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Sensory modulation and behavioral choice during feeding in the Australian frog, *Cyclorana novaehollandiae*

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Abstract This study investigates how visual and tactile sensory information, as well as biomechanical effects due to differences in physical characteristics of the prey, influence feeding behavior in the frog *Cyclorana novaehollandiae*. Video motion analysis was used to quantify movement patterns produced when feeding on five prey types (termites, waxworms, crickets, mice and earthworms). Twelve kinematic variables differed significantly among prey types, and twelve variables were correlated with prey characteristics (including mass, length, height and velocity of movement). Results indicate that *C. novaehollandiae* uses a different strategy to capture each prey type. Visual assessment of prey characteristics appeared to be more important in modulating feeding behavior than tactile cues or biomechanical effects. We propose a hierarchical hypothesis of behavioral choice, in which decisions are based primarily on visual analysis of prey characteristics. In this model, the frogs first choose between jaw prehension and tongue prehension based on prey size. If they have chosen jaw prehension, they next choose between upward or downward head rotation based on length and height of the prey. If they have chosen tongue prehension, they next choose between behavior for fast and slow prey. Final decisions may be the result of behavioral fine tuning based on tactile feedback.

Key words Feeding behavior · Sensory modulation · Behavioral choice · Visual guidance · Tactile cues

Introduction

Previous studies have shown that most vertebrates, including fishes, amphibians, reptiles and mammals, exhibit diversity in feeding behavior when feeding on different types of prey (Liem 1978; Lauder 1981; Gorniak et al 1982; Hiiemae and Crompton 1985; Wainwright and Lauder 1986; Anderson 1993; Valdez and Nishikawa 1993). Whereas these studies have documented that the ability to modulate feeding behavior in response to prey type is widespread, few studies have attempted to investigate the mechanisms of behavioral modulation.

In general, the role that sensory information plays in motor control is to modify motor output to the current conditions experienced by the animal (Rossignol et al. 1988). By modulating their feeding behavior in response to prey stimuli, animals are able to display behavior patterns that are more appropriate for a given set of prey characteristics. In principle, differences in motor output during feeding may be responses to differences among prey types in sensory input (e.g., visual analysis of prey characteristics or tactile information about the prey) or to differences in biomechanical effects (i.e., purely physical effects of prey characteristics on feeding movements in the absence of compensatory adjustments) (Anderson 1993; Gray and Nishikawa 1995). Of course, biomechanical effects and sensory input usually interact, so that appropriate compensatory adjustments are made. Information about the role of sensory modulation in behavioral decision making can be obtained by determining the extent to which animals are capable of modulating their behavior in response to sensory stimuli.

Like most vertebrates, frogs display modulation of feeding behavior in response to prey type (Honigmann 1944; Weerasuriya 1989; Nishikawa et al. 1992; Anderson 1993; Valdez and Nishikawa 1993). The goal of this study was to investigate the sensory basis for modulation of feeding behavior in frogs. The feeding behavior of frogs has been characterized as stereotyped, ballistic and comprised of a limited number of fixed action patterns (Ewert 1987). Ewert(1987) investigated the visual stimuli that elicit feeding behavior in the toad *Bufo bufo.* He found that toads exhibit feeding behavior more fre-

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quently when presented with elongate visual stimuli with the long axis parallel to the direction of movement (i.e., the "worm" configuration) than when presented with similar stimuli with the long axis perpendicular to the direction of movement (i.e., the "anti-worm" configuration), which were perceived as a threat (Ewert 1987). Whereas Ewert (1987) studied the efficacy of different visual stimuli as releasers of feeding behavior, we ask how feeding kinematics varies as a function of sensory information associated with different prey types.

Among frogs, highly protrusible tongues have evolved at least six times independently from tongues of limited protrusibility (Nishikawa et al 1992). *Rana pipiens* (family Ranidae), a member of the Neobatrachia (Fig. 1), possesses a long, highly protrusible tongue and also has been shown to modulate its feeding behavior in response to prey type (Anderson 1993). Previous studies have shown that *R. pipiens* exhibits two different behavior patterns (tongue prehension versus jaw prehension) when feeding on two different types of prey (Anderson 1993; Anderson and Nishikawa 1993). In tongue prehension, the prey is captured with the tongue and transported to the esophagus without contacting the jaws. In jaw prehension, the prey is first contacted with the tongue, but the head rotates downward, the prey is grasped with the jaws, and is transported into the oral cavity with the forelimbs. During tongue prehension, the head remains nearly level with respect to the horizon, the lunge distance is relatively short, the tongue is protracted to a greater distance and the mouth remains open for a longer time than during jaw prehension (Anderson 1993). Thus, it appears that the frogs modulate their feeding behavior in response to prey type in order to match feeding behavior with prey characteristics.

