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Effects of Prey Type on Motor Pattern Variance in Tetraodontiform Fishes

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ABSTRACT It is unclear whether the high variance of electromyographic parameters measured in feeding teleost fishes reflects functionally significant motor variation that is under control of the fish, or functionally insignificant variation characteristic of EMG data. We addressed this issue by examining the effect of three prey, differing in physical characteristics, on the feeding motor pattern in three fishes of the Order Tetraodontiformes: the filefish, *Monacanthus hispidus*; the triggerfish, *Balistes capriscus*; and the puffer, *Sphoeroides nephelus*. EMG recordings were made from subdivisions of the mouth closing adductor mandibulae muscle and the mouth opening levator operculi muscle in four fish from each species feeding on live fiddler crabs, live shrimp, and pieces of cut squid mantle. Analysis of variance was used to test for effects of prey type on the standard deviation of muscle burst duration, burst onset time, and average burst amplitude in the adductor muscles. The filefish exhibited a doubling of standard deviation of burst duration in all muscles when feeding on fiddler crabs; triggerfish showed increased standard deviations in onset times and duration of two muscles when feeding on squid mantle; and the puffer showed no effects of prey on motor variability. The observation that prey type can elicit more than a doubling in the standard deviation of some EMG traits indicates that a large portion of the within-prey type variance is under direct control of the individual fish, suggesting an even greater level of fine motor control in teleost feeding mechanisms than previously recognized. *J. Exp. Zool. 286:563–571, 2000.* © 2000 Wiley-Liss, Inc.

The muscle activation patterns underlying feeding behavior of teleost fishes have been a focus of research for over two decades (Ballintijn et al., ’72; Liem, ’78, ’79, ’80; Lauder, ’80, ’83a; Sibbing, ’82; Sibbing et al., ’86; Wainwright and Lauder ’86; Wainwright, ’89; Friel and Wainwright, ’98, ’99). Two general observations are pervasive in this literature: (1) motor patterns are highly variable, and (2) individual fish can alter motor patterns in response to prey type. The high variability of muscle activity patterns was noted by early workers (Osse, ’69; Ballintijn et al., ’72; Elshoud-Oldenhave and Osse, ’76) and has emerged as a dominant theme of electromyographic studies of fish feeding behavior (Lauder, ’81, ’83a; Wainwright and Lauder, ’86; Sanderson, ’88; Wainwright ’89; Turingan and Wainwright, ’93; Friel and Wainwright, ’98, ’99). Even under relatively controlled laboratory conditions electromyographic parameters that are used to describe motor patterns, such as muscle burst duration, relative onset time, or burst rectified integrated area, typically have coefficients of variation on the order of 0.3, or a standard deviation that is one-third the mean parameter value (e.g., Wainwright, ’89). This motor variability has often been assumed to represent fine tuning of the motor pattern by the individual fish in response to a variety of environmental and physiological factors that may vary from one prey capture event to another (Lauder, ’83a; Wainwright and Lauder, ’86; Sanderson, ’88), but there have been no direct attempts to test this assumption or explore alternatives.

One factor that can have a substantial impact on motor pattern traits and that has received considerable attention is prey type. Beginning with the observations of Liem (’78, ’79, ’80), workers have repeatedly shown that teleost fishes alter the mean value of muscle activation parameters in response to prey type (Lauder, ’81, ’83a; Wainwright and Lauder, ’86; Sanderson, ’88; Wainwright, ’89; Wainwright and Turingan, ’93). This

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result applies to prey capture (Sanderson, ’88; Wainwright and Lauder, ’86) and various prey processing behaviors (Sibbing et al., ’86; Wainwright, ’89; Wainwright and Turingan, ’93; Friel and Wainwright, ’98, ’99), and appears to be a universal attribute of teleost feeding systems as no well-documented cases are known of species that will not alter motor pattern in response to prey.

Without exception these studies of the effects of prey type on muscle activation patterns have focused on average parameter values, such as mean burst duration or relative time of burst onset. Typically, analysis of variance is used to test for effects of prey type on the mean value of EMG variables (e.g., Sanderson, ’88; Wainwright and Turingan, ’93).

