MOTOR CORRELATES OF LEARNING BEHAVIOUR: FEEDING ON NOVEL PREY BY PUMPKINSEED SUNFISH (*LEPOMIS GIBBOSUS*)

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SUMMARY

The functional basis of learning in prey capture was investigated in the pumpkin-seed sunfish (*Lepomis gibbosus*). Feeding performance of sunfishes was assessed when the fish were first fed a novel, elusive prey (guppies) and compared with their performance after several weeks of experience with capturing guppies. During these feedings electromyographic recordings were made to document the pattern of activity in four jaw muscles at the strike. With experience, the *L. gibbosus* improved their ability to capture guppies, and several changes in the pattern of muscle activity were associated with this improved performance. Average duration and maximum amplitude of activity in all muscles increased between trials. Previous studies of muscle activity modulation in fishes indicate that these changes could improve feeding performance on an elusive prey. Thus, specific modifications of muscle activity appear to be one functional determinant of feeding success in fishes.

INTRODUCTION

Neuroethologists have devoted considerable attention to the motor basis of learning in vertebrates (Gray & Lissmann, 1946; Gray, 1950; Bullock, 1961; Held, 1963; Konishi, 1965, 1978; Shashoua, 1969; Dufosse, Macpherson & Massion, 1982). A primary goal of this work has been to elucidate the physiological processes that underlie the acquisition of learned behaviour. In some studies, improved performance of a task gained through experience (i.e. learning) has been found to be directly associated with alterations of the muscle activity pattern of the behaviour (Konishi, 1965; Dufosse *et al.* 1982). The mechanisms of sensory feedback and integration of new information involved in this phenomenon are of central interest to the neurobiologist, but this type of learning also presents an opportunity to investigate the functional significance of specific motor patterns. Examination of the changes in muscle activity that are associated with improved performance should provide insights into the biomechanical basis of proficiency in the behaviour. In the

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present study this approach is used to interpret the functional role of jaw muscle activity patterns used by feeding fishes.

Electromyographic studies of prey capture in teleost fishes have shown that many species are capable of altering the activity pattern of jaw muscles during feeding on different prey (Ballintijn, Van Den Berg & Egberink, 1972; Elshoud-Oldenhave & Osse, 1976; Elshoud-Oldenhave, 1979; Liem, 1978, 1979, 1980; Lauder, 1981, 1983a; Wainwright & Lauder, 1986). This ability to modulate muscle activity has usually been interpreted as a functional response which allows the fish to 'fine tune' its behaviour to feed more effectively on a given prey type. A persistent finding in these studies is that capture of elusive prey by suction feeding, in comparison to capture of slow or dead prey, is associated with increased activity and increased overlap of activity in jaw muscles (Elshoud-Oldenhave, 1979; Liem, 1979; Lauder, 1981; Wainwright & Lauder, 1986). Increasing magnitude and overlap of muscle activity is thought to increase the suction pressure inside the buccal cavity of the fish and thereby improve the fish's ability to capture more elusive prey. Experimental evidence from aquatic salamanders (Lauder & Shaffer, 1985) and fishes (Lauder, Wainwright & Findies, 1986) supports this presumed relationship between muscle activity and buccal pressure since durations of activity of several head muscles were found to be positively correlated with negative buccal pressure. However, while sound biomechanical evidence links muscle activity and buccal pressure, no data exist which directly relate muscle activity patterns or buccal pressure to feeding performance.

In the present study the motor basis of prey capture was characterized by quantifying the activity patterns of four key feeding muscles in the pumpkinseed sunfish (*Lepomis gibbosus*). Electromyograms were recorded during each fish's first feedings on a novel, highly elusive prey (guppies), and again after several weeks of exposure to the guppies. Concomitant measures of feeding performance were made during the experiments which document that, with experience, the fish improved their ability to capture the guppies. The main purpose of this study is to test two hypotheses. First, it is predicted that as the *L. gibbosus* improve their performance, changes will occur in the motor basis of the feeding mechanism. Second, changes that do occur should be those expected on the basis of earlier modulation work: improved feeding performance on this elusive prey is predicted to be associated with an overall increase in and overlap of activity in the muscles examined.