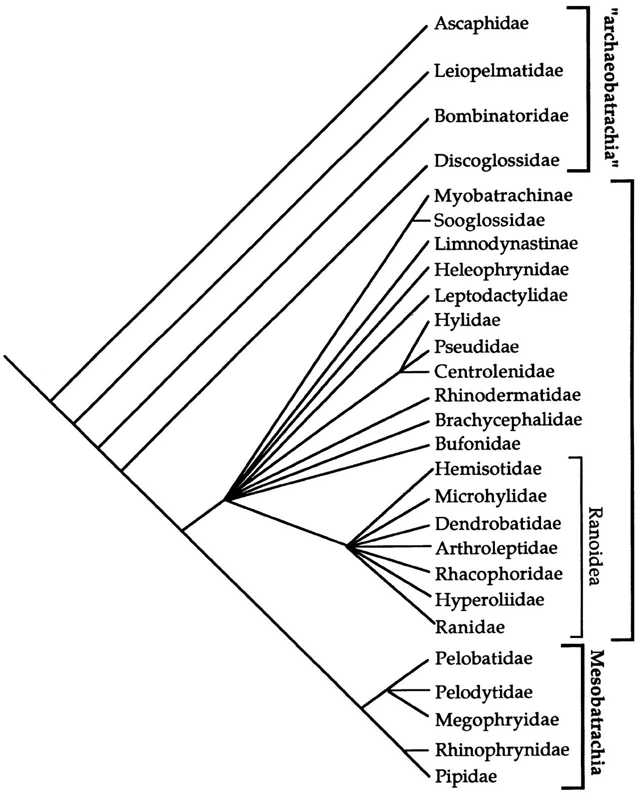


Fig. 1 A phylogeny of the living anurans modified from Ford and Cannatella (1993). The "archaeobatrachians" are a grade group that share many primitive characteristics but are not closely related to each other. *Cyclorana novaehollandiae* is a member of the family Hylidae and *Rana pipiens* is a member of the family Ranidae. Both are members of the group Neobatrachia. *Cyclorana* possesses a short tongue which is a primitive characteristic, whereas *Rana* possesses a long tongue which is derived among frogs

The first objective of this study was to investigate the extent to which feeding behavior is modulated by sensory information in *Cyclorana novaehollandiae.* In the present study, we ask whether additional prey types will elicit new behavior patterns in addition to those observed in *R. pipiens.* To answer this question, individuals of *C. novaehollandiae* were offered five different prey types (waxworms, earthworms, newborn mice, crickets and termites). Because these prey types exhibit a wide range of sizes, shapes and speeds of movement, it was also possible to analyze correlations between prey characteristics and prey capture kinematics, which is not possible if only two prey types are examined.

The second objective was to investigate the mechanisms used by *Cyclorana* to modulate feeding behavior patterns, including 1) the effects of visual assessment of prey characteristics on feeding kinematics; 2) the effects of tactile information on feeding kinematics; and 3) the purely biomechanical effects due to physical differences among the prey types on feeding movements. We investigated whether sensory information, visual or tactile, is used to modulate feeding behavior and whether physical differences among prey types affect feeding behavior.

Similarities between the feeding behavior of *Rana pipiens* when feeding on large prey (i.e., downward head rotation and jaw prehension) and the feeding behavior of frogs with short tongues led Anderson (1993) to hypothesize that *R. pipiens* had retained the plesiomorphic behavior pattern (i.e., jaw prehension) and used it to catch large prey, but had evolved a new behavior pattern (i.e., tongue prehension) to catch small prey (Anderson 1993). The third objective of this study was to test Anderson's (1993) hypothesis by investigating whether or not the short-tongued frog, *C. novaehollandiae* (family Hylidae), possesses the ability to modulate its feeding behavior in response to prey type. We chose to study *C. novaehollandiae* because it is a neobatrachian frog (Fig. 1) that possesses a short tongue, and because it is a feeding generalist that readily consumes a wide variety of prey types.

Materials and methods

Juvenile *Cyclorana novaehollandiae* (n = 5) were obtained from an animal supplier. The kinematics of feeding behavior was studied using five different prey types, including termites, crickets, waxworms, earthworms and newborn mice. All individuals were first fed termites, then earthworms, mice, waxworms and crickets, respectively. A display Integration Technologies model DIT 660 high-speed, multi-framing video camera was used to film feeding attempts at 120 fields per second. Filming was done from June 1992 through February 1993. The frogs were filmed at room temperature (approximately 21–23 °C) on a wet paper towel placed on a flat stage. The frogs were allowed to feed unrestrained on the stage.

The feeding sequences were digitized using Peak Performance Technologies motion analysis software on a Rycom 2050 IBM compatible computer. Only feeding sequences in which the frog successfully captured the prey item, remained in the field of view of the camera, and remained with the long axis of its body oriented perpendicular (± 10°) to the camera were analyzed. For each individual, at least five feeding sequences were analyzed for each of the five prey types. There were 25 feeding sequences for each prey type, except for mouse sequences, for which there were 26, for a total of 126 digitized sequences.

For each digitized sequence, the *X, Y* coordinates of the prey, a non-moving reference point and seven points on the frog were digitized from the video monitor. The digitized points included: 1) upper jaw tip, 2) midpoint of upper jaw, 3) jaw point, 4) midpoint of lower jaw, 5) lower jaw tip, 6) tongue height, and 7) tongue reach (Deban and Nishikawa 1992). The following variables were measured in milliseconds (ms), relative to the onset of mouth opening (time = 0): 1) onset of forward movement, the field in which forward movement of the upper jaw tip was first observed; 2) onset of tongue protraction, the field in which the tongue pad was first observed; 3) time of prey contact, the field in which the tongue first contacted the prey; 4) completion of tongue protraction, the field in which the tongue was maximally extended toward the prey; 5) onset of tongue retraction, the field in which the tongue first began to retract into the mouth; 6) completion of mouth opening, the field in which the gape angle was greatest; 7) completion of tongue retraction, the field in which the tongue completed its retraction into the floor of the mouth; 8) completion of forward movement, the field in which the frog's upper jaw tip reached its maximum forward position; 9) onset of mouth closing, the field in which the mouth first began to close; and 10) completion of mouth closing, the first field in which the mouth was fully closed.

