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MOTOR PLASTICITY IN THE FEEDING MECHANISM OF THE PINFISH *LAGODON RHOMBOIDES* (TELEOSTEI; SPARIDAE)

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ABSTRACT

Some fishes have been found to have the ability to alter, or modulate their feeding muscle activity patterns in different feeding situations. Other research has shown that some fishes have the ability to activate their feeding motor patterns in a bilaterally asymmetric manner. This is the first analysis of a possible prey type effect on the degree of bilaterally symmetric and asymmetric modulation of the feeding motor patterns in a lower vertebrate. Using three individuals of the pinfish, *Lagodon rhomboides*, the activity of three head muscles on each side of the head was measured during two phases of feeding, the initial strike and manipulation of the prey. Electromyographic (EMG) recordings were made from the epaxialis, the adductor mandibulae, and the sternohyoideus muscles. Feedings involved three prey types: small squid pieces, live fish, and large dead shrimp. Eleven variables, muscle activity durations and relative onset times, were measured to quantify the muscle activity patterns of each feeding event. Most of the individual EMG variables did not differ significantly in response to prey type. However, bilaterally symmetric and asymmetric manipulatory activities were affected by prey type. Specifically, asymmetric activity during manipulation was most common with large prey (shrimp and fish) and more cycles of activity were used when manipulating large prey. The results of this study reveal that *Lagodon rhomboides* uses fairly stereotypic patterns of muscle activity when feeding on different prey types, even though it has been characterized as an omnivorous feeder. *Lagodon* was also found to have the

ability to use asymmetric manipulation, especially when feeding on large prey types.

INTRODUCTION

Recent research in functional morphology has shown that many species of fish are not restricted to one stereotypical pattern of muscle activity during feeding as was previously believed, but instead possess the ability to select different motor patterns for different feeding situations from a repertoire of functionally distinct muscle activity patterns (Liem, 1978; Lauder, 1981; Wainwright and Lauder, 1986). This alteration or modulation of the feeding mechanism has been shown to be a consequence of variation in the size, shape, or elusiveness of the prey (Liem, 1978; Wainwright and Lauder, 1986). Consequently, it has been proposed that this modulatory ability has certain ecological implications on the trophic habits of organisms (Liem, 1980; Lauder 1981). One such hypothesis states that species which exhibit a broad range of distinct motor patterns for different prey types will have broader ranges of dietary capabilities (trophic generalists) and may utilize larger ranges of resources than species which cannot modulate (trophic specialists).

For this study, the pinfish *Lagodon rhomboides* was used because of its known ability to essentially "run the prey type gamut" as far as its omnivorous feeding habits are concerned. As a member of the family Sparidae, pinfish are heterodontous with four pairs of upper and lower incisors (allowing for a chisel-type biting behavior, probably used for herbivory (Stoner and Livingston, 1984)) and many smaller posterior, conical shaped teeth. They have been found to be the most populous fish species in the local area where collected for this study

(Stoner and Livingston, 1984), and to be extremely abundant in temperate zones and subtropical seagrass meadows along the Atlantic and Gulf coasts of North America (Caldwell, 1957). *Lagodon* experiences many diet shifts throughout ontogeny and feeds on seasonally available prey types within each trophic stage (Carr and Adams, 1973; Stoner and Livingston, 1984; Huh and Kitting, 1985). It has been found in these studies to have many distinct, dietary stages during ontogeny: herbivorous as a major consumer of seagrasses and macroalgae; planktivorous on copepods and larval invertebrates; carnivorous on amphipods and mysids; and generally omnivorous on shrimp, fish, and epiphytes. The ontogenetic order of each trophic stage was variable according to the location of study.

If a generalist-type fish such as *Lagodon* were found to possess the ability to modulate its muscle activities in response to different prey, to what extent would the control be? Would it be able to manage its motor patterns to the extent of apportionment of activity for the left and right sides of the head? This type of asymmetric activity has been found in only a few fish species. The more primitive gar, *Lepisosteus oculatus*, was found to show asymmetrical activity during prey manipulation stages in the sternohyoideus, obliquus superiorus and epaxial muscles, while re-orienting fish prey before swallowing (Lauder and Norton, 1980). African cichlid fishes have also been found to show asymmetries in the algae-scraping, pharyngeal jaw mechanism (Liem, 1978). This study seeks to determine if bilaterally asymmetric muscle activity behavior is present in

pinfish, and if so, is there a relationship between prey type and the degree of asymmetric control. Therefore, the two primary objectives in this study are: (1) to investigate the effect of prey type on the modulatory capabilities of the feeding mechanism in pinfish, and (2) to investigate the effect of prey type on the degree of the pinfish's ability to control asymmetric and/or symmetric patterns of muscle activity.

