder, '90a) indicated no kinematic or EMG differences in captures vs. misses at the strike (but did show significant variation among individual animals), we pooled all strikes (captures and misses) per individual to construct EMG area strike profiles

for each muscle. Therefore, each illustration of muscle activity profiles (see Figs. 5 to 7) is based on the average of 9 to 18 synchronized strikes per individual.

To compare motor patterns for transport cycles and strikes statistically, seven variables that described the timing, amplitudes, and numbers of EMG spikes were measured from each muscle. These variables are: 1) BURAR, the area of the muscle burst, in millivolts\*ms; 2) BURDUR, the burst duration, in ms; 3) MAXSP, the maximum number of spikes per 5 ms bin within the burst; 4) TMAXSP, the time, in ms, to the bin with the maximum number of spikes; 5) MAXAR, the maximum area per 5 ms bin within the burst, in millivolts\* ms; 6) TMAXAR, the time, in ms, to the bin with the maximum area; 7) ONSET, the onset of EMG activity in the muscle relative to the beginning of mouth opening (video time zero).

Two-way analysis of variance (ANOVA) was used to compare motor patterns for those muscles which were recorded in more than one individual (see Table 1). The experimental design used individuals as a random effect and feeding behavior (strike or transport) as a fixed effect. Because testing the fixed effect involves deriving the F-value from the ratio of the fixed effect mean square to the interaction mean square (Sokal and Rohlf, '81), the degrees of freedom available for determining significance levels were small (1, 1 to 2). This means that we may fail to detect a significant difference between feeding behaviors when one exists, and we caution that our conclusions in this regard are conservative.

One-way ANOVA was used to compare motor patterns for those muscles that were recorded only in single individuals (see Table 2). Feeding behavior (strike vs. transport) was used as the main effect. Because multiple comparisons (7) were made for each muscle we used a Bonferroni adjusted significance level of 0.007 ( $P = 0.05/7$ ) for both the one- and two-way ANOVAS.

#### *Myology*

Detailed anatomical descriptions of the salamander muscles chosen for analysis are provided elsewhere (Druner, '02, '04; Lauder and Shaffer, '88; Reilly and Lauder, '88, '89b). The eleven muscles include all the major head muscles involved in jaw movements during prey transport and the initial strike. In order to facilitate interpretation of the data on motor patterns, a brief summary of the major actions of the muscles is provided here with a schematic diagram to indicate generally

TABLE 1. Two-way analysis of variance for variables describing electromyographic patterns recorded from four cranial muscles and one hyoid muscle during strikes and transports in *Ambystoma tigrinum*<sup>1</sup>

Muscle (# individuals) (strikes/transport)	BURAR	BURDUR	MAXSP	TMAXSP	MAXAR	TMAXAR	ONSET
Adductor mandibulae externus (3)	1.83	25.69*	0.10	0.66	3.35	0.89	0.66
(38/28)	24.27**	10.24**	110.79**	1.06	56.34**	11.15**	28.63**
Depressor mandibulae (3)	1.13	1.14	3.21*	8.00**	6.41**	8.03**	8.25**
(34/24)	1.42	15.78	0.63	4.76	0.001	0.27	1.21
Adductor mandibulae internus (2)	69.82**	23.02**	13.30**	19.87**	174.34**	38.09**	37.38**
(19/14)	17.23**	2.85	3.49*	0.81	5.13*	0.51	23.03**
Expaxial (2)	0.90	0.59	1.11	0.48	156.38	0.05	2.21
(25/17)	185.35**	9.77**	12.67**	7.04*	386.69**	5.84*	2.26
Subarcualis rectus one (2)	3.65	15.84**	68.51**	25.60**	0.03	44.64**	24.70**
(24/17)	4.65	113.30	0.55	3.61	0.02	0.86	6.59
	41.86**	16.19**	15.29**	30.95**	44.56**	12.38**	37.34**
	7.49*	0.79	0.88	2.09	8.90**	4.76*	0.87
	0.93	0.007	0.162	0.05	1.37	0.001	3.66
	11.88**	100.61**	38.27**	14.22**	10.92**	2.30	0.65
	1.86	96.27**	0.000	7.40*	1.07	12.47**	3.66

<sup>1</sup>Triplets of F values for tests of behavioral effects (strikes vs. transports), individual effects (center), and their interaction (bottom) are 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). Degrees of freedom: behavior effect (1, 1-2), individual and interaction effects (1-2, 29-60).

\* $P < 0.05$ .

\*\* $P < 0.007$  (row adjusted Bonferroni significance level, 0.05/7).

TABLE 2. One-way analysis of variance for variables describing electromyographic patterns recorded from six tongue and hyoid muscles during strikes and transports in *Ambystoma tigrinum*<sup>1</sup>

Muscle (strikes/transport)	BURAR	BURDUR	MAXSP	TMAXSP	MAXAR	TMAXAR	ONSET
Geniohyoideus (9/8)	3.92	129.02**	13.04**	12.86**	10.40**	4.32	10.81**
Genioglossus (13/10)	153.81**	52.49**	8.32*	0.005	43.81**	5.52*	30.95**
Intermandibularis (10/7)	4.40	15.91**	11.74**	0.48	10.97**	6.75*	2.46
Interhyoideus (14/10)	18.90**	34.11**	0.000	3.53	2.86	2.13	7.08*
Rectus cervicis superficialis (15/10)	4.88*	12.99**	12.60**	5.64*	0.55	2.90	12.93**
Rectus cervicis profundus (14/10)	0.50	19.02**	0.03	5.52*	6.47*	7.06*	3.30

<sup>1</sup>F values for tests of strikes vs. transports 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, and burst onset relative to mouth opening (ONSET). Degrees of freedom (1, 15-23).

\* $P < 0.05$ .

\*\* $P < 0.007$  (row adjusted Bonferroni significance level, 0.05/7).

the lines of muscle action. Interpretations of muscle functions are based on muscle stimulations (Druner, '02, '04; Reilly and Lauder, '89b), functional analyses of homologous muscles in larval tiger salamanders (Lauder and Shaffer, '85, '88), and anatomical data such as muscle lines of action.

Mouth opening and closing is mediated by four principal pairs of cranial muscles (Fig. 1). The

lower jaw is rotated around the jaw joint by the depressor mandibulae muscle (DM), which originates on the cranium and inserts on the mandible just posterior to the jaw articulation. The mouth is closed by two large adductor muscles (adductor mandibulae externus, AMe, and the adductor mandibulae internus, AMi) which both originate on the dorsolateral aspect of the cranium and insert on the mandible (Fig. 1). The epaxial muscles