From the variables listed above, the following durations (ms) were calculated: 11) approach (ms), the time from the onset to the completion of forward movement of the upper jaw tip; 12) mouth opening, the time from the onset to the completion of mouth opening; 13) tongue protraction, the time from the onset to the completion of tongue protraction; 14) tongue at target, the time from prey contact to the onset of tongue retraction; 15) tongue retraction, the time from the onset to the completion of tongue retraction; 16) mouth closing, the time from the onset to the completion of mouth closing; 17) body recovery, the time from maximum displacement of the upper jaw tip to the completion of mouth closing; and 18) feeding sequence, the time from first forward movement to the completion of mouth closing.

The following angles (degrees) and distances (cm) were also calculated from the digitized points: 19) maximum gape angle, the maximum angle subtended by the upper and lower jaw tips with the jaw joint at the vertex; 20) maximum upward head rotation, the maximum angle above the horizon between a line from the upper jaw tip to the jaw joint and the horizon line; 21) maximum downward head rotation, the maximum angle below the horizon between a line from the upper jaw tip to the jaw joint and the horizon line (note that upward and downward head rotation may result from either craniovertebral extension and flexion or from changes in the orientation of the body during the lunge); 22) gape distance, the greatest distance between the upper and lower jaw tips; 23) maximum tongue reach, the greatest distance between the lower jaw tip and tongue tip; 24) maximum tongue height, the greatest perpendicular distance between the highest point on the tongue and the midpoint of the lower jaw; 25) distance to prey, the distance between the upper jaw tip and a point on the prey nearest the frog; 26) lunge length, the distance between the upper jaw tip in the first field and the upper jaw tip in the field in which the completion of forward movement occurred; 27) overshoot distance, the amount of forward movement of the head that occurred from prey contact to maximum forward displacement; 28) maximum angular velocity (degrees ms^{-1}) of mouth opening; and 29) maximum angular velocity of mouth closing.

During the study, the frogs increased in size as estimated by changes in jaw length. Jaw length increased from an average of 1.5 cm at the beginning of the study to an average of 2.6 cm at the end of the study. To account for this growth, the data were analyzed using two-way analysis of covariance (ANCOVA; type III sums of squares, $\alpha = 0.05$). The main effects were prey type (fixed) and individual (random), and the covariate was jaw length. The denominator mean square for the *F*-tests was the interaction between prey type and individual. The 19 dependent variables were the 8 duration variables (11–18), 3 angles (19–21), 6 distances (22–27) and the 2 angular velocities (28–29). The interaction terms in the ANCOVA model were prey type × individual, prey type × jaw length, individual × jaw length and prey type × individual × jaw length. When non-significant, interaction terms involving the covariate were removed from the model. If the covariate was not significant, it was also removed from the model. For most of the variables, the covariate was not significant so the data were analyzed using two-way ANOVAs. For variables that showed overall differences among prey types, an a posteriori Student-Newman-Keuls test ($a = 0.05$) was used to determine which prey types differed from each other. A test that considered experiment wide error was necessary because 19 kinematic variables were included. The sequential Bonferroni test was used because a regular Bonferroni test was considered to be too conservative and would have greatly increased the chance of a type II error (Rice 1989).

To determine if the behavior patterns diverged prior to prey contact, upward head rotation was measured in the field before prey contact for feeding sequences involving earthworms, waxworms and mice. The data were analyzed with a two-way ANOVA using type III sums of squares with prey type and individual as the main effects.

A discriminant function analysis was used to classify feeding sequences for different prey types on the basis of the kinematic variables. This analysis was used on an exploratory basis because it did not take into account individual variation or growth, and because more dependent variables were included in the analysis than individuals. The first analysis included feeding sequences from all five prey types. Because a previous study found differences in how frogs capture earthworms and waxworms (Anderson 1993), a second analysis was performed that included only these two prey types. All 29 kinematic variables were included in the discriminant function analyses.

To look for associations between prey characteristics and prey capture kinematics, five living individuals of each of the five prey types were weighed (g) and measured for length (mm) and height (mm). Earthworms were anesthetized with ether before being measured because they tended to curl up, which made it difficult to get an accurate measurement of their length. For each prey type, five movement velocities (cm s^{-1}) were calculated from videotapes of prey capture. One-way ANOVAs using type III sums of squares with prey type as the main effect were used to compare mass, length, height and movement velocity among the five prey types. For variables that showed overall differences among prey, a posteriori Student-Newman-Keuls tests ($a = 0.05$) were used to determine which prey types differed from each other.

Pearson product moment correlation coefficients ($a = 0.05$) were used to test for associations between the means of characteristics of the prey (n = 5 for each prey type) and the means of kinematic variables (n = 25–26 for each prey type). The prey characteristics were the mean movement velocity, length, height and mass of the five prey types. The kinematic variables included the same 19 dependent variables used in the ANCOVA.