MATERIALS AND METHODS

Research Specimens

The pinfish *Lagodon rhomboides* was selected for this study because of its local abundance and its notoriety for being a generalized predator with a wide trophic breadth. Three live specimens of *L. rhomboides*, ranging from 128 to 142 mm standard length (SL), were collected from the sea-grass beds of the Gulf of Mexico near Tallahassee, FL. Fish were transported from the field immediately after capture and housed separately in 30 or 100 l aquaria at room temperature for at least three weeks prior to experimentation. Anatomical observations were made on one specimen which was dissected to determine the precise position of the muscles used for electrode implantation. Pinfish were fed a mixture of the three prey types used in the experiments: small cut pieces of squid about 1 cm square were classified as prey type 1; live sailfin mollies (*Poecilia latipinna*) about 2.5 cm SL were classified as prey type 2; decapitated, peeled shrimp about 4 cm in length were classified as prey type 3. These prey types and their constant shapes and sizes were selected to represent various characteristics of prey which may function to maximize the possibility of eliciting different patterns of feeding behavior. The squid used represent a prey which is non-elusive, small and suspended in the water column. Sailfin mollies were chosen to represent an elusive prey, and large dead shrimp represent immobile, benthic prey, that could not be swallowed whole.

Electromyography

The electromyographic (EMG) recordings of muscle activity were made from each pinfish during two phases of feeding: the initial strike, and subsequent manipulation of the prey. During recording sessions the fish were allowed to swim freely about the tank. The EMG recordings were made through bipolar electrodes constructed from two 120 cm sections of 0.002 gauge (0.051 mm diameter) insulated stainless-steel wire (California Fine-Wire). After the two wires were threaded through a 26 gauge, 13 mm hypodermic needle, the wires were glued together along the first 15 cm of one end. Tips of approximately 0.5 mm were exposed by scraping away the insulation with a blade underneath a dissecting microscope. The tips were then bent back against the shaft of the needle forming a hook functioning for anchorage of the electrode in the muscle following percutaneous insertion of the hypodermic needle into the fish.

Electrodes were implanted into each of the three fish immediately following anesthesia in a gradually increasing solution of tricaine methanesulfonate that never reached concentrations higher than 1 g l^{-1} of MS-222. Six muscles were implanted and the wires were glued together into a common cable and tied to a loop of suture located slightly anterior to the fish's dorsal fin. Following electrode implantation, each fish was returned to its aquarium and allowed to recover from anesthesia. Recording sessions did not begin until 2-3 hours after recovery in order to minimize possible behavioral or motor pattern effects of the

anesthesia. After each experiment, the fish was killed by over-anesthesia and electrode position was confirmed by dissection.

Prey (squid, mollies, or shrimp) were placed in the aquarium and the pinfish was permitted to roam freely to pursue and capture them. During recording sessions, electrical signals were amplified 10,000 times with Grass P511 preamplifiers and filtered with a bandpass between 100 and 3000 Hz. The 60 Hz notch filter was always used. Electromyographic data and a simultaneous voice description of fish behavior were recorded on high-grade VHS tapes with a TEAC XR-5000 tape recorder. Following the experiments feeding sequences were played back at one-quarter recorded speed on a Western Graphtec mark-11 thermal array recorder running at 50 mm s^{-1}. This produced a resolution of 5 ms mm^{-1} of chart paper.

Three muscles were selected for this study (Fig. 1) based on their prominent roles in the feeding mechanism (especially for capture and manipulation of prey) of generalized percomorph fishes (Lauder 1985). Electrodes were implanted in both left and right side members of each muscle. The sternohyoideus (SH) is a muscle that spans from the hyoid bar to the pectoral girdle. When contracted, it depresses the hyoid bar, a major suction generating movement during the expansive phase of feeding. This muscle also depresses the lower jaw through a ligament that connects the hyoid bar to the mandible. The epaxialis (EP) is attached to the neurocranium which elevates the head when contracted during mouth opening. The adductor mandibulae portion 2 (AM) is a muscle

connecting the suspensorium to the dentary, functioning as a primary jaw closer. Therefore, two mouth opening muscles (SH and EP) and one mouth closing muscle (AM) were monitored. Care was taken during implantation to ensure that electrodes were placed in the same region within each muscle on left and right sides to minimize the possibility that bilaterally asynchronous muscle activities were due to variation in regional muscle activity instead of being true asymmetric muscle contraction efforts.

From the chart recordings of each prey capture or prey manipulation event, 11 variables were measured with a digital caliper that quantified the timing of muscle activity (Figs. 1 and 2 as examples). For each of the three muscles and for each lateral half of the head, the duration of the single activity burst which occurred during the strike or manipulation was measured in milliseconds (SHLdur = sternohyoideus- left duration, SHRdur, EPLdur, EPRdur, AMLdur, and AMRdur). Also, the onset of activity of the sternohyoideus-left was used as reference time to generate five more EMG variables measured as the time from SHLonset to the onset of the other muscles in milliseconds (SHRons, EPLons, EPRons, AMLons, and AMRons).

Experimental design

Three prey types were fed to the pinfish which produced EMG recordings that were categorized into three behavioral types: behavior 1 - defined as the initial strike and successful capture of the prey. This varied between a rapid, suction generating activity and a slow biting movement; behavior 2 - defined as a type

of subsequent manipulatory activity recorded in a bilaterally symmetric manner which enabled the pinfish to reorient or masticate the prey before glutition; behavior 3 - defined as a type of subsequent manipulatory activity recorded in an asymmetric manner which usually occurred when the pinfish was reorienting or shaking off pieces of the prey before swallowing.

There were two primary objectives of the statistical comparisons: (1) to determine if there was a prey type effect on the patterns of muscle activity (the EMG variables themselves) within each behavior, and (2) to determine if there was a prey type effect on the degree of symmetric or asymmetric control. The basic experimental design consisted of a two-way analysis of variance for each behavior with individual crossed by prey type.