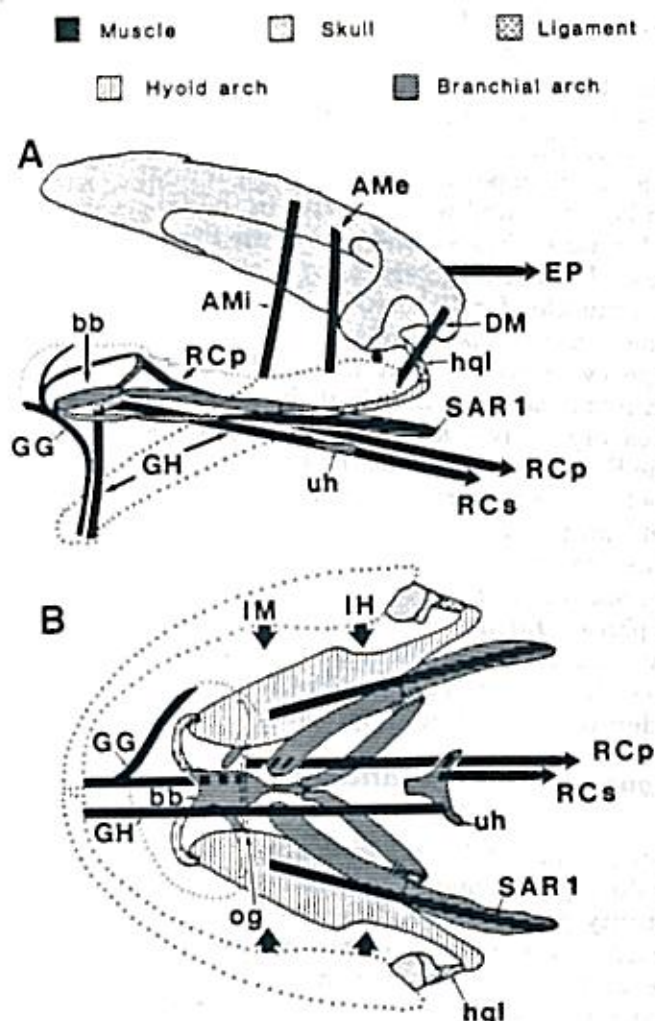


Fig. 1. Schematic diagrams of the major functional components of the prey transport mechanism in *Ambystoma tigrinum* in (A) lateral and (B) ventral views. The black dot indicates the jaw articulation. Dotted lines indicate the lower jaw and the tongue surface. The intermandibularis and interhyoideus muscles span the mandibular rami ventrally in the direction indicated by the arrows. Modified from Reilly and Lauder ('89a).

(EP) extend from the vertebrae to the dorsal surface of the skull and elevate the skull on the vertebral column.

Two transverse muscles span the mandibles and elevate the buccal floor, the intermandibularis posterior muscle (IM) and the interhyoideus muscle (IH). Four pairs of muscles attach to the hyobranchial apparatus and serve to protract and retract the tongue. The rectus cervicis superficialis muscle (RCs) inserts on the free floating urohyal element of the hyobranchial apparatus (Fig. 1: uh) while the rectus cervicis profundus muscle (RCp) extends anteriorly to the root of the

tongue, inserting on the medial basibranchial element (bb) of the hyobranchial apparatus. Muscle fibers of the RCp extend dorsally onto the otoglossal cartilage of the tongue (Fig. 1: og).

Two muscles extend to the hyobranchial apparatus from the lower jaw. The geniohyoideus muscle (GH) functions to advance the hyoid apparatus and to elevate the floor of the buccal cavity. It passes posteriorly from the mental symphysis to make a weak fascial connection with the bb and continues posteriorly to insert on the urohyal cartilage (Fig. 1). The genioglossus muscle (GG) also extends from the mental symphysis and inserts solidly on the bb, but many fibers of this muscle also extend above the hyobranchial apparatus to the ventral surface of the tongue and form the bulk of the muscular part of the tongue pad. The GG advances the tongue toward the lower jaw and flips the tongue pad forward and out beyond the rim of the lower jaw.

The subarcualis rectus one muscle (SAR) is an intrinsic hyobranchial muscle that protracts the hyobranchial apparatus and tongue forward by advancing the first branchial arch forward relative to the hyoid arch (Fig. 1). This muscle is postulated to be a protractor of the hyobranchial apparatus. Hyobranchial protraction has been suggested to occur when the SAR acts in concert with other hyobranchial muscles that contribute to elevation and advancement of the hyobranchial apparatus during tongue projection (Reilly and Lauder, '89b, '90a).

### Terminology

The terminology used in this paper to describe the prey transport cycle is that presented in Reilly and Lauder ('90b) on the basis of their kinematic study of prey transport. The *transport cycle* is composed of a long preparatory period followed by a rapid gape cycle when the prey is transported toward the esophagus by the tongue. Transport cycles occur *after* the strike and act to move prey that has been caught from the mouth into the esophagus and stomach. Typically in tiger salamanders between three and ten transport cycles are required to move a 4 cm earthworm into the esophagus; from 4 to 8 mm of the prey are transported with each cycle. The transport cycle encompasses the time from the start of one Preparatory phase to the start of the Preparatory phase of the next cycle (Reilly and Lauder, '90b).

The prey transport cycle is divided into four major phases which are defined on the basis of jaw and hyoid movements. The Preparatory phase

begins the transport cycle and is divided into two parts. The first part (P1) is a long phase of variable duration during which the gape changes only slightly and the hyoid may be slightly protracted under the prey. During the second part (P2) of the Preparatory phase no change in gape or hyoid position occurs. During the Fast Opening phase (FO) the gape rapidly increases and the hyoid is rapidly retracted. During the Closing phase (C), the gape decreases rapidly and the hyoid reaches maximum retraction. The Recovery phase (R) is characterized by constant gape accompanied by hyoid protraction. Unless the prey has been swallowed, the Recovery phase is followed by P1 again and the entire cycle repeats.

The term *gape cycle* refers to the Fast Opening and Closing phases during which the mouth opens and closes on the prey while the hyoid is retracted. The gape cycle is thus a portion of the transport cycle when posterior movement of the prey occurs. It is important to distinguish prey transport (which involves only movement of the prey toward the esophagus and stomach) from chewing or prey manipulation cycles which are associated with intraoral prey processing. In tiger salamanders very little or no prey reduction occurs within the oral cavity; the intact prey is simply transported to the esophagus. In addition, swallowing is a distinct action which occurs at the end of prey transport and appears to involve a distinct kinematic and motor pattern. Prey transport in tiger salamanders should not be equated with intraoral prey manipulation behaviors or swallowing events in amniotes.

## RESULTS

### *The transport cycle: An overview*

The pattern of muscle activity during the prey transport cycle in tiger salamanders may be described on the basis of the four major phases defined by kinematic attributes (Figs. 2, 3). Figure 2 illustrates sample electromyographic (EMG) recordings for ten muscles of the feeding mechanism during an entire prey transport cycle. The transport cycle begins with the first part of the Preparatory phase (P1) which may last up to 5 seconds. Preparatory phase 1 is associated with activity in the genioglossus, geniohyoideus, interhyoideus, and intermandibularis (muscles involved in compressing the tongue and prey item against the palate) as well as occasional low level activity in the epaxial and adductor mandibulae muscles. The subarcualis rectus is silent. During P1 the gape is usually held constant (closed on the

prey) but in about 10% of transport cycles there is a small (< 1 mm) but consistent increase in gape prior to the start of the P2 phase. Figure 4 illustrates these two types of gape profiles during the P1 phase. Beginning about 500 ms prior to Fast Opening, a small gape increase may occur that appears to be correlated with activity in the GH, IH, and IM muscles. The second part of the Preparatory phase (P2) is characterized by complete silence in all muscles for 70 to 100 ms prior to the onset of the next transport cycle.

The gape cycle occurs next and includes the Fast Opening phase (Figs. 2, 3: FO), during which all muscles are active, and the Closing phase. During the Fast Opening phase the hyoid apparatus begins to move posteroventrally and pulls the tongue and prey into the mouth. After the jaws close on the prey the hyobranchial apparatus and tongue recycle forward under the prey during the Recovery phase. During the Recovery phase (Figs. 2, 3) many muscles are silent (e.g., the SAR, DM, RCs, AMi) while others such as the GG and AMe show moderate levels of activity.