MATERIALS AND METHODS

Experimental animals

Ten *Lepomis gibbosus* (Centrarchidae) were collected with seines in Three Lakes, Kalamazoo County, Michigan, USA. The fish were maintained in the laboratory in 35-l aquaria at 17 °C. Standard lengths of the fish ranged from 116 to 142 mm. Since larger fish may be inherently better at capturing elusive prey (Werner, 1974) the 10 fish were divided into two groups of roughly equal size structure (Table 1);

Table 1. *Means for eleven electromyographic variables measured during feedings on guppies by five experimental and five control fish (Lepomis gibbosus) during two trials*

Experimental group

Variable	1	2	3	4	5
LOPDUR (ms)	80·5 (86·7)	48·1 (51·6)	71·3 (99·3)	33·5 (63·5)*	48·3 (83·7)
AM2DUR (ms)	33·1 (114·6)**	22·5 (145·8)**	78·9 (155·3)*	91·8 (156·3)*	85·5 (63·5)
EPDUR (ms)	24·2 (63·4)**	30·3 (50·8)*	20·4 (34·8)	37·5 (117·5)**	73·3 (55·4)
SHDUR (ms)	29·7 (74·1)*	32·9 (95·0)	40·3 (71·7)	63·4 (67·1)	66·9 (62·1)
LOPAMP (µV)	294 (413)	519 (137)**	254 (398)*	102 (605)**	258 (359)
AM2AMP (µV)	234 (573)***	215 (572)**	241 (511)**	210 (603)	443 (381)
EPAMP (µV)	137 (1092)**	383 (611)	163 (750)***	315 (734)***	781 (718)
SHAMP (µV)	136 (643)***	169 (550)**	383 (252)	316 (554)***	298 (421)
LOP–AM2 (ms)	36·5 (23·2)	15·3 (2·7)	9·4 (25·7)	11·5 (24·9)	16·9 (24·8)
LOP–EP (ms)	21·7 (10·8)	2·6 (−3·1)	15·6 (10·8)	−2·2 (10·3)	7·4 (5·4)
LOP–SH (ms)	8·9 (9·3)	14·6 (−4·0)*	11·0 (18·7)	4·0 (13·4)	7·9 (2·7)
Strikes per capture	4·1 (1·5)*	3·8 (1·5)*	4·6 (1·8)*	5·6 (1·6)*	2·9 (2·1)
Standard length (mm)	136	142	133	116	120

Control group

Variable	6	7	8	9	10
LOPDUR (ms)	58·6 (59·7)	56·5 (37·1)	125·7 (107·8)	55·2 (78·5)	43·5 (86·5)*
AM2DUR (ms)	75·0 (104·6)*	86·0 (104·1)	104·8 (59·2)	72·8 (131·7)*	155·1 (68·9)**
EPDUR (ms)	32·0 (39·7)	32·5 (54·4)**	88·1 (43·9)	29·0 (33·0)	56·3 (47·4)
SHDUR (ms)	75·5 (33·4)*	38·7 (74·6)**	51·1 (80·3)	31·5 (57·2)	45·0 (62·5)
LOPAMP (µV)	592 (198)**	313 (210)	596 (500)	226 (236)	268 (312)
AM2AMP (µV)	442 (490)	465 (495)	301 (310)	322 (583)*	453 (382)
EPAMP (µV)	419 (373)	362 (1014)*	533 (504)	95 (202)	495 (732)*
SHAMP (µV)	415 (163)*	294 (426)	307 (503)	93 (264)	613 (543)
LOP–AM2 (ms)	32·0 (35·1)	11·9 (4·1)	27·8 (44·0)	21·8 (21·2)	2·9 (1·2)
LOP–EP (ms)	13·1 (12·2)	1·3 (−1·2)	12·9 (28·8)	10·61 (23·7)	0·6 (−3·8)
LOP–SH (ms)	17·6 (12·0)	0·8 (−0·4)	15·72 (28·6)	4·4 (11·1)	0·8 (−1·9)
Strikes per capture	3·1 (3·2)	3·5 (4·39)	3·67 (3·4)	2·25 (3·5)	3·8 (3·7)
Standard length (mm)	127	142	125	133	117

* Significantly different at $P<0.01$; ** different at $P<0.001$.
Means for trial two are given in parentheses after means for trial one.
Feeding performance, measured by the number of strikes per capture is also given.
See text for experimental treatments and descriptions of EMG variables.

an experimental group (mean standard length = 128 mm) and a control group (mean = 129 mm) composed of five fish each. All fish were fed a diet of earthworms (*Lumbricus* sp.) during the 3 weeks between their capture and the first experiments.