RESULTS

The means for the 11 EMG variables for the strike behavior are listed in Table 1a. Results of the ANOVA tests of the prey type effect for the strike behavior are presented in Table 2. The only electromyographic variables which showed a significant prey type effect were EPLDUR and EPRDUR. Missing F-ratios for three variables in Table 2 indicated by "--" are due to insufficient EMG data for proper statistical analysis (loss of those muscles in one fish).

The means and ANOVA results for the symmetric manipulation behavior are shown in Table 1b. and Table 2, respectively. In Table 1b., the absence of data for the squid variable (prey type 1) is due to the fact that squid were never manipulated in a symmetric or asymmetric manner. The only behavior used in squid feedings was the strike behavior. Squid were always swallowed immediately following a suction-type strike. Again, only two variables showed a significant prey type effect- EPLDUR and EPRDUR.

Means for the asymmetric manipulation behavior are listed in Table 1c. Again, there is no data for squid because the pinfish never manipulated this prey. ANOVAs could not be run for the asymmetric behavior because: (1) There weren't any cases of the asymmetric behavior for squid and (2) only 1 of the individuals used the asymmetric behavior on mollies (prey type 2), and even in that case there were very few cycles of activity. Therefore, the individual EMG variables themselves did not receive a test for prey type significance, for the asymmetric manipulation behavior.

Symmetric and asymmetric manipulatory events were typically comprised of 1 to 5 cycles of biting or shaking (each cycle, by definition, began with a burst of the reference muscle SHL for onset variable measurements) within each manipulatory event. For instance, Figure 2 was classified as one symmetric manipulatory event comprised of three cycles. Each cycle is characterized by the nearly synchronous activation of the left and right sides of the SH, EP, and AM. Figure 3 was classified as one asymmetric event comprised of four cycles. Each asymmetric cycle is characterized by asynchronous activation of the left and right sides of the SH and EP only, while the AML and AMR usually remained activated for long bursts throughout more than one cycle of shaking. Long absences of muscle activity before or after these events would typically differentiate separate manipulatory events.

To determine if the degree of asymmetric or symmetric manipulation was affected by prey, other methods were employed. Figure 4 shows the mean number of asymmetric cycles which occurred per feeding event (y-axis), for all three prey types. Results of a pairwise ANOVA (see figure legend for values) revealed that shrimp feedings required a significantly larger number of asymmetric cycles than either squid or mollies. Figure 5 shows a similar result for the symmetric behavior. Again, the pinfish used significantly more symmetric cycles per shrimp feeding than squid or mollies required.

Figure 6 is a bar graph showing that the frequency of asymmetric occurrence also was affected by prey type. The y-axis gives the percentage of total feedings

which included at least one cycle of asymmetric manipulation, for different prey types (x-axis). Notice again that the shrimp feedings required much more asymmetry (75%) than either the molly or the squid. Also, mollies elicited more frequent use of asymmetry (17%) than the squid. These results indicate that shrimp elicited both a higher frequency of symmetric and asymmetric activity, and an increased repetition of asymmetric cycles to engulf prey.

For examples of the chart recordings for symmetric and asymmetric behaviors, refer to Figures 2 and 3, respectively. Figure 2 shows a typical event of symmetry, this one including three cycles of activity bursts. Symmetric manipulation usually occurred with prey that were too large to swallow immediately, and occurred while the fish bit or crushed down on the prey while held between the jaws. Figure 3 shows a typical event of asymmetry, this one including four cycles of activity. Vertical lines are the reference points for SHL initiation used to measure the onset variables. The SHL and EPL fire in a synchronous manner followed by the SHR and EPR muscles firing synchronously for each cycle. Asymmetry usually occurred as the shrimp or molly was being shaken laterally while still lodged between the jaws. This resulted in small pieces of the peeled shrimp being ripped loose, as the main body became smaller and smaller for swallowing. Once the shrimp was completely swallowed, the extraneous pieces were eaten immediately.

DISCUSSION

By use of electromyographic experimentation on the patterns of activity of three cranial muscles used for feeding, this study was able to quantitatively provide some insight on two major questions: (1) Does the pinfish have the ability to modulate its feeding motor patterns (symmetric or otherwise) in response to different prey?, (2) Does the pinfish have the ability to use asymmetric muscle activities for feeding, and if so, is it a stereotypic type of behavior or can the pinfish "pick and choose" the degree of usage of this behavior for different feeding situations?

In response to the first question, the EMG variables show that *Lagodon* does not modulate its motor patterns to a very large degree. From ANOVAs on two feeding behaviors (strikes and symmetric manipulations), only the epaxial muscle durations on both sides of the head showed a significant prey type effect for each behavior. Even though the pinfish obviously has the ability to feed on many prey types, the durations and onsets of those feedings do not alter. In response to the second question: yes, pinfish do have the ability to fire the sternohyoideus and epaxial muscles in an asymmetric manner (see Fig. 3). The adductor mandibulae portion 2 muscle was not found to fire asymmetrically, though. Instead, the AM muscle remained constantly active during the cycles of the asymmetric firing of the SH and EP, probably in order to hold the prey in the mouth during rapid shaking.