Although prey type has been shown to affect mean EMG trait values, variance within prey type is considerable (Wainwright, ’89; Friel and Wainwright, ’98, ’99) and it remains unclear whether these high levels of variance reflect fine control of the fish or an inherently high measurement error for electromyographic parameters. In this study, we investigate the interaction between prey type and motor pattern variability by experimentally asking if some prey elicit a more variable motor response from fishes than others. We use a commonly employed experimental design in our analysis of prey type effects, the analysis of variance, but rather than test for prey type effects on mean values of EMG variables, we instead test for effects of prey type on the standard deviation of EMG variables.

MATERIALS AND METHODS

This study was part of a broader investigation of the evolution and function of jaw adductor muscles in tetraodontiform fishes (Turingan and Wainwright, ’93; Wainwright and Turingan, ’93; Turingan et al., ’95; Friel and Wainwright, ’97, ’98, ’99). Members of this cosmopolitan teleost order have relatively small, powerful jaws with stout teeth and they frequently subdue larger prey by repeatedly biting off small, manageable pieces that are swallowed. This cyclical biting behavior, termed buccal manipulation (Lauder, ’83b; Turingan and Wainwright, ’93; Friel and Wainwright, ’98, ’99) was the focus of the current study.

We studied feeding behavior in three species representing as many families of the Tetraodontiformes: the planehead filefish, *Monacanthus hispidus* (Monacanthidae) (standard length [SL] = 117–136 mm); the gray triggerfish, *Balistes capriscus* (Balistidae) (SL = 240–270 mm); and the Southern puffer, *Sphoeroides nephelus* (Tetraodontidae) (SL = 110–147 mm). These species were selected to represent a phylogenetic sampling of this diverse order of fishes, because they have been the focus of previous research on feeding functional morphology (Friel and Wainwright, ’97, ’98, ’99), because they were amenable to the experimental procedures, and because the species were readily available locally. All specimens were collected offshore from the Florida State University Marine Laboratory near Turkey Point, Florida, under a Scientific Collecting Permit from the State of Florida. Immediately after capture, fish were transported back to the laboratory in Tallahassee, Florida where they were housed separately at 24 ± 2°C in 100-liter aquaria and fed a mixed diet that included the three experimental prey types. All experimental procedures used were reviewed by the Florida State University Animal Care and Use Committee.

Electromyographic recordings were made from subdivisions of sections 1 and 2 of the adductor mandibulae muscle and the levator operculi muscle (LOP) (Fig. 1). The study focused on activity of the adductor muscles with the LOP muscle used as a reference point for measures of adductor mandibulae activity. The evolutionary history of the adductor mandibulae muscle in tetraodontiform fishes has involved a series of subdivision events that resulted in phylogenetic increases in the number of separate subdivisions of this muscle (Winterbottom, ’74; Friel and Wainwright, ’97). As a result of this history, the three species included in this study each possess a unique set of adductor mandibulae subdivisions. The phylogenetic history and nomenclature for these muscles is reviewed by Friel and Wainwright (’97). From the filefish we recorded activity from three A1 subdivisions and two A2 subdivisions: $A1\alpha b'$, $A1\alpha b''$, $A1\alpha b'''$, $A2\alpha$, and $A2\beta$ (Fig. 1A, B). We recorded from two A1 subdivisions and three A2 subdivisions in the triggerfish; $A1\alpha b$, $A1\beta b$, $A2\alpha$, $A2\beta'b$, and $A2\beta''b$ (Fig. 1C). From the puffer we recorded from two A1 subdivisions and three A2 subdivisions; $A1\alpha t$, $A1\beta t$, $A2\alpha$, $A2\beta' t$, $A2\beta'' t$ (Fig. 1D). We also recorded activity from the levator operculi muscle in all species. This muscle is the primary abductor of the lower jaw in tetraodontiform fishes (Turingan and Wainwright, ’93).