### *The gape cycle: Kinematics and motor patterns*

High-speed video fields showing prey transport behavior during the gape cycle with synchronized EMG activity patterns are illustrated in Figure 3. Posterior movement of the prey occurs during the gape cycle when the mouth rapidly opens (0–20 ms) and closes (20–80 ms) while the tongue with the adhering prey item is retracted. The hyobranchial apparatus is pulled posteriorly and rotates to bulge the throat ventrally during prey transport (Fig. 3: hyoid depression). Kinematic profiles for prey position and hyoid depression (Figs. 3, 5) indicate that the tongue and prey begin to move rapidly posteriorly about halfway through the Fast Opening phase with most of prey movement occurring in the first half of the Closing phase. During hyobranchial retraction the prey is transported about 8 mm as indicated by the change in prey position relative to the plane of the gape (Fig. 3). The gape cycle lasts about 80 ms and the prey begins to move posteriorly about 15 ms after the onset of mouth opening.

The average activity patterns of the cranial muscles during the gape cycle relative to the beginning of mouth opening (time 0), are presented in Figures 5–7. The cranial muscles controlling jaw opening (EP, DM) become active prior to mouth opening (Fig. 5; –10 to –5 ms) and peak in activity during mouth opening (+5 to 10 ms).

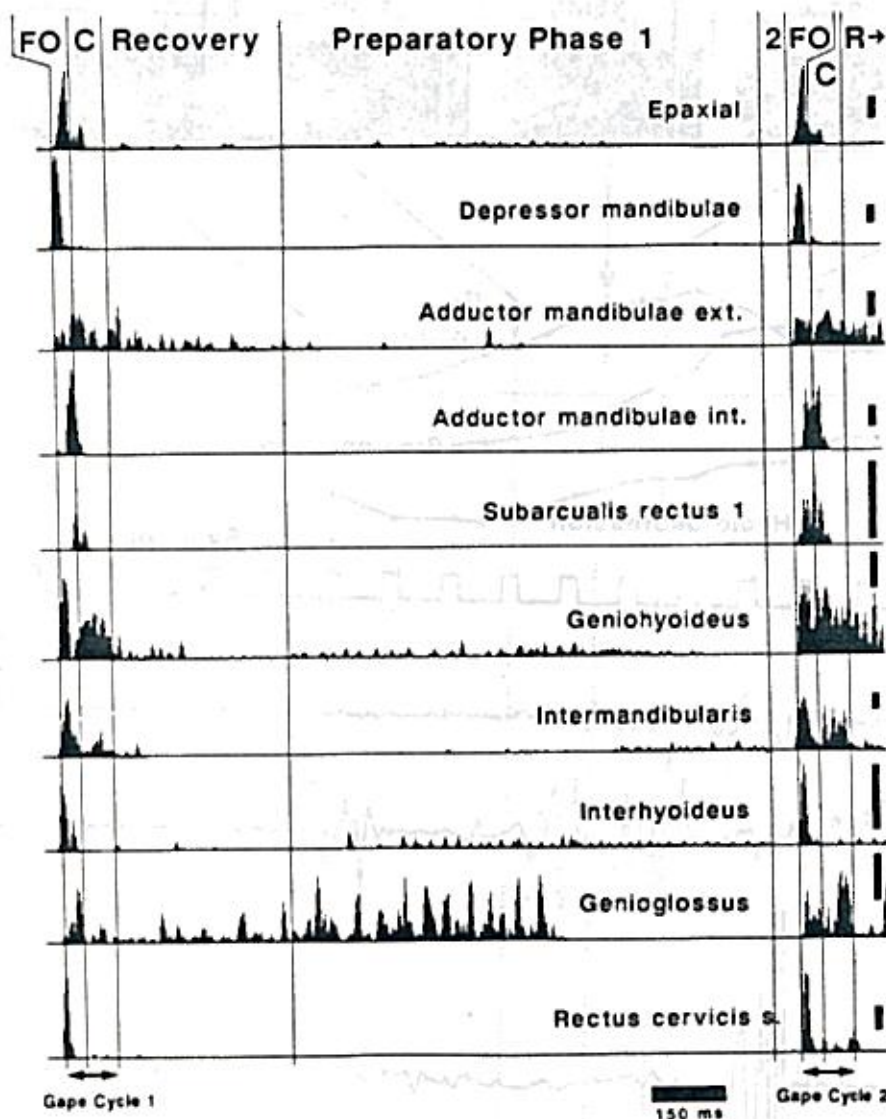


Fig. 2. Phases of the prey transport cycle in the tiger salamander, *Ambystoma tigrinum*, with a composite of rectified electromyographical activity patterns for ten muscles involved in feeding. All ten muscles are active during the gape cycle (Fast Opening (FO) and Closing (C) phases) when the prey is moved posteriorly. Activity of the adductor mandibulae externus, geniohyoideus, and genioglossus continues into the Recovery phase (R) when the tongue is recycled forward under the prey item. The long Preparatory phase of little or

no movement extends until the subsequent onset of the next gape cycle (Gape cycle 2). Muscles involved in prey compression (geniohyoideus, intermandibularis, interhyoideus, genioglossus) are active during Preparatory phase 1 while all muscles are silent for about 100 ms prior to the next Fast Opening phase (Preparatory phase 2). Vertical scale bars represent 0.1 mv. The transport cycle and its kinematic phases are defined in the Materials and Methods section following Reilly and Lauder ('90b).

Both muscles become silent by peak gape but the EP has a second peak in activity during the middle of the Closing phase. The two jaw adductor muscles (AMe, AMi) also become active prior to jaw opening but their patterns during transport differ. The AMe (Figs. 5, 6, 7) ramps to a high level of activity just before or after peak gape and remains moderately active well after jaw closing until the end of the Recovery phase (Fig. 2). Activ-

ity in the AMi (Fig. 7) begins to develop about 15 ms after the onset of mouth opening and peaks at the time of peak gape and then ceases by the time the jaws close. The AMi is silent during the Recovery and Preparatory phases.

The three buccal muscles, IM, GH, and IH (Figs. 6, 7), become active 5–15 ms before the onset of mouth opening, peak in activity early in mouth opening, and then activity tapers off by the