Asymmetric manipulatory behavior was not tested for a prey type effect because the pinfish used the behavior mostly for shrimp, marginally for fish, and never for squid. Therefore, the answer to the next part of the second question must be that the asymmetric behavior is not used uniformily for all prey types, but instead is selected and fine tuned for different situations. For instance, as in Figures 4 and 6, *Lagodon* uses the behavior more often in shrimp than for squid or mollies, and uses more cycles per behavior for shrimp (i.e., the very quick and distinct shaking event lasted longer when shaking shrimp) than for squid or mollies. So, the pinfish can pick and choose from its neuromuscular feeding repertoire particular symmetric and asymmetric activity patterns which in themselves do not differ much in duration or onset of firing, but in frequency and duration of usage.

One remark to be included about the effect of prey type in this study is that the effect of prey probably involved characteristics such as size and shape, and not the particular taxa itself. It is unlikely that the squid taxon in general would illicit a stereotypic response, for it is speculated that had the squid pieces used for this study been large, 3 cm^2 pieces instead of the 1 cm^2 ones used, surely the feeding response would have been different (much more manipulation would probably have occurred, including asymmetrically). Likewise, if the shrimp used in this study were smaller pieces (such as halves or thirds of the entire body), less manipulation would probably have occurred. Let it be stressed that the prey

types used were constant in size and shape, and that their taxonomic positions are likely of minor importance here.

Lagodon is an interesting species as well as an economically important link within the complex ecological realm of the grass bed flats and other shallow, vegetated areas where they have been found in the largest densities compared with any other habitat (Caldwell, 1957). What are the factors responsible for their enormous abundance and success? Is it possible that one factor is their abilities to utilize asymmetric activity in order to shake and tear oversize prey apart affords them the luxury to have access to many prey sizes? Another important factor is likely to be their ability to readily graze on seagrasses when seasonally available. Due to their chisel-like incisors and their abilities to non-enzymatically rupture macrophyte cell walls via acid lysis in the stomach (Montgomery and Targett, 1992), pinfish living in vegetated areas have an almost constant overabundance of available food. Future research is clearly needed to transcend these speculations.

This study should reiterate and reinforce the warning made by Lauder and Norton (Lauder and Norton, 1980) that variations between right and left side activity must not be ignored when unilateral muscles are recorded. Bilateral asymmetry may be widespread and recording of muscle pairs is essential.

The results of this study do not support the prediction that generalist feeders will have a high capacity for modulating motor activity. Here is a known ultra-

generalist feeder whose motor patterns are only slightly altered when feeding on different prey.

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Table 1a. List of means for the 11 electromyographic variables within each prey type for the strike behavior only. Prey 1 = squid; Prey 2 = molly; Prey 3 = shrimp. Significance of ANOVA between prey types (including individual effects) indicated by an asterisk on EMG variable.

Table 1b. List of means for the EMG variables within each prey type for the symmetric manipulation behavior only. Prey type assignments same as Table 1a.

Table 1c. List of means for the EMG variables within each prey type for the asymmetric manipulation behavior only.

Table 2. List of F-ratios following an ANOVA between prey types (including individual effects) on the prey strike behavior and on the symmetric manipulation behavior for all 11 electromyographic variables. Prey type significance indicated by an asterisk.

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Figure 1. Anatomical diagram of the feeding musculature and osteology of a representative Sparid fish (Genus:Calamus) showing the major muscles used for electromyography. **Muscles**: The dorsally located epaxialis muscles contract to elevate the head during the expansive phase of feeding. The adductor mandibulae is one of the principle oral jaw muscles responsible for mouth closing. The ventrally located sternohyoideus muscle contracts to depress the hyoid bone which in turn causes lower jaw depression during the expansive phase of feeding. **Abbreviations**: AM = adductor mandibulae muscle; DN = dentary; EP = epaxialis muscle; HY = hyoid bone; MX = maxilla; NC = neurocranium; OP = opercle; PG = pectoral girdle; PMX = pre-maxilla; SH = sternohyoideus muscle; SUS = suspensorium.

Figure 2. Electromyograph of a typical symmetric manipulatory event comprised of three individual cycles. SHL: sternohyoideus left. SHR: sternohyoideus right. EPL and EPR: epaxialis left and right. AML and AMR: adductor mandibulae (portion 2) left and right. Note the closely synchronal occurrence of the lateral halves of the SH, EP, and AM muscles for each independent manipulatory cycle.

Figure 3. Electromyograph of a typical asymmetric manipulatory event. Muscle abbreviations the same as above. Note the asynchronous occurrence of the lateral halves of the SH and EP muscles for each independent cycle while the

AML and AMR muscles are symmetrically contracted for the duration of the manipulatory event including each cycle and the intervals between.

Figure 4. Bar graph showing the mean number of asymmetric cycles per feeding event (y-axis) for each prey type (x-axis). Actual means are as follows: prey type 1 (squid) mean = 0.00 (n=8); prey type 2 (molly) = 1.71 (n=7); prey type 3 (shrimp) = 14.25 (n=4). A Pairwise ANOVA test on the prey type means concluded that prey 1 and 2 are not statistically different (p-value = 0.563) but prey 1 and 2 each are statistically different from prey 3 (p-value < 0.001 for both cases).