Recordings were made during the repeated biting events that characterized feeding on three experimental prey types that challenged the abilities of the fishes in different ways. Live fiddler crabs (*Uca*) were attacked by first subduing the prey with lethal bites and then biting off smaller parts

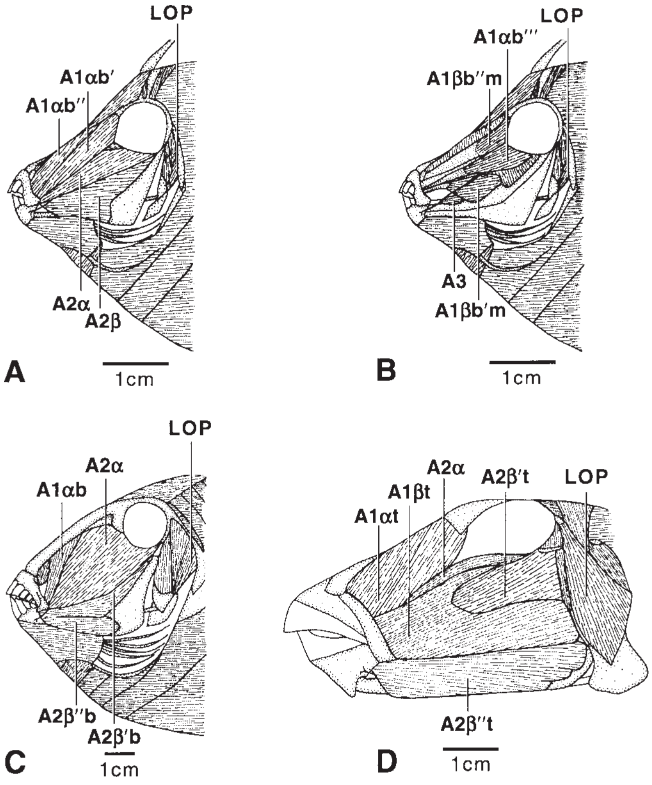

Fig. 1. Adductor-mandibulae muscles and levator operculi (LOP) of three tetraodontiform fishes. (**A, B**) Planehead filefish, *Monacanthus hispidus*, A1 is subdivided into five muscles: A1αb′, A1αb″, A1αb‴, A1βb′m and A1βb″m. A1αb‴, A1βb′m and A1βb″m lie deep. A2 is subdivided into two muscles, A2α and A2β (**C**) Gray triggerfish, *Balistes capriscus*, A1 is subdivided into two muscles, A1αb and A1βb. A1βb lies deep to A1αb and is not shown. A2 is subdivided into three muscles, A2α, A2β′b, and A2β″b. (**D**) Southern pufferfish, *Sphoeroides nephelus*, A1 is subdivided into A1αt and A1βt. A2 is subdivided into three muscles, A2α, A2β′t, and A2β″t.

to swallow. Live shrimps (*Penaeus*) were more elusive than the crabs but had no significant structural defenses. Squid mantle (*Loligo*) was cut into pieces of about 2 × 2 cm and were the toughest prey item, challenging the biting strength of the fish, though they were of consistent texture. Of these prey we predicted that the fiddler crab, with its structurally diverse body parts, would elicit the most variable motor response. In contrast, we expected that the homogeneous squid mantle would elicit the least variable feeding response.

Data were collected from four individuals of each species feeding on the three prey types. Each prey item elicited several cycles of buccal manipulation or biting behavior and for most individuals we analyzed cycles from feedings on 2–4 prey items per prey type. The mean number of cycles analyzed per individual varied slightly among prey types with means of 31.8 cycles of feeding on fiddler crabs analyzed per individual, 22.8 cycles of feeding on squid mantle, and 39.3 cycles of feeding on shrimp. A total of 1,127 cycles of buccal manipulation behavior were analyzed for this study. This data set includes a subset of that used to explore evolutionary diversification of adductor muscles following subdivision (Friel and Wainwright, '99) with the addition of data collected from six fishes not discussed previously.

In preparation for electromyographic experiments, fishes were anesthetized gradually in a solution of tricaine methanesulfonate (<1.0 g/liter) and electrodes mounted in hypodermic needles were inserted through the skin into the target muscles. Electrodes were constructed from paired 1.2-m pieces of plastic-coated 0.051 mm diameter stainless steel wire (California Fine Wire). The paired wires were glued together and 0.5-mm tips of steel were exposed by removing insulation with a razor blade under a dissecting microscope. Hooks of 3-mm length were formed by bending the tips back against the shaft of the needle. This configuration anchored the electrode in the muscle when the hypodermic needle was inserted and withdrawn. The electrodes from all muscles were bundled together and glued into a cable that was tied to the dorsum of the fish behind the eyes with a piece of suture. Following electrode implantation the fish was returned to its aquarium and allowed to recover. Recording sessions commenced at least 2–3 hr following complete recovery from the anesthesia. Electrodes were attached to the probes of Grass P511 preamplifiers, the signal was amplified 10,000 times, and a band width of 100–3,000 Hz was used. A 60-Hz notch filter was always employed. Data were recorded on a multitrack TEAC XR-5000 FM recorder with a simultaneous voice track that documented the behavior of the fish. Because the adductor muscles all lie in close proximity to each other in the region ventral to the eye, each specimen was euthanized following the experiment and the position of each electrode was confirmed visually during a postmortem dissection.