Results

A statistical approach using analysis of covariance, discriminant function analysis, and correlations between kinematic variables and prey characteristics was used to investigate how movement patterns differed among prey types. We first present the results of the statistical tests, followed by a description of the prey capture behavior patterns that were observed for each of the prey types.

Results of analyses of covariance

Analysis of covariance was used to test for effects of jaw length, individual and prey type on prey capture kinematics (Table 1). The effect of jaw length was significant only for maximum tongue height ($F = 12.769$, $P = 0.0005$). There were no significant effects of individual, and no significant interactions between individual and jaw length or between prey type and jaw length after sequential Bonferroni tests.

Cyclorana novaehollandiae exhibited different patterns of feeding behavior that varied in many kinematic variables depending on the prey type that was presented (Figs. 2, 3). After the sequential Bonferroni adjustment, 12 of the 19 kinematic variables tested with ANCOVA differed significantly among prey types (Table 1). (Details are given below after summary statistics.)

Results of discriminant function analysis

When all five prey types were included in the discriminant function analysis (Analysis 1), the prey were classified correctly on the basis of prey capture kinematics in 119 of 126 (91.3%) trials (Wilks' Lambda = 0.0167, $P < 0.0001$). There was no consistent misclassification of any of the prey types.

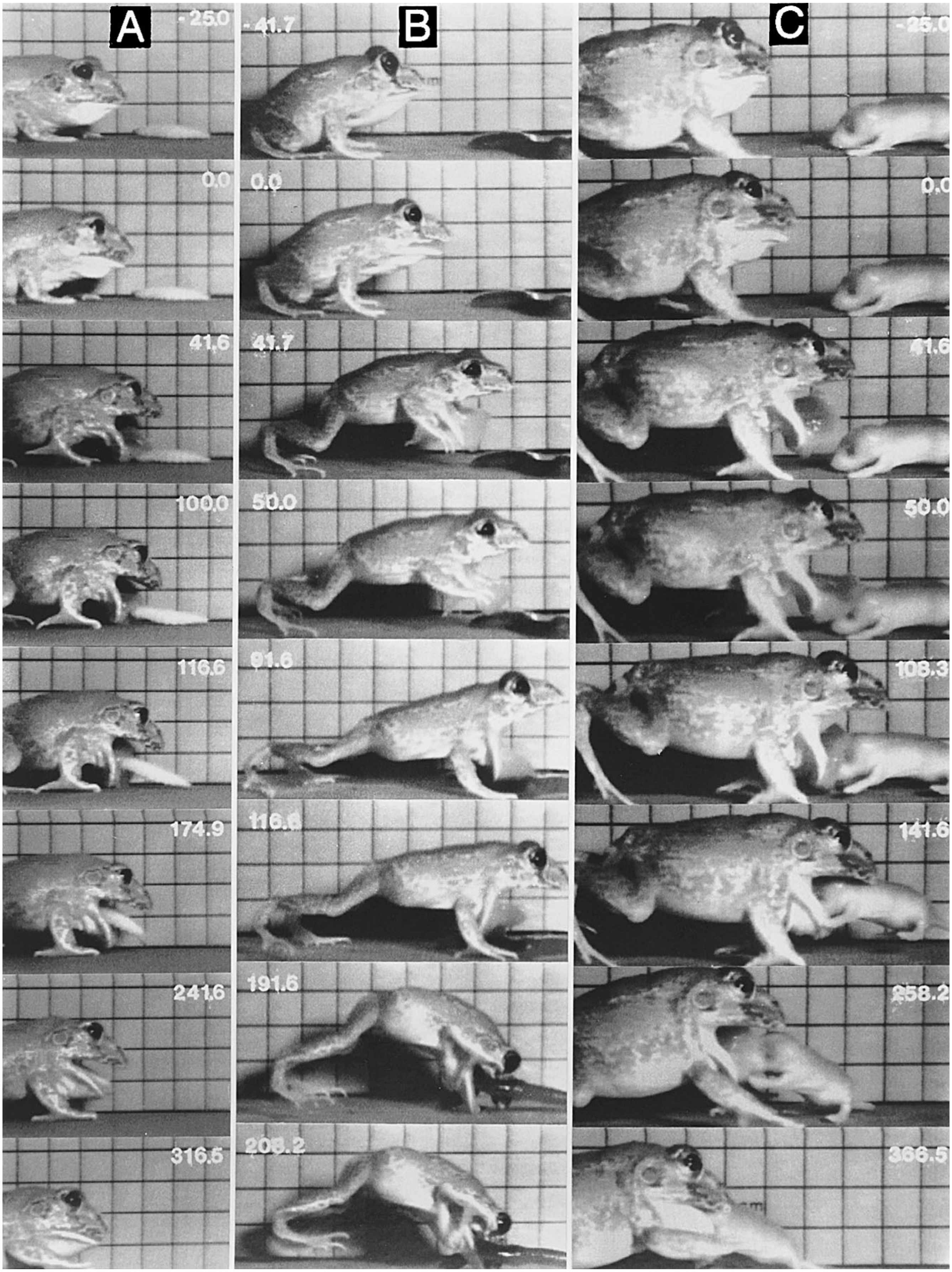
Table 1 Means ± 1 SE of kinematic variables for each prey type (in order of increasing mass) and results of two way ANCOVAs ($a = 0.05$), with prey type (fixed) and individual (random) as the main effects and jaw length as the covariable. F-and P-values are for the overall effect of prey type. A total of 126 feeding sequences was included in the analysis. Letters M,L,H and V denote prey characteristics mass, length, height and velocity and the sign (±) denotes the direction of significant correlations between the kinematic variables and prey characteristics. (Abbreviations: *c* crickets, *e* earthworms, *m* mice, *t* termites, *w* waxworms). The letters next to the mean and standard error signify that the prey type in that column differs significantly from the prey type represented by the letter