Figure 5. Bar graph showing the mean number of symmetric cycles per feeding event for each prey type. Pairwise ANOVA test on prey type effect concluded that prey 1 and 2 are not statistically different (p-value = 0.702) but prey 1 and 2 each are statistically different from prey 3 (p-value < 0.005 for both cases).

Figure 6. Bar graph showing the percentage of total feeding events which included any asymmetric manipulation (y-axis) for each prey type (x-axis). Prey type assignments the same as Figure 4.

TABLE 1a. -- STRIKE

VARIABLE	PREY TYPE 1	PREY TYPE 2	PREY TYPE 3
	mean (± S.E.)	mean (± S.E.)	mean (± S.E.)
SHLDUR	27.125 (4.7) N=8	40.500 (4.3) N=7	64.875 (17.6) N=2
EPLDUR*	5.679 (2.0) N=7	24.607 (6.7) N=7	16.125 (16.1) N=2
AMLDUR	55.844 (17.9) N=8	86.393 (31.6) N=7	120.000 (63.0) N=2
SHRDUR	25.000 (7.5) N=8	31.500 (8.4) N=7	19.750 (3.25) N=2
EPRDUR*	22.844 (6.7) N=8	47.643 (11.6) N=7	28.125 (28.1) N=2
AMRDUR	88.656 (18.7) N=8	126.929 (28.6) N=7	104.000 (34.5) N=2
EPLONS	1.938 (0.8) N=4	1.500 (1.0) N=6	0.000 (--) N=1
AMLONS	12.500 (4.7) N=8	13.429 (3.5) N=7	8.625 (0.1) N=2
SHRONS	-6.333 (3.9) N=6	1.717 (2.1) N=7	6.750 (0.7) N=2
EPRONS	-1.542 (1.8) N=6	-3.792 (5.6) N=6	0.000 (--) N=1
AMRONS	10.063 (4.9) N=8	13.500 (3.9) N=7	13.750 (3.7) N=2

TABLE 1b. -- SYMMETRIC MANIP.

VARIABLE	PREY TYPE 1	PREY TYPE 2	PREY TYPE 3
		mean (± S.E)	mean (± S.E.)
SHLDUR	--	52.071 (4.4) N=7	40.315 (3.7) N=23
EPLDUR*	--	36.607 (4.3) N=7	10.663 (2.7) N=23
AMLDUR	--	137.036 (27.4) N=7	127.533 (7.3) N=23
SHRDUR	--	78.286 (18.0) N=7	39.315 (7.0) N=23
EPRDUR*	--	57.064 (8.2) N=7	19.359 (4.9) N=23
AMRDUR	--	162.893 (29.8) N=7	130.250 (8.7) N=23
EPLONS	--	3.714 (1.7) N=7	6.750 (1.5) N=13
AMLONS	--	9.536 (3.2) N=7	12.705 (1.7) N=22
SHRONS	--	-7.825 (3.5) N=6	-7.083 (3.0) N=18
EPRONS	--	-3.421 (4.7) N=7	0.712 (2.2) N=13
AMRONS	--	8.714 (3.2) N=7	12.875 (1.8) N=22

TABLE 1c. -- ASYMMETRIC MANIP.

VARIABLE	PREY TYPE 1	PREY TYPE 2	PREY TYPE 3
		mean (± S.E.)	mean (± S.E.)
SHLDUR	--	41.042 (8.6) N=6	30.152 (2.4) N=28
EPLDUR	--	32.250 (7.0) N=6	17.223 (1.2) N=28
AMLDUR	--	410.708 (27.5) N=6	249.875 (33.0) N=28
SHRDUR	--	34.958 (9.0) N=6	18.170 (3.3) N=28
EPRDUR	--	32.083 (3.6) N=6	15.848 (3.0) N=28
AMRDUR	--	438.750 (34.2) N=6	274.375 (32.7) N=28
EPLONS	--	7.100 (1.0) N=5	4.148 (0.7) N=27
AMLONS	--	-20.542 (6.2) N=6	-12.838 (7.0) N=20
SHRONS	--	72.000 (16.0) N=6	30.988 (2.3) N=21
EPRONS	--	74.750 (16.4) N=6	32.671 (2.6) N=19
AMLONS	--	-39.000 (9.5) N=6	-4.795 (5.9) N=28

* Significant at $P<0.05$.

TABLE 2.

EMG VARIABLE	F-RATIO FOR PREY TYPE EFFECT IN STRIKE BEHAVIOR	F-RATIO FOR PREY TYPE EFFECT IN SYMMETRIC MANIPULATION BEHAV.
SHLDUR	4.138 (1,9)	0.521 (1,18)
EPLDUR	8.878* (1,8)	12.386* (1,18)
AMLDUR	0.891 (1,9)	0.075 (1,18)
SHRDUR	1.325 (1,9)	1.845 (1,18)
EPRDUR	11.844* (1,9)	7.100* (1,18)
AMRDUR	1.336 (1,9)	0.446 (1,18)
EPLONS	--	1.506 (1,15)
AMLONS	0.021 (1,9)	0.005 (1,17)
SHRONS	--	0.828 (1,18)
EPRONS	--	1.788 (1,15)
AMRONS	0.156 (1,9)	0.054 (1,17)

* Significant at $P<0.05$. ( ) = degrees freedom

FIGURE 1.