Guppies (*Poecelia*) were chosen as the experimental prey because they represent a novel, elusive prey type for *L. gibbosus*. *L. gibbosus* found in Three Lakes, Michigan are virtually never piscivorous and instead feed on gastropods and various arthropods (Mittlebach, 1984). Therefore, at the onset of the experiment the *L. gibbosus* were assumed to have no experience in attempting to capture small fish.

Experimental techniques

Electromyographic (EMG) recordings were made simultaneously from four cranial muscles following a procedure described in detail elsewhere (Lauder, 1983*b*). Briefly, bipolar fine-wire electrodes (Basmajain & Stecko, 1962) were implanted directly into the belly of each muscle while the fish was anaesthetized with tricaine methane sulphonate. The exact location of entry, angle of penetration and depth of insertion of electrodes was standardized for each muscle to minimize any effects of differences in experimental preparation on overall variation in EMG parameters among individuals. The electrode wires from each muscle were glued together into a common cable which was sutured to the back of the fish slightly anterior to the dorsal fin, so that slight tension on the cable would not dislodge the electrode tips from the muscle.

Electrical activity from the muscles was recorded on a Bell & Howell 4020A tape recorder. The amplifier bandwidth (Grass P511J) was 100–3000 Hz and the electromyograms were amplified 10 000 times. Feeding sequences were digitized at a sample rate of 1272 Hz using a DAS 12-bit analogue-to-digital converter and stored on an IBM XT microcomputer. A chart record for visual inspection was made from the computer file of each feeding.

In the two experimental trials recordings were made from all fish during feedings on at least 10 guppies. Feeding performance was assessed by counting the number of strikes that was required to capture each prey. At the time of the first trial none of the fish had ever been fed guppies. During the 6 weeks between trials the five control fish were maintained on a diet of earthworms and were never fed fish while the five experimental group fish were fed guppies almost daily. A total of 228 feedings was analysed.

Four muscles were chosen for this study, based on their role in the feeding mechanism, their ease of experimental accessibility and the large amount of previously reported data on their modulatory activity during feeding. A brief description of their function follows (see Lauder, 1983*c* for anatomy and a more detailed functional discussion). All muscle names follow Winterbottom (1974). The levator operculi (LOP) is the primary jaw opening muscle. Division 2 of the adductor mandibulae (AM2) is the main jaw closer. The anterior epaxial musculature (EP) inserts into the back of the neurocranium and lifts the head, contributing to jaw

opening. Lastly, the sternohyoideus (SH) depresses the hyoid apparatus thus forcing down the floor of the mouth and expanding the oral cavity; an important suction-generating action in the feeding mechanism.

A computer program was used to measure 11 variables from the myogram file of each feeding. These variables summarized the overall pattern of activity in the four muscles. For each muscle the duration of activity was measured in milliseconds (LOPDUR, AM2DUR, EPDUR, SHDUR). Also, the maximum amplitude of each muscle burst was recorded in microvolts (LOPAMP, AM2AMP, EPAMP, SHAMP). EMG electrodes of the type used in this study record regional, extra-cellular changes in electrical potential summed over all local motor units undergoing depolarization. The maximum amplitude variables then represent peak summations of activity in the vicinity of the electrode tips and were taken as one measure of overall intensity of muscle activity. Finally, the temporal sequence of muscle activity was characterized by choosing LOP as a reference muscle and measuring the difference in time of onset of activity between it and each of the other three muscles (LOP–AM2, LOP–EP, LOP–SH). The eight duration and maximum amplitude variables were taken to represent the amount of activity each muscle puts into the strike while the three relative onset times estimated the degree of overlap in activity among the four muscles.