Kinematic variables	*Termite*	*Cricket*	*Waxworm*	*Mouse*	*Earthworm*	*F*	*P*
Time of prey contact[b]	27 ± 1.4	38 ± 3.9	40 ± 3.1	36 ± 2.3	42 ± 9.1		
Durations (*ms*)							
approach (+L)	123 ± 6.7	126 ± 4.1	121 ± 7.4	124 ± 7.6	154 ± 8.6	3.19	0.0418
mouth opening	78 ± 7.0	121 ± 8.6	125 ± 14.4	100 ± 9.4	110 ± 9.1	4.10	0.0179
tongue protraction (+V)	56 ± 6.4	85 ± 10.5	63 ± 4.8	58 ± 4.9	61 ± 7.4	1.96	0.8787
tongue at target	51 ± 5.9 cmw	30.6 ± 2.0 et	32.3 ± 3.6 et	29 ± 3.2 et	54 ± 6.2 cmw	6.89	0.0020[a]
tongue retraction (−M)	123 ± 17.5	115 ± 7.2	107 ± 11.7	77 ± 12.4	69 ± 6.4	2.72	0.0671
mouth closing (−M)	167 ± 16.6 em	148 ± 14.5 e	172 ± 13.77 em	109 ± 10.7 tw	72 ± 4.6 ctw	10.40	0.0002[a]
body recovery (−M)	195 ± 15.7 em	204 ± 13.7 em	232 ± 12.6 em	142 ± 13.6 cetw	87 ± 11.0 cmtw	13.69	0.0001[a]
feeding sequence (−M)	318 ± 17.2 em	336 ± 12.1 em	351 ± 12.9 em	275 ± 12.9 ctw	242 ± 7.9 ctw	10.27	0.0003[a]
Angles (*degrees*)							
maximum gape angle (+M)	62 ± 1.6 em	75 ± 3.3 e	66 ± 3.3 em	85 ± 3.7 tw	94 ± 4.1 ctw	10.60	0.0002[a]
upward head rotation (+H)	3 ± 0.9 m	7 ± 1.4 m	4 ± 1.2 m	21 ± 2.4 cetw	6 ± 2.2 m	12.02	0.0001[a]
downward head rotation (−L)	−24 ± 1.4 e	−16 ± 1.4 e	−22 ± 1.6 e	−23 ± 1.9 e	−46 ± 2.2 cmtw	32.11	0.0001[a]
Distances (*cm*)							
gape distance	1.8 ± 0.05 cemw	2.7 ± 0.07 wt	2.3 ± 0.06 cmt	2.7 ± 0.08 tw	2.5 ± 0.09 t	21.51	0.0001[a]
maximum tongue reach	0.5 ± 0.02	0.6 ± 0.04	0.5 ± 0.05	0.4 ± 0.03	0.5 ± 0.04	3.63	0.0274
maximum tongue height (+V)	1.1 ± 0.04	1.6 ± 0.06	1.3 ± 0.04	1.3 ± 0.06	1.3 ± 0.07	3.03	0.0489
distance to prey	2.2 ± 0.13 cmw	3.5 ± 0.24 et	2.9 ± 0.21 mt	3.4 ± 0.25 etw	2.4 ± 0.17 cm	9.89	0.0003[a]
lunge length	2.8 ± 0.13 cemw	5.0 ± 0.30 tw	3.9 ± 0.27 cmt	5.01 ± 0.33 tw	4.5 ± 0.30 t	17.24	0.0001[a]
overshoot distance (+M)	0.4 ± 0.08 cem	0.7 ± 0.08 emt	0.5 ± 0.07 em	1.0 ± 0.11 ctw	1.1 ± 0.11 ctw	15.09	0.0001[a]
Angular velocities (*degrees/ms*)							
mouth opening	2.4 ± 0.07	2.5 ± 0.08	2.1 ± 0.10	2.5 ± 0.11 cetw	2.5 ± 0.10 cmtw	1.56	0.2329
mouth closing (+M)	−1.13 ± 0.09 em	−1.34 ± 0.09 m	−1.34 ± 0.35 em	−1.94 ± 0.25 wt	−2.19 ± 0.12 cwt	5.66	0.0049[a]

[a] Significant effect of prey type after sequential Bonferroni tests

[b] This variable was included in the table to enable readers to determine if a given behavior occurred before or after prey contact

Fig. 2A–E Selected video frames from typical sequences of *Cyclorana novaehollandiae* feeding on: (**A**) a waxworm; (**B**) an earthworm; (**C**) a mouse; (**D**) a cricket; and (**E**) a termite. Numbers in upper corners indicate time (ms) relative to the onset of mouth opening. The frogs use jaw prehension to capture earthworms and mice, but use tongue prehension to capture waxworms, crickets, and termites. When feeding on mice, the frogs rotate the head upward more than when feeding on any other prey type. When feeding on earthworms, the frogs rotate the head downward more than when feeding on any other prey type. The frogs exhibit the smallest maximum gape angle when feeding on crickets