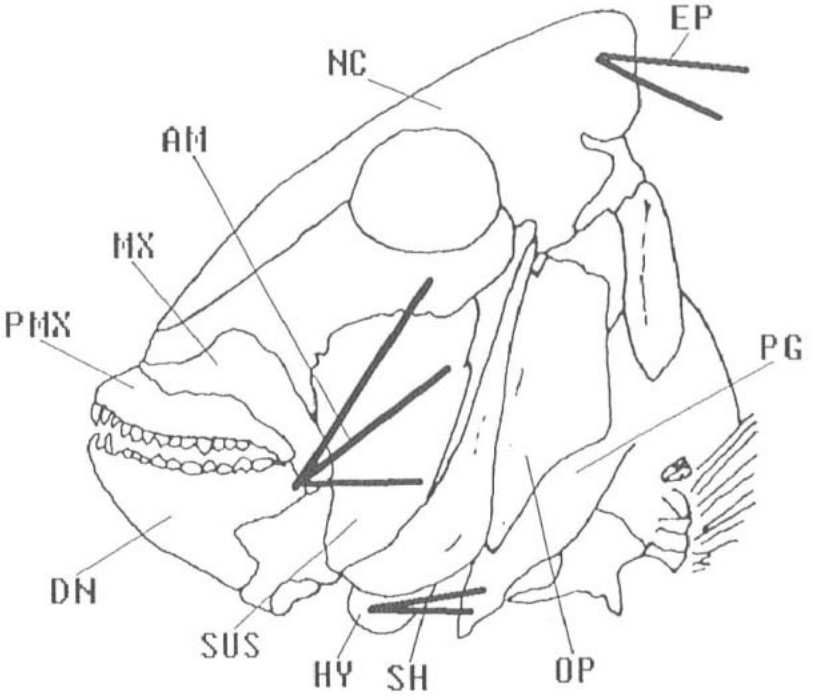


FIGURE 2.

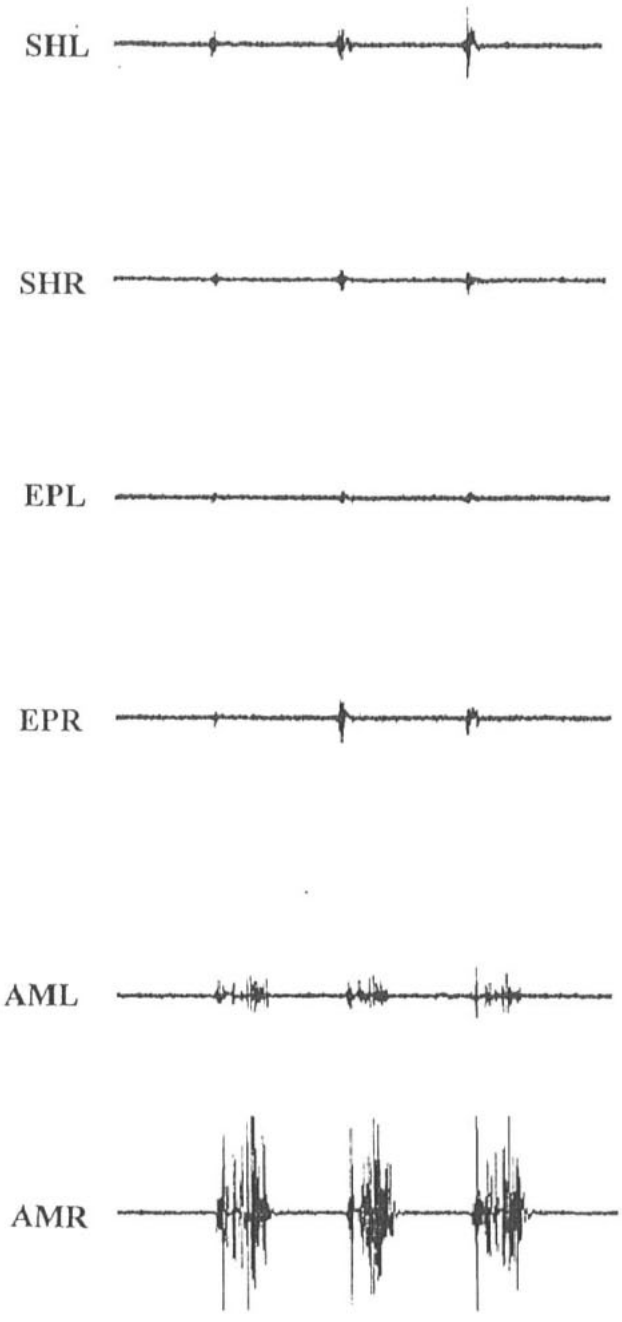
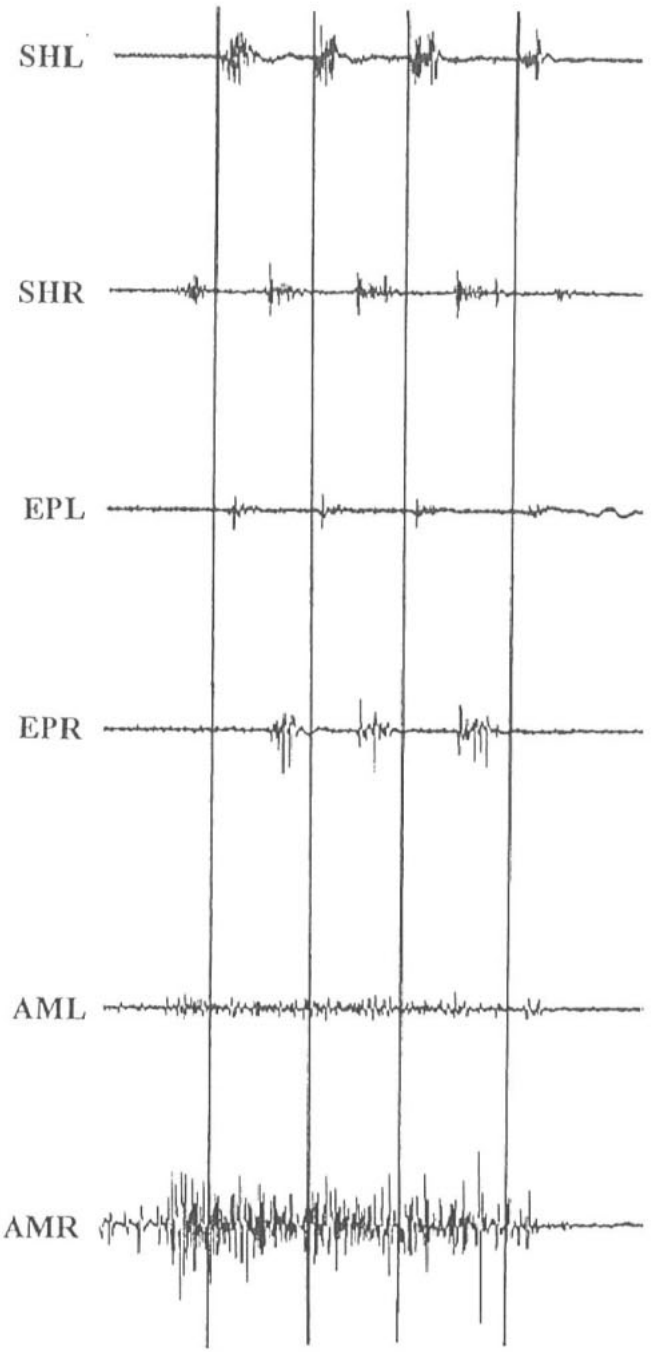