In addition to these experiments comparative data were obtained from several individuals of three other centrarchid species, *Lepomis macrochirus*, *Micropterus salmoides* and *Pomoxis nigromaculatus*, during feeding upon worms (*Lumbricus* sp.) and small fish (*Pimephales* sp.).

Data analysis

In this study five experimental and five control fish were used to ensure that individual variation was not the cause of any inter-group differences (Shaffer & Lauder, 1985; Wainwright & Lauder, 1986). The overall experimental design used was a two-way analysis of variance (ANOVA) with a nested level. Overall differences in the EMG variables were first sought between the control and experimental groups. None was found so the data set was divided into these two groups for subsequent analyses. Next, two-way mixed model ANOVAs were employed with each group to compare the average value of each variable for all individuals across the two trials. In all of these ANOVAs the interaction term was a significant effect so all tests of the difference between trial one and two were calculated using the interaction error term in the denominator of the F ratio (Sokal & Rohlf, 1981). Finally, one-way ANOVAs were performed on the data from each fish to explore muscle variable changes between trials for every individual. Because many significance tests were performed a probability value of $P < 0.01$ was used as the minimum criterion for significance.

Assumptions about distributions and equality of variances were met satisfactorily with the untransformed data set. All data manipulations and statistical calculations were done with SYSTAT (Evansville, Illinois) on an IBM XT microcomputer.

RESULTS

Feeding performance of the experimental group improved significantly between the two trials, as the number of strikes per capture decreased, while control group fish were significantly less proficient in trial two (both $P < 0.01$, Tables 1, 2). In addition, within the experimental group all eight of the EMG activity variables increased in magnitude between trials (Table 2; Fig. 1). Half of these changes were statistically significant. In contrast, for the control fish these variables varied equally in both directions and never yielded a significant change (Table 2). No pattern of change was observed in the relative onset time variables. These means were compared to values of the same relative onset time variables obtained from other centrarchids feeding on immobile worms and elusive fish (Table 3). The relative onset times of *L. gibbosus* were most like those seen in other species feeding on fish.

All variables in both groups were significantly different among individuals (all $P < 0.01$). In both groups, means for all variables varied by as much as a factor of 5 among individuals (Table 1). Nevertheless, group trends were reflected in tests at the individual level. Four fish of the experimental group showed significant changes in at least four of the 11 EMG variables (Table 1). Most of these were among the eight activity variables and all but one of these 20 significant changes matched the direction of predicted change. All four of these fish improved in feeding performance between trials. The fifth experimental fish did not improve in performance and none of its EMG variables changed significantly between trials. Within the control group no individual had more than four variables which changed significantly and never more than two of these matched the predicted direction of change. No pattern in direction of change was observed in the eleven significant EMG alterations in this group, since about half increased and half decreased.

Table 2. *Means for eleven electromyographic variables averaged across five experimental and five control fish* (Lepomis gibbosus) *in two feeding trials*

| Variable | Experimental group | | Control group | |
	Trial 1	Trial 2	Trial 1	Trial 2
LOPDUR (ms)	54·3	77·5*	67·4	74·5
AM2DUR (ms)	66·0	122·4	100·0	100·0
EPDUR (ms)	39·7	64·4	48·8	44·3
SHDUR (ms)	50·1	84·3*	48·1	61·4
LOPAMP (μV)	272	382	297	294
AM2AMP (μV)	277	522*	398	445
EPAMP (μV)	378	791*	558	387
SHAMP (μV)	266	492	355	377
LOP–AM2 (ms)	18·7	29·1	18·7	22·2
LOP–EP (ms)	6·7	7·5	7·1	12·3
LOP–SH (ms)	7·4	9·1	7·9	10·5
Strikes per capture	4·0	1·7*	2·9	3·6*