The analog recordings were digitized with a Keithley 500A converting system operating at an effective sampling rate of 8,000 Hz. A custom computer program was used to measure the burst duration, burst rectified integrated area, and burst onset time relative to onset of the levator operculi for the muscular activity associated with each cycle of buccal manipulation behavior. Average amplitude, hereafter termed 'intensity', of each burst (μV) was calculated by dividing the integrated area under the rectified myogram (μV · s) by the burst duration(s). Our observations had revealed that different electrodes can have slightly different recording properties, particularly regarding the maximum voltage recorded during experiments. To eliminate variation resulting from this difference in absolute scale of the recording electrodes, we standardized each intensity by expressing it as a fraction of the maximum intensity observed in that electrode.

Muscle activity burst duration and intensity were selected because previous research has shown that modifications of both attributes, together or independently, by fishes (Wainwright and Turingan, '96; Grubich and Wainwright, '97; Korff and Wainwright, '98) and other vertebrates (Moritani and DeVries, '78) are used to modulate the mechanical properties of the muscle contraction, including both the force exerted and the time course of tension. Onset time of the adductor muscles relative to the LOP is affected by prey type in tetraodontiforms and other teleost fishes (Wainwright and Lauder, '86; Sanderson, '88; Friel and Wainwright, '99), and this variable has been interpreted as having considerable implication for the speed of feeding kinematics (Sanderson, '88, Grubich and Wainwright, '97).

Statistical analysis

Our major aim in this study was to quantitatively test for effects of prey type on the variability of electromyographic parameters. In previous work with these species we analyzed the effects of prey type on the mean values of motor pattern variables (Friel and Wainwright, '98, '99). Here, we measured variability of the motor pattern by calculating the standard deviation of each EMG variable for each individual fish feeding on each prey type (see Fig. 2 for sample distributions). We note that the standard deviation is the average absolute value of the distance from each observation to the sample average. Thus, for each individual fish and each prey type, we reduced our 20–30 cycles of analyzed activity to a single measure that characterized the variability of the motor pattern during feeding on that prey type.