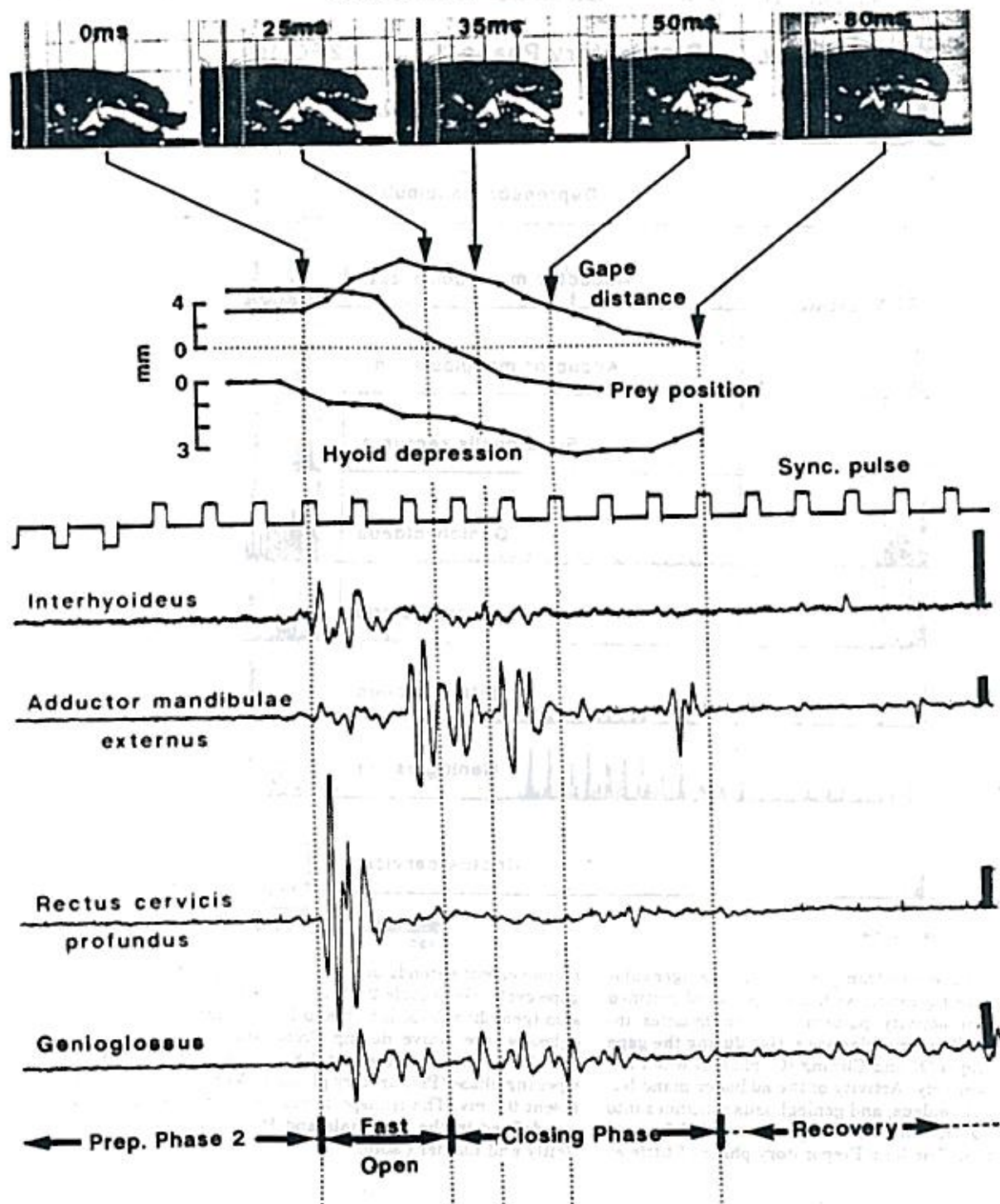


Fig. 3. Synchronized kinematic and EMG patterns during prey transport in the tiger salamander. Video fields depict tongue and head movements relative to digitized gape, prey position, and hyoid depression distances and correspond to the EMG bursts shown for four muscles from single transport event below (vertical dotted lines). Video fields represent the following events: 0 ms, the field before the mouth begins to open; 25 ms, maximum posterior prey movement at peak mouth opening; 35 ms, prey moves into the oral cavity as jaws

begin to close; 50 ms, prey approaches maximum retraction as hyoid depression reaches its maximum; 80 ms, tongue and prey reach maximum retraction and the mouth closes on the prey. The synchronization (Sync.) pulse (10 ms long) was used to align kinematic (video) and EMG recordings, and the white dots on each video field represent the top of the sync pulses shown below. EMG amplitudes are indicated by the black bars representing 0.1 mv.



beginning of the Closing phase. The GH and IM show a moderate increase in activity as the jaws close and into the Recovery phase.

The SAR (Fig. 5: SAR) has a large burst of activity beginning with mouth opening, peaking before maximum gape when the tongue is moving posteriorly, and then activity tapers off during mouth closing. The GG shows low amplitude bursts of activity from the onset of mouth opening through the Recovery phase with increasing bursts of activity during Preparatory phase 1 (Fig. 6). The two parts of the rectus cervicis (Figs. 5, 6: RCs, RCp) exhibit similar patterns of activity. Both muscles become active with the onset of mouth opening and have a sharp peak in activity early in mouth opening and then activity tapers to a low level by the end of the Closing phase.

#### Strike vs. transport muscle activity

Comparisons of EMG activity during the initial strike and during prey transports are presented in Tables 1 and 2 and Figures 8 and 9. Because the recordings were made from the same electrodes in the same muscles from several contiguous capture/transport feeding sequences, these comparisons directly illustrate the similarities and differences in the timing and amplitude of EMG activity for the same muscles used in the two behaviors.

The two-way ANOVA shows mostly small F-values (31 of 35  $< 5.0$ ) for the behavior effect, and indicates considerable similarity between the motor patterns in strikes and transports for these variables and muscles (Table 1:30 of 35 comparisons). Because of the low degrees of freedom in testing for the behavior effect, large F-values may indicate significant differences which we did not have the sample size to detect. Thus, F-values of 15 to 200 reflect longer burst durations in the AMe, DM, and EP muscles during the initial strike. In addition, the AMi shows a strong trend toward having 5 ms intervals with a larger burst area during prey transport. Two-way ANOVA results (Table 1) also indicate that there is significant inter-individual variation for most variables and muscles (29 out of 35 comparisons), and that the ANOVA interaction term (indicating that individuals vary in their differences between strikes and transports) shows differences in 14 of 35 comparisons.

One-way ANOVA results indicate that the duration of the EMG burst differs considerably between strikes and transports (Table 2: BURDUR). Electromyographic activity in prey transport is

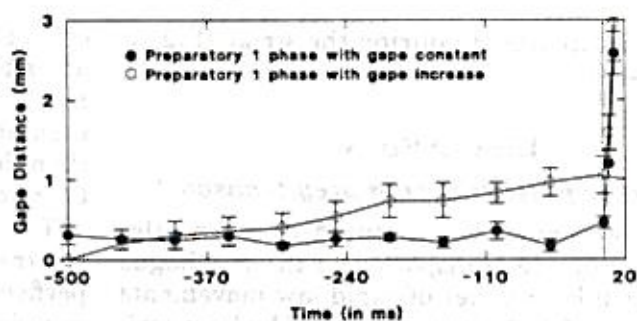


Fig. 4. Variability of gape distance during the Preparatory phase. About 10% of Preparatory phases exhibit a long gradual increase in gape of less than 1 mm prior to the onset of mouth opening. The Fast Opening phase begins at time 0 (vertical dotted line). Each point represents the mean ( $\pm$ SE) of 10 feedings.

longer for the GH and IM muscles, while the reverse is true for the GG, IH, and rectus cervicis muscles. The GH achieves significantly greater number of EMG spikes during the strike and does so more rapidly than during prey transport (10 ms vs. 46.3 ms). In addition, the onset times are closer to time 0 for the GH, GG, and RCs muscles during prey transport, that is, during the strike these muscles begin activity earlier.

Comparisons of the entire EMG profile for eleven muscles during the initial strike and during transport behaviors within individuals are presented in Figures 8 and 9. These profiles show differences in the EMG patterns not captured by the statistical variables analyzed above. The DM and SAR muscles both show double-burst patterns during the initial strike but only have a single burst during prey transport (Fig. 8). In both cases the first strike burst is similar in relative timing to the single burst observed during transport. The second burst in the EP (associated with jaw closing) is shifted to the right in initial strikes to match the longer gape cycle. The second peak of activity in the DM during the strike is associated with the plateau in gape, and this plateau is not present during prey transport (Figs. 3, 5). The AMe shows a large second burst of activity during transports in contrast to a longer low-level burst during the strike.

The AMi and RCp both show large high-amplitude initial bursts during prey transport that are not present during the strike where peak activity is much delayed (Fig. 9). The IM also tends to show higher activity earlier in the Fast Open phase during prey transport. The GG shows only very low activity during the prey transport gape cycle in contrast to a rapid rise to a much

greater peak in activity during the strike (Fig. 9: genioglossus).

## DISCUSSION

### *The motor pattern during prey transport*

After prey have been captured by tiger salamanders, they are transported to the esophagus and stomach by a series of rapid jaw movements (occurring in 80 to 100 ms) separated by long periods with very little jaw movement lasting from 1 to 5 seconds. Except for jaw closing "bites" at the end of the Closing phase of the transport cycle, there is little or no chewing or intraoral manipulation of the prey. Thus, the transport of prey items involves a set of rhythmic movements that moves a relatively unmodified prey item toward the esophagus.