* Significantly different at $P < 0.01$.
Feeding performance, measured as number of strikes per capture, is also given.
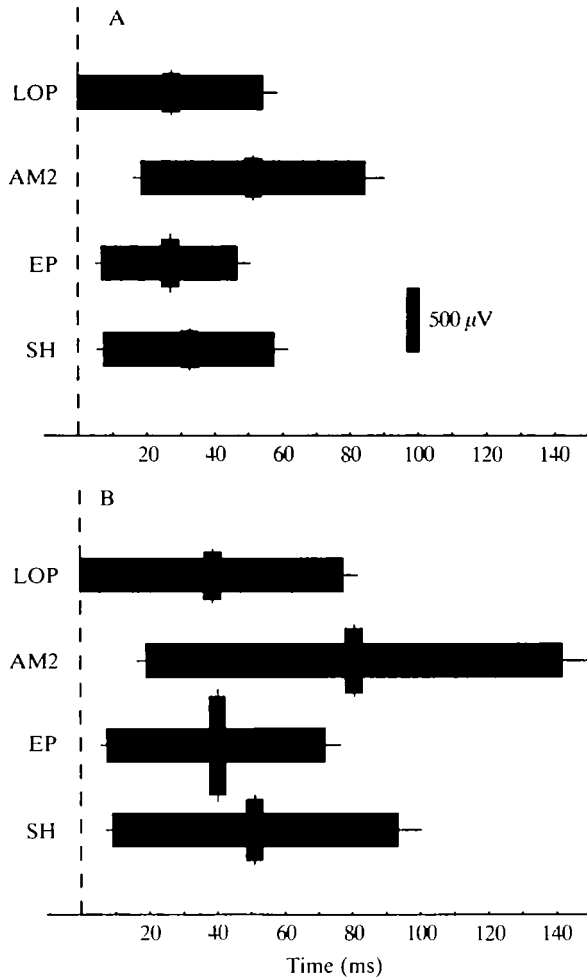See text for experimental treatment and variable descriptions.

Fig. 1. Electromyographic bar diagrams of muscle activity in four head muscles averaged over five fish (*Lepomis gibbosus*) during (A) the first feedings on a novel prey and (B) after several weeks of experience feeding on the new prey. Length of horizontal bars is mean duration of activity (±S.E.M.) of each muscle. Distance between vertical broken line and start of activity is the relative onset time. Vertical bars are mean maximum amplitude (±S.E.M.). See text for key to muscles. ($N = 54$ feedings in A, $N = 58$ feedings in B).

DISCUSSION

Motor basis of feeding performance

L. gibbosus showed a significant improvement in the ability to capture guppies after several weeks of exposure to this novel, elusive prey. This was associated with several conspicuous alterations in the pattern of activity of the four head muscles (Table 2; Fig. 1). Durations of activity and maximum amplitudes increased in all muscles as predicted on the basis of previous modulation studies of other teleostean fishes. Thus, the present study directly demonstrates (for the first time) experience-induced alterations of a motor pattern in fishes. The contrast between jaw muscle

activity patterns before and after improved performance was achieved suggests that these changes were an alteration of the feeding mechanism that contributed to the fish's increased feeding success.

Elusive prey are better able than less mobile types to escape the field of water movement created during suction feeding. A predatory fish can make prey escape more difficult by increasing the negative pressure inside its buccal cavity thus increasing the velocity of incoming water. Quantitative studies show a positive correlation between durations and maximum amplitudes of muscles and negative buccal pressure in salamanders (Lauder & Shaffer, 1985) and other centrarchid fishes (Lauder et al. 1986). Thus, it appears that L. gibbosus exhibited improved feeding performance, at least in part, through an increase in jaw muscle activity and hence, greater suction.

While modulation of jaw muscle activity may be one determinant of a fish's ability to capture elusive prey, there are other factors which have not been considered here. For example, it is important that the fish be able to move close enough to the prey that the strike has the potential of being successful. Maximum swimming speed and manoeuvrability are two variables that have been proposed to influence approach ability and thus feeding success in piscivores (Webb, 1978). In a study of swimming speed during feeding in four teleost fishes, Webb (1984) showed that the centrarchids Ambloplites and Micropterus swam at only one-seventh maximum speed during pursuit of minnows (Pimephales). He suggested that these fish sacrifice swimming speed for manoeuvrability as a predatory tactic. In light of the results of the present study one goal of future research will be to test experimentally the relative contributions of buccal suction pressures, maximum swimming speed and manoeuvrability to the feeding performance of piscivorous fishes exhibiting different foraging strategies.