FIGURE 3.



——— = 160 msec.

FIGURE 4.

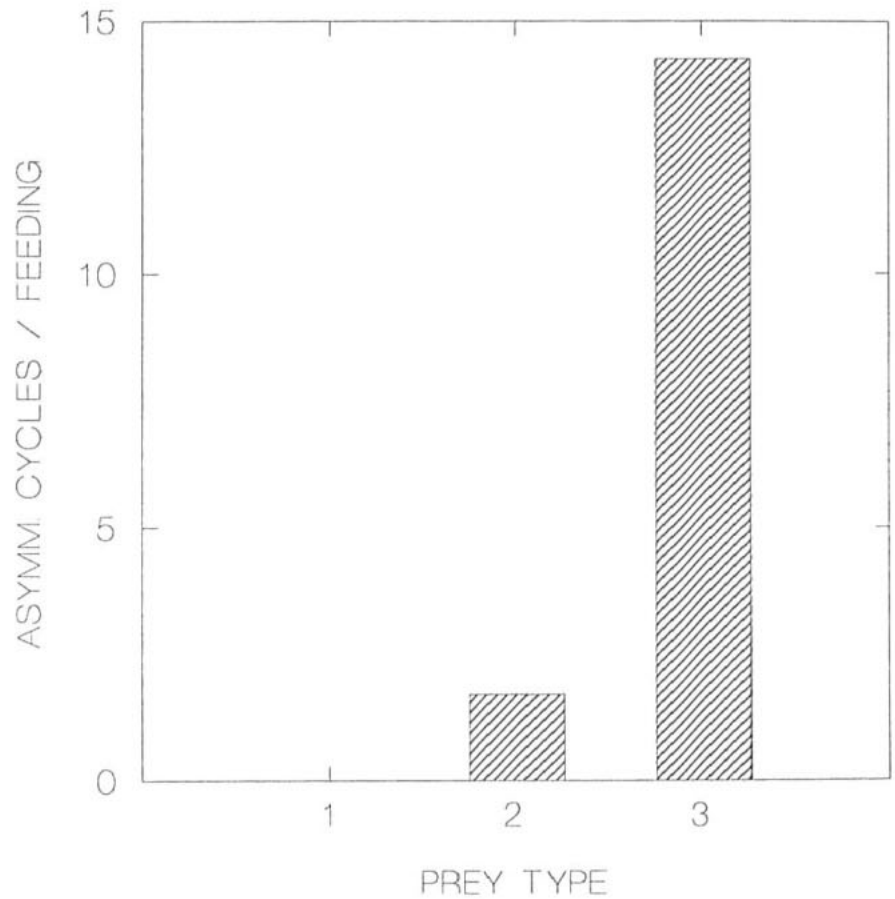


FIGURE 5.