The motor pattern that controls transport behavior exhibits a number of distinctive features. The Preparatory phase (P1) is characterized by activity in muscles of the buccal floor such as the GH, IH, and IM, and the GG muscle exhibits relatively high activity during the early part of this phase. In addition, the SAR, rectus cervicis muscles, and AMi are completely silent during the P1 phase (Fig. 2). These EMG data, in conjunction with kinematic data on prey transport (Reilly and Lauder, '90b) and a kinetic model of jaw muscle function (Reilly and Lauder, '89b), suggest that the buccal floor is being elevated during this phase pressing the prey against the roof of the mouth. The relatively high level of GG activity during the preparatory phase suggests that the tongue pad itself plays a significant role in applying pressure to the prey well before the gape cycle. No consistent EMG correlates were found during the small percentage of Preparatory phases in which small increases in gape were present (Fig. 4). Activity of the muscles of the buccal floor during this time suggests that dorsal pressure on the prey may force the mandible ventrally thus opening the gape slightly. The DM was silent during the P1 phase and thus this muscle is not contributing to the slight gape change noted in about 10% of the feedings.

During the second part of the Preparatory phase (P2) all muscles are silent (Fig. 2). This corresponds to a time during which no movement is seen in any jaw bones just before the Fast Open phase (Fig. 3; Reilly and Lauder, '90b).

During the Fast Opening phase of the gape cycle all jaw muscles become active within 15 ms before the mouth begins to open. Even anatomi-

cally antagonistic muscles (such as the DM and adductor mandibulae muscles, Fig. 5) show nearly synchronous activity onsets. Depressor mandibulae activity, however, peaks rapidly and then declines while the AMe exhibits strong activity during the Closing phase (Fig. 5).

The opening and closing of the mouth during the transport cycle is a rapid behavior that is superficially similar to terrestrial strike as all jaw muscles begin activity at nearly the same time and both behaviors last between 80 and 130 ms. However, this similarity is illusory as many features of both jaw kinematics and the motor pattern are different. The most obvious kinematic difference occurs in the gape profile which peaks near the middle of the gape cycle during prey transport (Figs. 3, 5) in contrast to the gape profile during the strike which exhibits a prolonged plateau as the tongue is extended toward the prey (Reilly and Lauder, '89b). This kinematic difference is mirrored by the depressor mandibulae EMG profile which exhibits only a single (early) burst of activity during transport in contrast to the double burst shown during the initial strike.

The main action of actual prey transport is accomplished during the gape cycle by the rectus cervicis muscles which show high levels of activity as the mouth begins to open (Figs. 2, 5). These muscles (Fig. 1) retract the hyobranchial apparatus and move the base of the tongue (with the prey adhering to it) posteriorly toward the pharynx. The video fields at the top of Figure 3 clearly show the prey moving posteriorly during the time between 25 ms and 50 ms. During the initial strike at prey, the peak of RCp muscle activity is delayed considerably due to the time necessary for tongue extension toward the prey. During transport, the prey and tongue are located within the buccal cavity and posterior movement of the tongue and prey begins with the onset of Fast Opening.

The most unexpected finding from the recordings of transport muscle EMG patterns is the large burst of activity in the SAR (Figs. 5, 8). We had not initially expected to find any activity in this muscle during transport as the SAR is currently hypothesized to function to project the tongue out of the mouth during the strike (Findeis and Bemis, '90; Lauder and Shaffer, '88; Lombard and Wake, '76, '77; Reilly and Lauder, '89b; Severtsov, '72; Thexton et al., '77). During prey transport, no tongue projection occurs (Fig. 3) and yet the SAR shows a large burst of activity that subsides by the end of the Closing phase. The SAR

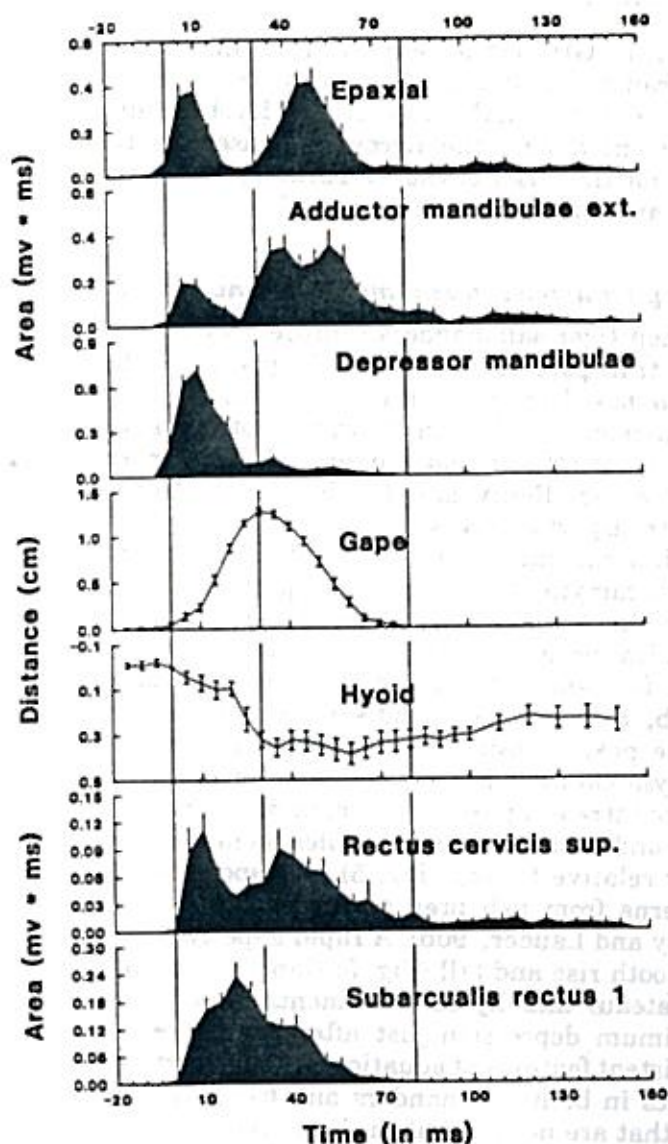


Fig. 5. Average muscle activity profiles for 5 muscles during prey transport in the tiger salamander illustrated for one individual along with average gape and hyoid kinematics. Levels of muscle activity (Area) are plotted as the mean rectified integrated EMG area ( $mv \cdot ms \pm SE$ ,  $n = 17$  transports) for each 5 ms bin corresponding to synchronized video fields. Gape distance and hyoid depression are indicated in cm. Kinematic events are indicated by vertical lines for mouth opening (time 0), mean peak gape (30 ms), and mean time to mouth closing (80 ms). Note especially the bell-shaped gape profile, the peak in hyoid depression after peak gape, the single burst in the subarcualis rectus one and depressor mandibulae muscles, and the double burst profiles in the epaxial and adductor mandibulae muscles.

muscle may function to stabilize the hyobranchial apparatus by rigidifying the connection between the first ceratobranchial and the ceratohyal (Fig. 1), and in so doing may aid in the rapid posterior movement of the entire hyobranchial apparatus