Modulation

The ability of animals to improve, with experience, their success in feeding on novel prey types is a well-documented phenomenon in birds (Pietrewicz & Kamil, 1979), fishes (Ware, 1971; Werner, Mittlebach & Hall, 1981) and insects (Heinrich,

Table 3. *Mean relative onset time EMG variables for trials one and two from experimental* Lepomis gibbosus *(this study)*

Variable	L. macrochirus[1] Worms/fish		M. salmoides[2] Worms/fish		P. nigromaculatus[3] Worms/fish		L. gibbosus Trial 1	Trial 2
LOP–AM2 (ms)	63·8	29·2	57·5	41·8	80·0	43·5	18·7	29·1
LOP–EP (ms)	17·5	6·0	16·3	7·7	23·3	8·9	6·7	7·5
LOP–SH (ms)	23·5	6·3	24·0	6·9	7·2	10·9	7·4	9·1

[1]*Lepomis macrochirus*; [2]*Micropterus salmoides*; [3]*Pomoxis nigromaculatus*.
Shown for comparison are the same variables from three centrarchid species feeding on worms and fish.
See text for variable descriptions.

1979). Werner *et al.* (1981) have shown that other species of *Lepomis* require about 6–8 trials to reach their peak feeding performance on a new prey. This general lag time together with the results of the present study suggest that, while the capacity to modulate muscle activity may be inherent in many fish taxa (Elshoud-Oldenhave, 1979; Liem, 1980; Lauder, 1981; Wainwright & Lauder, 1986), specific patterns of muscle activity may be acquired largely through experience. Fishes used in modulation studies are typically maintained on a diet of what will be the experimental prey, thus allowing them an opportunity to learn appropriate feeding responses. A significant question concerns the extent to which intraspecific feeding repertoires (Liem, 1980) are an innate property of different fish taxa or if they are primarily experience-induced modifications of the basic suction feeding mechanism.

While some of the changes in muscle activity that were predicted in this study did occur, one type did not. Increased simultaneous activity of muscles, as measured by reduced relative onset times has been associated with elusive prey capture in several fish taxa (Liem, 1978; Lauder, 1981; Wainwright & Lauder, 1986). Comparison of the mean relative onset times in both trials of the present study with the same variables in three other centrarchids feeding on worms and fish reveal that, even in the first trial, *L. gibbosus* utilized a muscle overlap pattern more similar to other species feeding on fish than on non-elusive worms (Table 3). Modifications of the relative onset times of the first trial are not necessary to produce the typical centrarchid pattern exhibited during feeding on fishes.

Individual variation

Two types of individual variation were found in this study. First, the means for all 11 variables were remarkably variable among individuals (Table 1). It is evident that without several fish in each group erroneous differences would certainly have been found between treatment and control groups. Similar levels of intraspecific variation have been reported in other fishes (Wainwright & Lauder, 1986) and in aquatic salamanders (Shaffer & Lauder, 1985). It should be pointed out, however, that in the present study differences among experimental preparations contributed to 'individual' variation. About 22 % of the EMG variables changed between trials in the control group fish (Table 1). Shaffer & Lauder (1985) found that a similar proportion (20 %) of the EMG variables they measured on salamanders varied significantly between experimental days within the same individual. However, most variables still showed significant variation among individuals supporting the general pattern reported here.

Second, one of the five experimental individuals did not follow the pattern of significantly improved feeding performance or alteration of muscle activity between trials (Table 1, fish no. 5). Historically, functional studies involving electromyography have not assessed the intraspecific component of variation (see also Shaffer & Lauder, 1985). Recent work (Shaffer & Lauder, 1985; Wainwright & Lauder, 1986) has made clear the possible pitfalls of ignoring this source of variance when higher

level comparisons (e.g. experimental groups or species) are sought. The experimental design used in the present work made it possible for a quantitative assessment of muscle activity to establish differences in group trends, in spite of individual variation in EMG variable means and individual differences in tendencies to learn.

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