To test for prey type effects on the standard de-

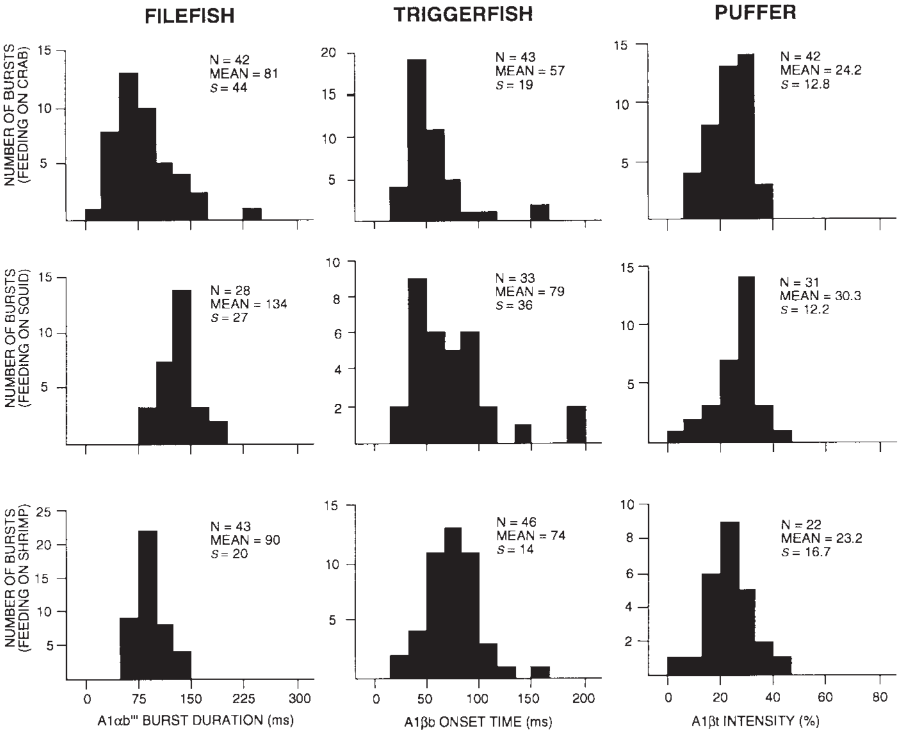

Fig. 2. Frequency histograms of electromyographic variables measured from bursts of activity in adductor mandibulae muscles of three species of tetraodontiform fishes feeding on three type of prey. Data shown for each species are the results obtained for one of the four individuals examined per species. The standard deviation(*s*) for each individual feeding on each prey type was calculated for each of four individual fish per species and analysis of variance used to test for effects of prey type on the standard deviation of EMG traits.

viation of EMG variables within each species, we ran a one-way analysis of variance on each EMG variable. In these ANOVAs there were four observations per prey type, each representing the standard deviation of the variable for that individual feeding on that prey. The four replicate individuals within each prey type permitted comparisons of the mean standard deviation among prey types, based on variation among individuals in this parameter. Hence, regardless of the number of original cycles of activity we analyzed for each individual, the test for the prey type effect in these ANOVAs always had d.f. = 2, 9.

RESULTS

Feeding behavior

The three fish species readily fed on the experimental prey but appeared to use slightly different feeding behaviors to overcome the specific challenges presented by each prey type. During feeding on squid pieces, fishes initially attacked the food by a combination of suction and biting, typical of tetraodontiform prey capture (Turingan and Wainwright, '93), that resulted in the prey being gripped firmly in the oral jaws. This was followed immediately by a rapid succession of buccal manipulation cycles as the squid piece was moved in and out of the mouth. During this process the tough squid was shredded and small pieces were eventually removed that were individually swallowed.

Shrimp were typically attacked in the mid-ventral region of the large tail musculature. Following the initial attack a rapid series of buccal manipulation cycles were used to dispatch the potentially elusive prey and smaller pieces were removed and swallowed. Shrimp frequently escaped several times during these feeding bouts before succumbing to the damage done by the repeated cycles of buccal manipulation.

Fiddler crabs were attacked differently by the three species. Triggerfish and puffers had notably larger mouths than the filefish species (filefish mean mouth width = 2.4 mm; triggerfish = 11.1 mm; puffer = 12.6 mm), and typically dispatched the crabs by directly biting them in the anterior aspect of the carapace, often bisecting the crab. The crab was then eaten in a succession of about six smaller bites. In contrast, filefish would attack the crabs first by biting off appendages followed by consumption of viscera inside the carapace. Filefish rarely consumed the carapace itself.

Effects of prey type on motor pattern variability

All fish exhibited high variability in burst onset, burst duration, and burst intensity of the adductor mandibulae muscles (Figs. 2 and 3). Coefficients of variation for the three variable types within individual ranged from about 0.2–0.7. Within individuals, distributions of variables were normal or slightly skew, and could be skew left or right (Fig. 2).

Prey type influenced the standard deviation of EMG variables, but the effects were not seen in all variables and differed between species. The greatest effects were seen in the filefish, which showed significant differences among prey types in the standard deviation of burst duration of all five adductor mandibulae subdivisions (Table 1). In all muscles, filefish showed higher variability when feeding on fiddler crabs than on the other two prey (Figs. 2, 3). There were no significant effects of prey on the variability of burst onset time or burst intensity in the filefish. In the triggerfish, prey type had a significant effect on the standard deviation of burst duration of only one adductor muscle, section A1αb, but there were significant effects of the burst onset time of A1αb and A1βb (Table 2). In both muscles, burst onset time was least variable in feedings on fiddler crabs and most variable when feeding on squid. The burst duration of A1α was most variable during feedings on squid and less, but equally variable when triggerfishes fed on crabs and shrimp. The puffer showed no significant effects of prey type on motor variability (Table 3) with mean standard deviations markedly consistent among prey. No cases were found in which prey type had a significant effect on the standard deviation of activity intensity (Table 1), although trends in this direction were observed in some individual fish (Fig. 2).