A
B
C
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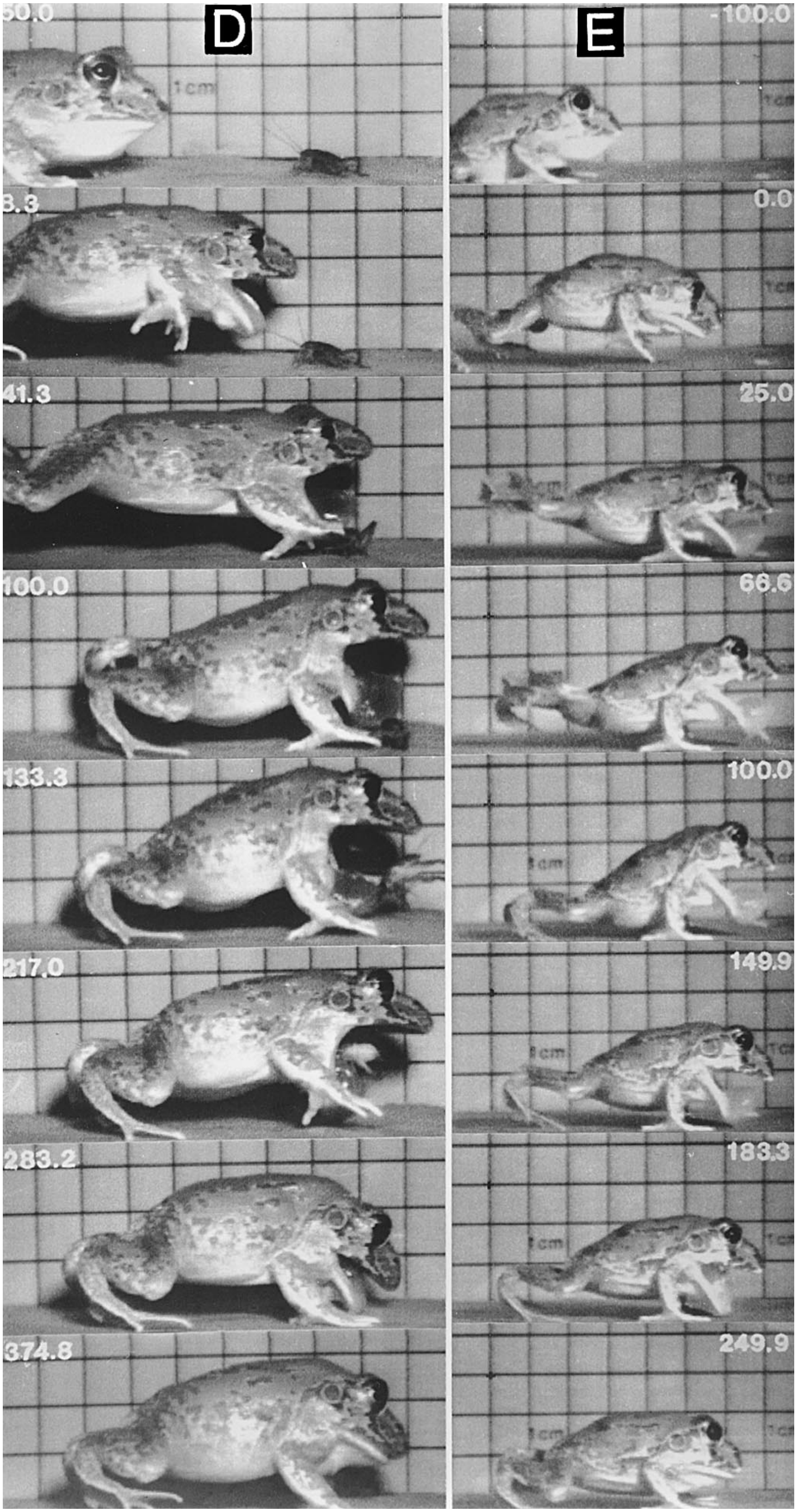
-41.7
-25.0
0.0
0.0
0.0
41.6
41.7
41.6
100.0
50.0
50.0
116.6
91.6
108.3
174.9
116.6
141.6
241.6
191.6
258.2
316.5
208.2
366.5

Fig. 2D–E


D
E
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8.3
41.3
100.0
133.3
217.0
283.2
374.8
-100.0
0.0
25.0
66.6
100.0
149.9
183.3
249.9
1cm