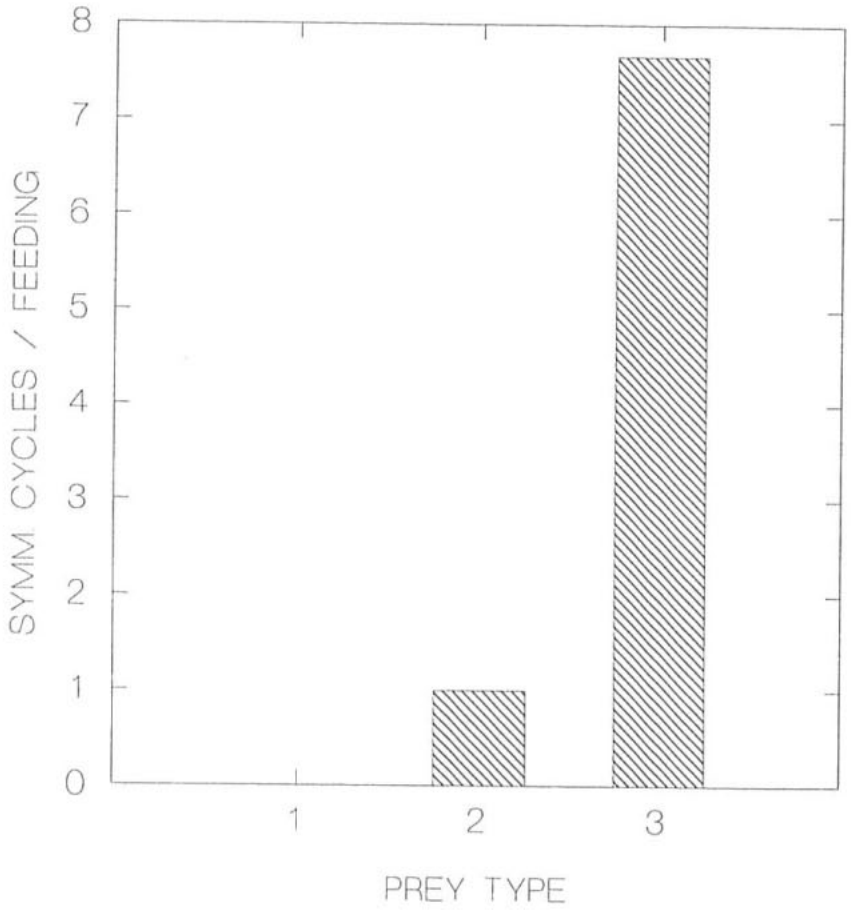
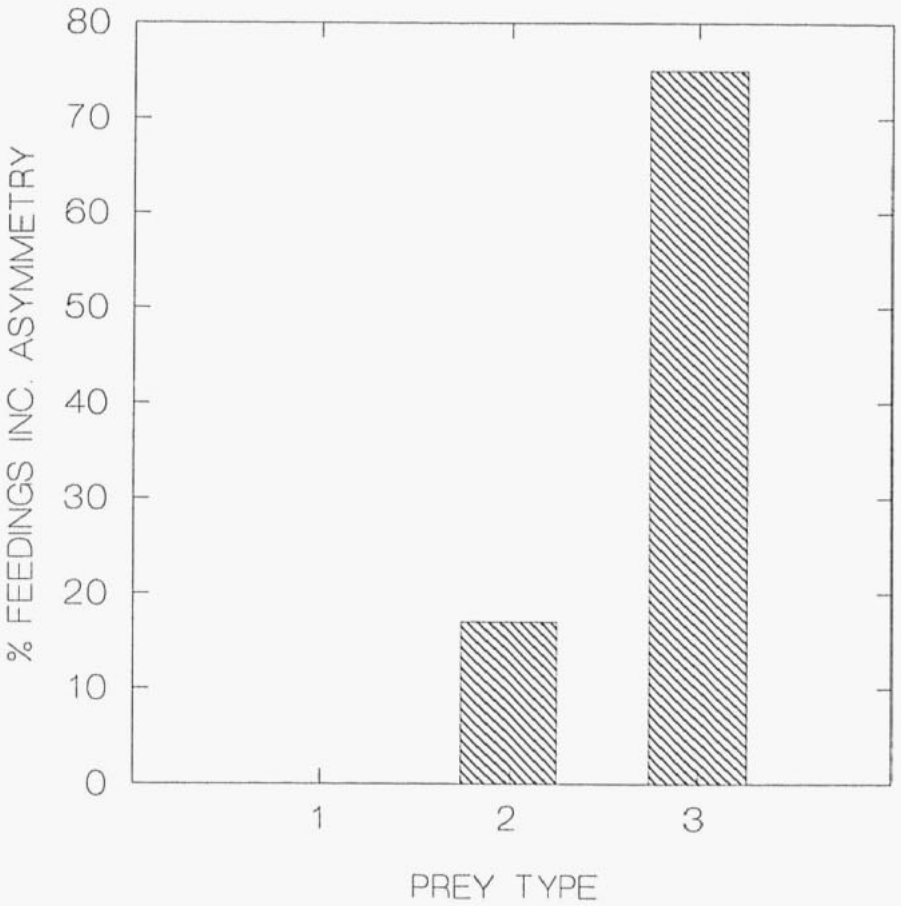



FIGURE 6.