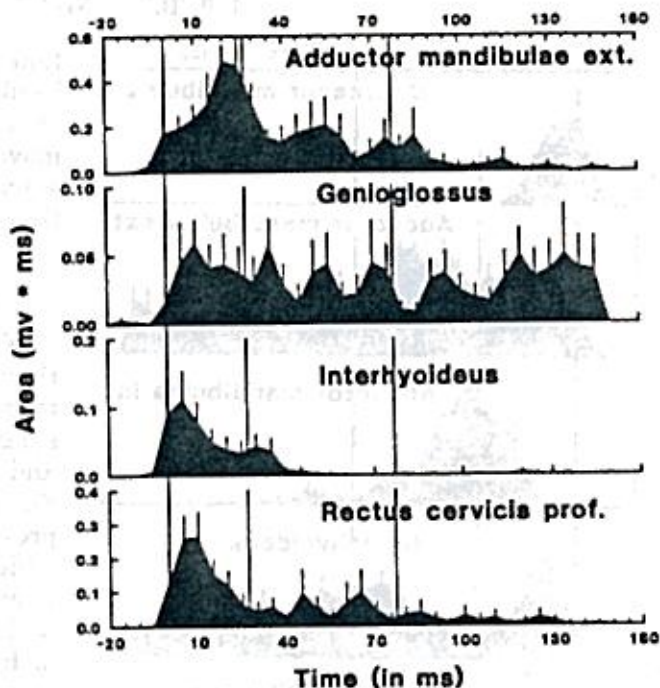


Fig. 6. Average muscle activity profiles for 4 muscles during prey transport in the tiger salamander for one individual. Levels of muscle activity (Area) are plotted as the mean rectified integrated EMG area ( $mv \cdot ms \pm SE$ ,  $n = 10$  transports) for each 5 ms bin corresponding to synchronized video fields. Kinematic events for each individual are indicated by vertical lines for mouth opening (time 0), mean time to peak gape (27 ms), and mean time to mouth closing (77 ms).

that begins early in Fast Opening. The same possible function during tongue retraction at the strike is suggested by the second burst of SAR activity present in the strike profile at the time the tongue is being retracted (Fig. 8). The SAR muscle activity recorded during transport suggests that the function of this muscle may not be well understood. Although the SAR may, as is currently believed, aid in protraction of ceratobranchial one during the initial strike, it is also possible that the muscle may act to advance and stabilize the entire skeleton of the buccal floor by making a more rigid platform for tongue projection toward the prey. This hypothesis could be tested by experimental modification of the SAR muscle (i.e., by removing its innervation) to determine how tongue projection distance is affected.

Another interesting finding related to tongue projection is the difference in EMG activity in the genioglossus muscle during the strike and transport (Fig. 9). During prey transport the GG has very low levels of activity during the gape cycle when the prey is moved posteriorly and a higher,

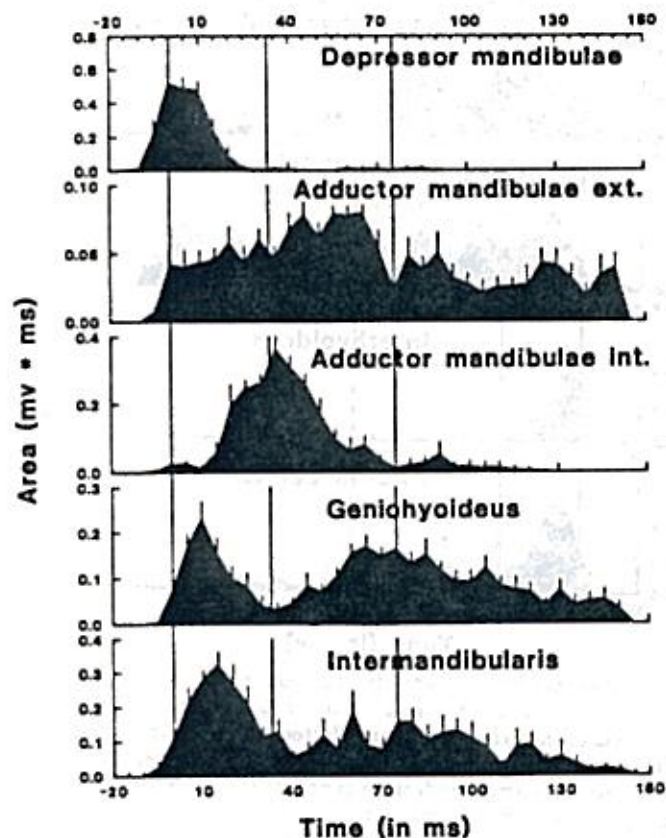


Fig. 7. Average muscle activity profiles for 5 muscles during prey transport in the tiger salamander for one individual. Levels of muscle activity (Area) are plotted as the mean rectified integrated EMG area ( $\text{mv} \cdot \text{ms} \pm \text{SE}$ ,  $n = 8$  transports) for each 5 ms bin corresponding to synchronized video fields. Kinematic events for each individual are indicated by vertical lines for onset of mouth opening (time 0), mean time to peak gape (33 ms), and mean time to mouth closing (75 ms).

longer burst of activity during the preparatory phase when the prey is compressed between the tongue and palate. However, during tongue projection, the GG exhibits a tenfold increase in EMG activity from that seen during the transport gape cycle. This indicates the significant role that the GG plays in tongue projection and that flipping of the tongue pad by the GG may be the primary mechanism responsible for projecting the tongue past the plane of the gape.

During the Recovery phase many muscles such as the DM, AMi, SAR, and rectus cervicis muscles are inactive, having ceased activity during the Closing phase. The AMe, GH, and GG are the major muscles active at this time. This pattern of muscle activity in conjunction with plots of jaw kinematics suggests that the Recovery phase is characterized by hyobranchial protraction and a recycling of the tongue under the prey. The por-

tion of the GH muscle between the mandible and basibranchial may act during this time to directly affect hyobranchial protraction. Hyobranchial movement during the Recovery phase sets the stage for the onset of the Preparatory phase and the start of the next transport cycle.

#### Prey transport in salamanders and fishes

When tiger salamanders capture prey on land they transport it to the esophagus using the tongue-based mechanism described above. Tiger salamanders also feed in the water, both as larvae and adults (Miller and Larsen, '86; Lauder and Shaffer, '88, Reilly and Lauder, '89b). Aquatic prey transport involves a hydraulic mechanism in which a current of water is created through the mouth carrying the prey to the posterior region of the pharynx where it is then swallowed. Details of hydraulic prey manipulation are best understood for fishes (Bemis and Lauder, '86; Lauder, '80a,b, '85; Liem, '70), and several of the phases of the prey transport process identified here in *Ambystoma tigrinum* are very similar to the process of intraoral prey transport in fishes. Both the gape and hyoid kinematic profiles themselves and their relative timing (Fig. 5) correspond well to patterns from fish prey transport (Lauder, '85; Reilly and Lauder, '90b). A rapid gape cycle with a smooth rise and fall (Fig. 5: Gape; i.e., without a plateau) and hyoid movements which reach maximum depression just after peak gape are consistent features of aquatic prey transport kinematics in both salamanders and fishes (Lauder, '85) that are not present in the strike.