DISCUSSION

Our observations reveal a previously unmeasured level of complexity and subtlety in the response of teleost fishes to alternative prey. Previous workers have repeatedly demonstrated an ability of teleost fishes to alter the mean value of motor pattern variables in response to feeding on different prey (Lauder, '81; Wainwright and Lauder, '86; Sanderson, '88; Wainwright and Turingan, '93; Friel and Wainwright, '98, '99). This study offers the first demonstration that the variability of the feeding motor pattern can also be affected by environmental cues; in this study, prey type.

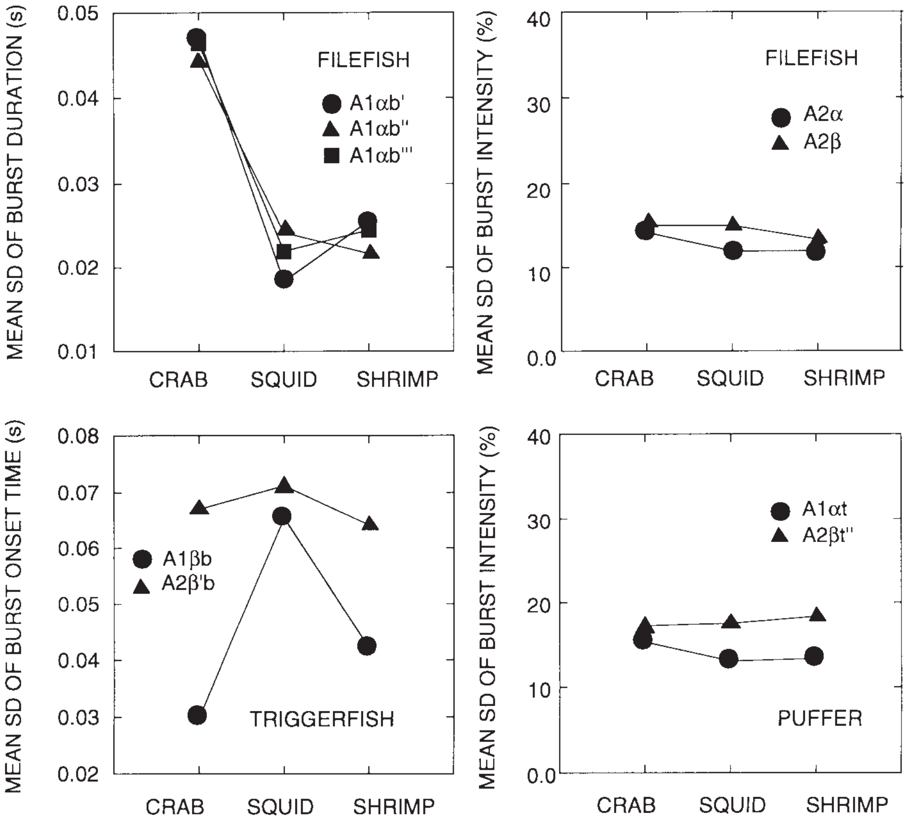

Fig. 3. Plots of the average standard deviation of electromyographic parameters for three species of tetraodontiform fishes feeding on three prey. Each point shown is the average standard deviation for that EMG variable across four individuals from the indicated species. In some species and muscles a more variable pattern of muscle activity was employed by fishes feeding on certain prey. Note, for example, that the standard deviation of burst duration in A1 muscles was about twice as high for filefish feeding on fiddler crabs as compared to the other prey type.