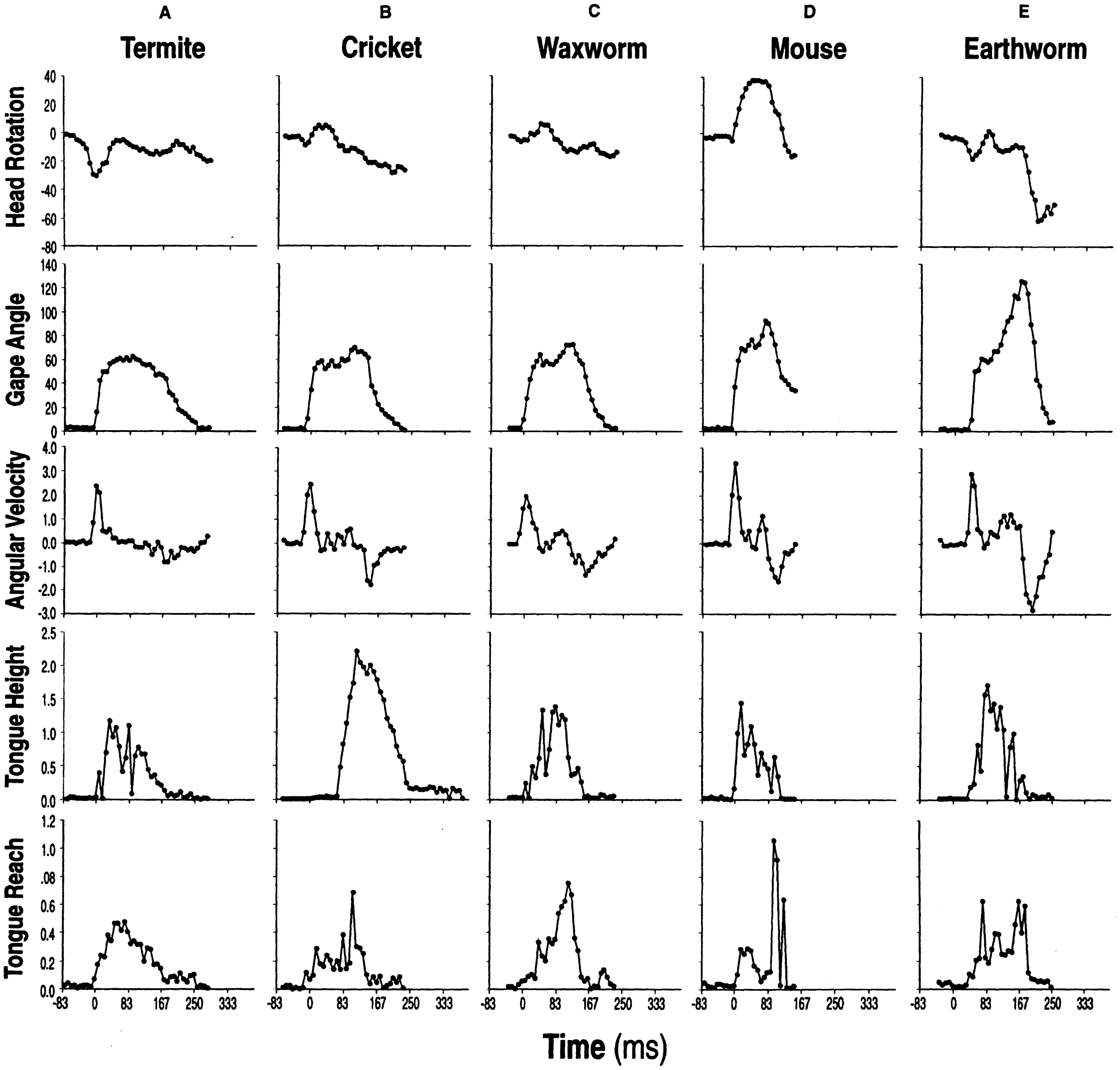

Fig. 3A–E Kinematic profiles for selected variables from typical feeding sequences of *Cyclorana novaehollandiae* feeding on: (**A**) a waxworm; (**B**) an earthworm; (**C**) a mouse; (**D**) a cricket; and (**E**) a termite. Sequences from multiple individuals are represented. The frogs exhibit greater downward head rotation when feeding on earthworms and a greater degree of upward head rotation when feeding on mice, whereas the head remains level with the horizon in feeding sequences for waxworms, crickets and termites. A greater maximum velocity of mouth closing occurs when the frogs feed on mice and earthworms than when they feed on crickets, waxworms or termites. The greatest tongue height occurs when the frogs feed on crickets. The frogs exhibit a smaller gape distance when feeding on termites than when feeding on any of the other prey types

Numerous kinematic variables were important in discriminating among prey types (Table 2). For Analysis 1, maximum downward head rotation ($r > -0.47$, $P < 0.05$) was most closely associated with discriminant function (DF) 1; gape distance ($r > 0.58$, $P < 0.05$) was most closely associated with DF2; maximum upward head rotation ($r > -0.61$, $P < 0.05$) was most closely associated with DF3; and gape distance ($r > 0.40$, $P < 0.05$) was most closely associated with DF4.

When only feeding sequences for earthworms and waxworms were included in the analysis (Analysis 2), 100% of the prey were classified correctly (Wilks' Lambda = 0.064, $P < 0.0001$). Maximum downward head rotation ($r > -0.33$, $P < 0.05$) and duration of body recovery ($r > -0.34$, $P < 0.05$) were most closely associated with DF1 (Table 2).

Associations between prey characteristics and prey capture kinematics

The five prey types differed in size, shape and speed of movement (Table 3). The mean maximum velocity was significantly greater for crickets than for all other prey types (Table 3). Mice were significantly greater in height than the other four prey types and earthworms had a significantly greater height than termites (Table 3). Mice and earthworms has a significantly greater mass than any of the other three prey types and earthworms had a significantly greater mass than mice (Table 3). Earthworms were significantly longer than any of the other prey types, and mice were significantly longer than termites (Table 3).