In addition to the similarities between aquatic and terrestrial prey transport, there are also considerable similarities between the process of initial prey capture by suction feeding in the water and the kinematics and motor patterns involved in terrestrial prey transport. For example, in contrast to the terrestrial strike, aquatic and terrestrial prey transport and aquatic prey capture (in both salamanders and fishes) share nearly identical gape and hyoid kinematic profiles (Reilly and Lauder, '90b), similar absolute and relative timings of jaw movement (Shaffer and Lauder, '88), the lack of tongue projection during the gape cycle (Lauder, '85; Reilly and Lauder, '89b; Shaffer and Lauder, '88), and many similarities in the motor pattern, including the same overall sequence of muscle activity (Wainwright, et al., '89), a single peak in jaw opening muscle EMG (Figs. 5, 7; Lauder '85), and short duration muscle

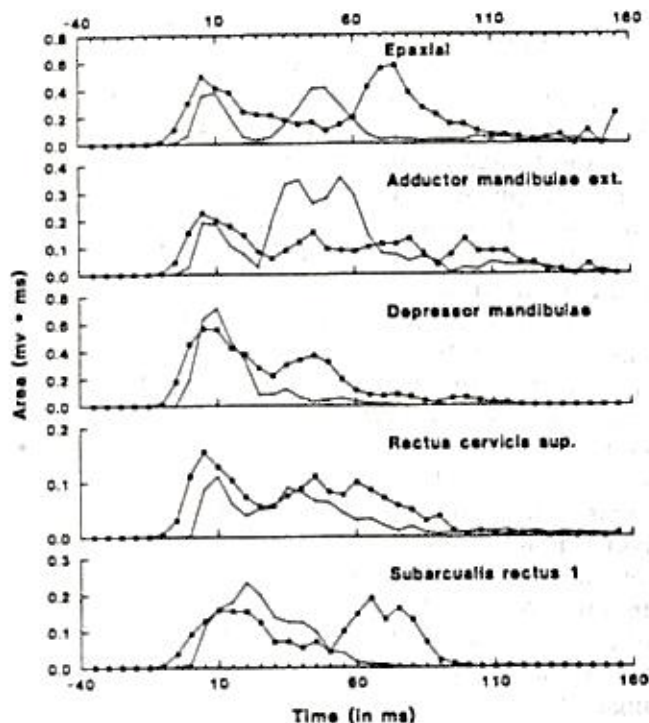


Fig. 8. Comparison of average EMG profiles for strike (squares) vs. prey transport (dots) behaviors recorded simultaneously from five muscles in one individual tiger salamander. Muscle activity (Area) recorded from the same electrode during interspersed strikes ( $n = 15$ ) and transports ( $n = 10$ ) is plotted as average rectified integrated EMG area per 5 ms bin ( $mv \cdot ms$ ). Note that the average profiles indicate considerable differences in motor patterns not detected by the analysis of variables measured from individual profiles.

bursts relative to terrestrial strikes (Figs. 8, 9; Lauder and Shaffer, '88).

These data suggest that the motor and kinematic patterns used for terrestrial prey transport by *Ambystoma tigrinum* are most similar to those used for initial prey capture by larvae and adults when they feed in the water. Lauder and Shaffer ('88) showed that adult tiger salamanders retain the larval motor pattern (in the DM, EP, RCs, AMe, AMi) after metamorphosis, and use it to capture prey in the water. We suggest that it is this motor pattern (or a slight modification of it) that is used by adults to transport terrestrial prey. Thus, we propose the hypothesis that post-metamorphic tiger salamanders retain the larval motor pattern used during aquatic suction feeding and employ it to accomplish terrestrial prey transport.

The following additional point supports this hypothesis. Lauder and Shaffer ('88) showed that the SAR muscle is active during aquatic prey capture by post-metamorphic salamanders. Although

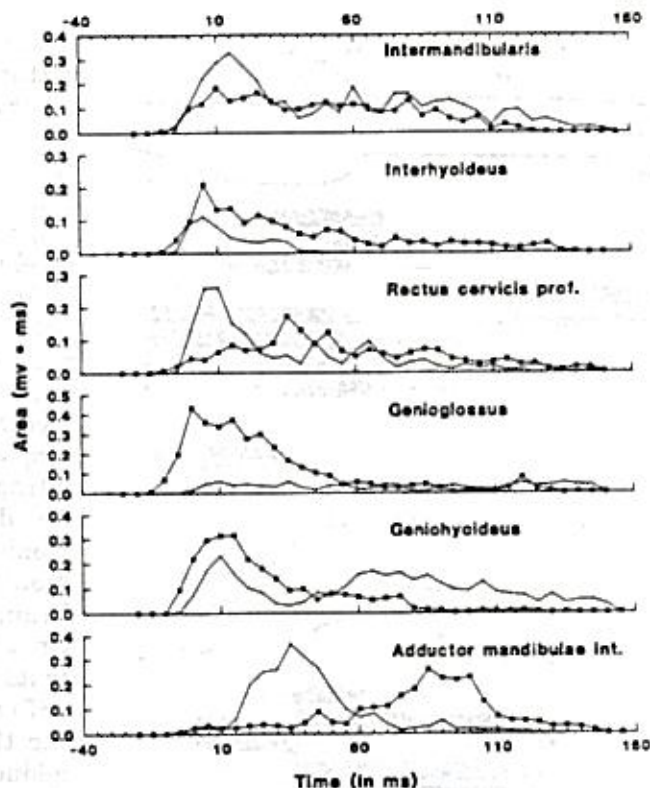


Fig. 9. Comparison of average EMG profiles for strike (squares) vs. prey transport (dots) behaviors in 6 additional muscles plotted as the average rectified integrated area per 5 ms bin ( $mv \cdot ms$ ) as in Figure 8. For each muscle EMG activity was recorded from the same electrode during interspersed strikes and transports. The intermandibularis profiles are from one individual ( $n = 10$  strikes, 7 transports); the interhyoideus, rectus cervicis profundus, and genioglossus profiles are from a second individual ( $n = 14$  strikes, 10 transports), and the geniohyoideus and adductor mandibulae internus profiles are from a third individual ( $n = 9$  strikes, 7 transports). Note that the average profiles indicate considerable differences in motor patterns not detected by the analysis of variables measured from individual profiles.

the EMG profile of the SAR in that study was not analyzed quantitatively, the pattern of SAR activity described by Lauder and Shaffer ('88: Figs. 8, 9) during aquatic feeding is similar to the motor pattern shown during terrestrial prey transport (Figs. 5, 8). This hypothesis could be explicitly tested by a direct statistical comparison of the EMG profile in homologous muscles among four behaviors: the initial strike in water, the initial strike on land, transport of prey in the water, and terrestrial transport of prey.

#### Models of prey transport in tetrapods

Models of prey capture and transport in tetrapods have been derived almost exclusively from data on amniotes (Bramble and Wake, '85;

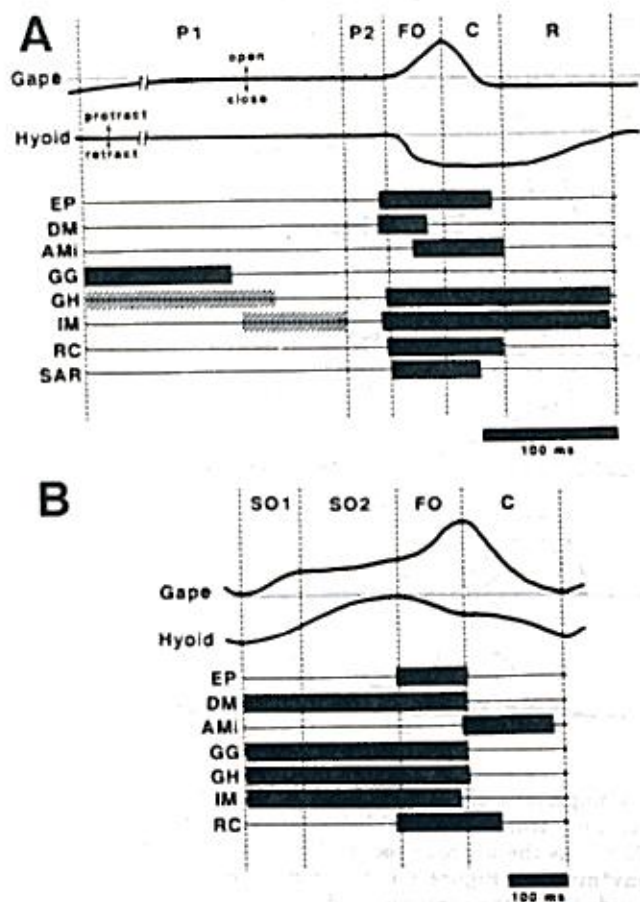


Fig. 10. Schematic diagram of (A) typical kinematic and motor patterns during prey transport in the tiger salamander and (B) a qualitative model of the intraoral transport cycle in generalized tetrapods. Black bars indicate muscle activity that is always present while hatched bars represent occasional activity. Note that neither the kinematic nor the motor patterns found in the tiger salamander fit the model for generalized tetrapods. Further discussion is provided in the text.