TABLE 1. Results of one-way analyses of variance for the effect of prey type on the standard deviation of electromyographic variables describing the activity pattern of the adductor mandibulae muscles in the filefish, Monacanthus hispidus[1]

Variable	Mean SD fiddler crab	Mean SD squid	Mean SD shrimp	F-ratio of prey type effect (d.f. = 2, 9)
A1αb′ onset (ms)	26.5	24.3	22.3	1.78
A1αb′ duration (ms)	47.2	19.2	25.8	17.54*
A1αb′ intensity (%)	18.0	19.1	20.1	0.47
A1αb″ onset (ms)	32.5	21.3	24.5	1.78
A1αb duration (ms)	45.1	24.3	21.2	14.51*
A1αb intensity (%)	16.6	13.3	11.0	0.48
A1αb‴ onset (ms)	32.3	21.8	22.3	1.92
A1αb‴ duration (ms)	46.8	20.7	24.9	12.64*
A1αb intensity (%)	14.1	16.3	11.9	0.63
A2α onset (ms)	30.2	19.9	22.0	1.61
A2α duration (ms)	51.4	33.5	22.6	14.70*
A2α intensity (%)	13.3	11.3	12.1	0.84
A2β onset (ms)	31.0	21.5	23.4	1.69
A2β duration (ms)	49.4	30.8	19.6	15.91*
A2β intensity (%)	14.7	14.5	12.8	0.95

[1] Table entries are the average standard deviation for each prey type across four fish, and the F-ratio for the prey type effect from the ANOVA.

*Table-wide Bonferroni correction of $P < 0.05$.

TABLE 2. Results of one-way analyses of variance for the effect of prey type on the standard deviation of electromyographic variables describing the activity pattern of the adductor mandibulae muscles in the triggerfish, Balistes capriscus[1]

Variable	Mean SD fiddler crab	Mean SD squid	Mean SD shrimp	F-ratio of prey type effect (d.f. = 2, 9)
A1αb′ onset (ms)	14.2	47.3	21.3	18.61*
A1αb duration (ms)	27.7	59.9	21.5	13.76*
A1αb intensity (%)	24.9	30.5	28.8	0.87
A1βb onset (ms)	29.9	65.2	41.5	21.26*
A1βb duration (ms)	27.3	40.3	22.9	10.54
A1βb intensity (%)	26.1	19.4	26.5	1.05
A2α onset (ms)	55.2	86.4	50.3	8.64
A2α duration (ms)	45.1	73.7	46.8	7.84
A2α intensity (%)	18.0	17.8	12.1	0.35
A2β′b onset (ms)	67.4	71.9	64.3	3.54
A2β′b duration (ms)	39.3	66.5	48.8	5.74
A2β′b intensity (%)	19.3	20.6	14.6	0.64
A2β″b onset (ms)	59.4	85.4	66.1	9.44
A2β″b duration (ms)	58.2	65.8	58.7	2.87
A2β″b intensity (%)	19.6	15.9	16.8	0.28

[1] Table entries are the average standard deviation for each prey type across four fish, and the F-ratio for the prey type effect from the ANOVA.

*Table-wide Bonferroni correction of $P < 0.05$.

Is the high variance of EMG parameters controlled by the individual?

The observation that prey type can affect the standard deviation of EMG parameters has implications for how we view the high variability of feeding motor patterns. High levels of variation in EMG parameters have been reported in most quantitative studies of the motor control of feeding in fishes (Ballintijn et al., ’72; Lauder, ’81, ’83a; Wainwright and Lauder, ’86; Sibbing et al., ’86; Sanderson, ’88; Wainwright, ’89; Turingan and Wainwright, ’93; Wainwright and Turingan, ’96; Grubich and Wainwright, ’97; Friel and Wainwright, ’98, ’99). The two chief candidates for the cause of this variation have different implications for the nature of teleost feeding behavior and our general interpretation of electromyographic data.

The first possibility is that the high variance of motor pattern traits is a manifestation of exten-

TABLE 3. Results of one-way analyses of variance for the effect of prey type on the standard deviation of electromyographic variables describing the activity pattern of the adductor mandibulae muscles in the puffer, Sphoeroides nephelus[1]