Schwenk and Throckmorton, '89). Based on models of amniote feeding and numerous experimental studies on amniote prey acquisition and transport behaviors, a terminology has been developed to describe kinematic patterns of jaw and hyoid movement and to partition motor patterns (e.g., Bels, '89; Bramble and Wake, '85; Byrd et al., '78; Cleuran et al., '89; Crompton, '89; Crompton et al., '77; Franks et al., '84; Gans et al., '78; Gorniak and Gans, '80, '82; Greet and De Vree, '84; Hiiemae and Crompton, '85; Hylander et al., '87; Schwenk and Throckmorton, '89; Smith, '82, '84, '88; Throckmorton, '80; Weijs, '75; Weijs and Dantuma, '81).

The amniote feeding cycle (Fig. 10B; Bramble and Wake, '85; Fig. 13-4) often begins with the Slow Open (SO) phase. During Slow Opening in

amniotes (when present), the gape reaches about a third of its peak value and then grades into the Fast Opening phase. The Slow Open phase typically involves a reasonably rapid initial increase in gape to about 30% of maximum (often called the SO1 phase) and then a brief pause where the gape is maintained at a nearly constant level (called the SO2 phase). Bramble and Wake ('85) and Schwenk and Throckmorton ('89) have suggested that the SO phase is a particularly important aspect of the tetrapod feeding cycle that has been subjected to considerable phylogenetic modification across vertebrate taxa. Muscles proposed to be active during Slow Opening in tetrapods include intrinsic lingual muscles, the depressor mandibulae, suprahyoid muscles (geniohyoideus and genioglossus), the intermandibularis, and internal adductors (Fig. 10B; Bramble and Wake, '85; Fig. 13-4). The Fast Opening phase begins as the gape opens rapidly to its maximum. The model of Bramble and Wake ('85) suggests that all muscles will be active during this phase except the internal and external adductors which become active only just prior to the start of the Fast Close phase (Fig. 10B). During Fast Close, while the jaws are moving rapidly together, the primary muscles proposed to be active are the adductor muscles and the infrahyoid group (rectus cervicis muscles). During the final phase (Slow Close and Power Stroke) the teeth engage the prey and the major muscles proposed to be active are the internal and external jaw adductors (Bramble and Wake, '85; Fig. 13-4).

Our results on the motor pattern used during terrestrial prey transport in an anamniote, *Ambystoma tigrinum*, as well as experimental results from separate studies of feeding and transport kinematics and motor output in *Ambystoma* and other amphibians (Bemis et al., '83; Findeis and Bemis, '90; Gans and Gorniak, '82a,b; Lauder and Shaffer, '88; Matsushima et al., '85; Reilly and Lauder, '89b, '90b; Shaffer and Lauder, '88; Thexton et al., '77), indicate that several of the above generalizations proposed for amniote prey transport cycles cannot be extended to anamniote tetrapod taxa (Fig. 10A).

First, we have not found a distinct Slow Opening phase that is part of the gape cycle (Fig. 10A). In *Ambystoma*, only about 10% of all transport cycles involve any gape increase prior to Fast Opening, and during this time the depressor mandibulae, intermandibularis, and internal jaw adductor show little or no activity (Fig. 10A). In other amphibians, the presence of an amniote

Slow Open cycle is equivocal at best (Bemis et al., '83; Gans and Gorniak, '82a,b) although data from prey transport cycles are not yet available. Based on currently available data in amphibians the Slow Opening phase cannot be regarded as an element of the primitive tetrapod transport cycle. In fact, a distinct Slow Opening phase is often absent from gape cycles of many amniote feeding behaviors including prey transport.

Second, the Fast Opening phase in *Ambystoma* involves the near simultaneous onset of activity in all jaw and hyoid muscles, and prior to this phase there is a time (Fig. 2: P2 phase; Fig. 10A) of total silence in all muscles. This result does not fit any current model of prey transport in primitive tetrapods.

Third, the Closing phase cannot be separated into distinct parts (i.e., the Fast Close and Power Stroke components of amniotes; Fig. 10A). The gape cycle rapidly rises to a peak and then smoothly declines in a bell-shaped pattern during prey transport (Figs. 3, 5; Reilly and Lauder, '90b). Recordings of the motor pattern during the Closing phase of prey transport in *Ambystoma* reveal that the rectus cervicis muscles are active throughout this phase as are the GG and GH (Figs. 5, 6, 7). Comparative data on prey transport in amphibians are only available for *Dermophis* (Bemis et al., '83). Although EMG data from individual muscles are not identified in that study, EMG recordings of the transport cycle do indicate that the infrahyoid musculature may be active during the Closing phase. In sum, current EMG data on the Closing phase in amphibians do not match predictions of general models of tetrapod feeding.

Fourth, the transport cycle in *Ambystoma* contains a distinct Recovery phase virtually identical to that of fishes (Figs. 5, 6, 7; Lauder, '85; Reilly and Lauder, '90b). During this phase the muscles of the buccal floor are active (Fig. 10A). The presence of this phase in amphibians has not previously been recognized in models of tetrapod feeding cycles.

Schwenk and Throckmorton ('89) have suggested that in amniotes there is considerable similarity between ingestion (the strike) and transport cycles and that the major difference between these behaviors is the extent of Slow Opening. Our data on terrestrial salamanders (Figs. 8, 9) show that the kinematics of the strike and subsequent prey transport cycles are quite different. Instead, terrestrial prey transport in salamanders appears to be most similar to aquatic prey capture

and transport (in fishes and salamanders before and after metamorphosis).

Given the many differences noted between our data on *Ambystoma* and the data available for amniotes, it is possible that no one model will be applicable to all tetrapods. In particular, it is obvious from our data that urodeles, by virtue of retaining many features of the motor pattern of aquatic feeding for use in terrestrial prey transport, do not conform to models proposed for amniotes. In addition, feeding cycles of non-mammalian amniotes (such as lizards) may not fit models based purely on mammals.

Reilly and Lauder ('90b) proposed a set of kinematic homologies among transport phases in tetrapods and suggested that the preparatory and Recovery phases of amphibian prey transport cycles have been compressed into the gape cycle (as the Slow Open phase) in amniotes. This hypothesis can now be tested indirectly by comparing the motor patterns recorded here during the Preparatory and Recovery phases (Fig. 10A) to those found during the amniote Slow Open phase (Fig. 10B). For example, activity of the lingual, intermandibular, and suprahyoid muscles is characteristic of the Slow Open phase in amniotes. In *Ambystoma*, these muscles are active during the Recovery and Preparatory phases. In addition, in the model of Bramble and Wake ('85; Fig. 13-4) epaxial muscle activity is the best basis for defining the start of Fast Open phase as epaxial activity does not occur elsewhere in the transport cycle. In *Ambystoma*, the epaxial muscles also show a rapid onset with the start of Fast Opening. If the onset of epaxial activity is used to define a comparable time in the transport cycle, then the motor pattern of the Recovery plus Preparatory phases is indeed similar to that of the Slow Opening phase in amniotes. Our understanding of the evolution of tetrapod feeding systems will improve as more comparative and quantitative data on prey transport for other amphibians and non-mammalian amniotes become available.

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