Variable	Mean SD fiddler crab	Mean SD squid	Mean SD shrimp	F-ratio of prey type effect (d.f. = 2, 9)
A1αt onset (ms)	37.7	31.0	24.2	1.94
A1αt duration (ms)	34.5	33.4	22.6	0.75
A1αt intensity (%)	15.3	12.3	12.6	0.23
A1βt onset (ms)	34.9	38.4	30.8	1.97
A1βt duration (ms)	30.8	24.7	30.3	0.55
A1βt intensity (%)	15.8	21.7	19.9	0.12
A2α onset (ms)	27.6	29.3	28.0	2.25
A2α duration (ms)	25.3	30.8	33.9	0.44
A2α intensity (%)	23.9	15.5	29.8	0.13
A2βt′ onset (ms)	30.5	30.5	38.1	2.00
A2βt′ duration (ms)	25.3	32.3	37.5	1.03
A2βt′ intensity (%)	16.4	9.3	12.7	0.36
A2βt″ onset (ms)	30.5	33.4	24.1	1.97
A2βt″ duration (ms)	26.5	33.1	40.5	0.79
A2βt″ intensity (%)	17.1	18.3	19.6	0.32

[1] Table entries are the average standard deviation for each prey type across four fish, and the F-ratio for the prey type effect from the ANOVA.

sive muscular control and represents functionally significant variation among feeding bouts in which the animal modulates motor activity in response to external (e.g., position of prey, activity of prey, experience with prey, physical characteristics of prey) and internal cues (e.g., level of satiation). Alternatively, high EMG variability may not be under control of the fish and essentially represents measurement error associated with the complex waveforms that are recorded and analyzed in electromyographic research. Under this view, the variation represents an imperfect coupling between the EMG parameters and the mechanical output of the muscles, tension and shortening. Thus, there are two elements to the problem: (1) whether the variance in EMG parameters represents functionally significant variation, and (2) whether the fish controls the variance.

Previous results indicate strongly that variation in EMG parameters does reflect mechanical output of the muscle. The statistical correlation between EMG parameters and integrated measures of muscular tension is usually high, reaching values of 0.9 and higher (Lauder et al., '86; Jayne et al., '90, Wainwright and Turingan, '96; Grubich and Wainwright, '97). In highly controlled experiments with humans on systems that involve a single muscle working isometrically across a single joint, over 95% of tension is explained by variation in EMG amplitude (Moritani and DeVries, '78; Lawrence and De Luca, '83). In a complex system like the jaws of tetraodontiform fishes the precise relationship between EMG activity and jaw movement might not be easily predicted, and empirical data describing this relationship are not yet available for this system. However, it is clear that standard EMG parameters reflect mechanical output of muscles.

Whether the high variance in EMG traits of feeding fishes represents individual control of the motor pattern has not previously been experimentally addressed. The finding that the magnitude of this variance is influenced by prey type implicates control by the fish. With the filefish, for example, there was about a 100% increase in standard deviation of burst duration in all adductor mandibulae subdivisions associated with feeding on fiddler crabs, as opposed to squid or shrimp (Table 1; Figs. 2 and 3). Thus, we can attribute this difference in variability to an effect of the prey type, some feature of fiddler crabs that the filefish responded to. In this case, at least 50% of the within-prey type standard deviation associated with fiddler crabs represents a functional response of the individual.

Why does prey type affect EMG variance?

Why might some prey elicit a more variable feeding response than other prey? Filefish showed a consistent pattern of highest variance in burst duration variables when feeding on fiddler crabs, a prey with extensive modularity in body parts that were removed individually by the small-mouthed filefishes during the repeated rounds of buccal manipulation. For filefish, fiddler crabs appeared to represent a heterogeneous prey compared to the squid pieces and the relatively soft-bodied shrimp. Filefish may have responded to this greater variability of the fiddler crab body with the use of a more variable motor pattern than when feeding on the other two prey types.

The pattern of greater variance during feeding on fiddler crabs was not followed by the triggerfish, which altered the standard deviation of burst duration of A1αb and the onset times of A1αb and A1βb. In all three variables it was squid, the most homogeneous of the three prey, that elicited the highest variance (Table 2; Fig. 3). Furthermore, the puffer showed no effects of prey type on EMG variable standard deviation (Table 3). Thus, the three species responded differently to the experimental prey. Our observation that filefish fed on fiddler crabs by removing body parts individually while triggerfish and puffers usually directly bit the carapace suggests that the difference in effective mouth size and robustness of these species may have affected how they interacted with each prey. Although the puffer did not alter EMG variability in response to prey, this species and the other two have previously been shown to alter mean EMG trait values in response to these prey (Friel and Wainwright, '98, '99) indicating that the lack of a prey type effect in the current study is not an indication of a lack of capacity to perceive or respond to differences among prey.

LITERATURE CITED

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