Twelve of the 19 kinematic variables showed significant correlations with characteristics of the prey (Figs. 4, 5). Four variables were negatively correlated with prey mass: duration of mouth closing ($r = -0.90$, $P < 0.05$); duration of tongue retraction ($r = -0.97$, $P < 0.01$); duration of recovery ($r = -0.96$, $P < 0.01$); and duration of feeding sequence ($r = -0.95$, $P < 0.05$). Maximum gape angle ($r = 0.94$, $P < 0.05$), overshoot distance ($r = 0.93$, $P < 0.05$) and maximum velocity of mouth closing ($r = 0.97$, $P < 0.01$) were positively correlated with prey mass (Fig. 4). Duration of approach ($r = 0.97$, $P < 0.01$) was positively correlated with prey length, whereas maximum downward head rotation ($r = -0.95$, $P < 0.05$) was negatively correlated with prey length (Fig. 5). Maximum upward head rotation ($r = 0.96$, $P < 0.01$) was positively correlated with prey height (Fig. 5). Maximum tongue height ($r = 0.91$, $P < 0.05$) and duration of tongue protraction ($r = 0.97$, $P < 0.01$) were positively correlated with prey velocity (Fig. 5).

Table 2 Correlation coefficients between kinematic variables and discriminant functions in each analysis. Only significant coefficients are given. For Analysis 1, the sample size was 126 sequences ($r > 0.174$, $P < 0.05$). For Analysis 2, the sample size was 50 sequences ($r > 0.273$, $P < 0.05$)

	Analysis 1				*Analysis 2*
Kinematic variable	*DF1*	*DF2*	*DF3*	*DF4*	*DF1*
completion of tongue protraction			+0.18		
completion of mouth opening		+0.20	+0.18		
completion of tongue retraction		−0.19	+0.18		
completion of forward movement		+0.27			
onset of mouth closing			+0.17		
completion of mouth closing	−0.19		+0.30	−0.29	−0.28
Durations (*ms*)					
tongue protraction				+0.24	
tongue at target	+0.20				
tongue retraction		−0.20			
mouth closing		−0.30	+0.18	−0.28	
body recovery	−0.24	−0.29	+0.27	−0.37	−0.34
feeding sequence	−0.19	−0.21	+0.28	−0.25	−0.27
Angles (*degrees*)					
maximum gape angle		+0.41	−0.20	+0.36	
downward head rotation	−0.47	−0.35			−0.33
upward head rotation		+0.20	−0.61		
Distances (*cm*)					
gape distance		+0.58	−0.18	+0.40	
maximum tongue reach			+0.29	+0.27	
maximum tongue height	−0.18	+0.21	+0.23	+0.41	
distance to prey	−0.19				
lunge length		+0.35		+0.33	
overshoot distance		+0.35	−0.23	+0.25	
Angular velocities (*degrees/ms*)					
mouth opening				+0.39	
mouth closing		+0.21			

Table 3 Results of one-way ANOVAs with prey type as the main effect. (Abbreviations: *c* crickets, *e* earthworms, *m* mice, *t* termites, *w* waxworms). The letters next to the mean and standard error signify that the variable for the prey type in that column differs significantly from the prey type represented by the letter

Characteristic	*Termite*	*Cricket*	*Waxworm*	*Earthworm*	*Mouse*	*F*	*P*
mass (g)	0.002 ± 0.0002 em	0.14 ± 0.025 em	0.18 ± 0.009 em	3.22 ± 0.17 cmtw	2.02 ± 0.01 cetw	317.26	0.0001[a]
length (cm)	0.48 ± 0.02 em	1.50 ± 0.11 e	2.18 ± 0.06 e	14.12 ± 1.19 cmtw	3.22 ± 0.22 et	105.56	0.0001[a]
height (cm)	0.16 ± 0.024 em	0.36 ± 0.024 m	0.4 ± 0.032 m	0.58 ± 0.07 tm	1.08 ± 0.15 cetw	20.28	0.0001[a]
velocity (cm/s)	4.57 ± 0.56 c	81.42 ± 16.29 emtw	4.87 ± 0.82 c	16.28 ± 5.88 c	9.87 ± 1.43 c	27.71	0.0001[a]

[a] denotes a significant effect of prey type after sequential Bonferroni tests

Kinematics of normal feeding behavior on waxworm prey

Previous studies of feeding behavior in frogs typically have used waxworms as prey (Nishikawa and Roth 1991; Deban and Nishikawa 1992; Gray and Nishikawa 1995). Therefore, we first present a kinematic analysis of the feeding behavior of *C. novaehollandiae* when feeding on waxworms and then the behavior patterns exhibited when capturing each of the four other prey types will be discussed. Data are reported as means ± SE unless otherwise noted (Table 1).

Head and body movements

The prey capture sequences began with orientation and visual fixation on the prey. The frogs then began to move forward by pushing off with their hind legs. Forward head movement began 50 ms before the onset of mouth opening (Table 1). The forelimbs always rose from the substrate. The completion of forward movement occurred 69 ms after the onset of mouth opening. The duration of approach was 121 ms. Distance to prey was 2.9 cm and lunge length was 3.9 cm. Overshoot distance was 0.5 cm. The frogs returned to their original position by alternately lifting up each forelimb and pulling it backwards. The duration of body recovery was 232 ms. Maximum downward head rotation was −22° and maximum upward head rotation was 3.9° (Table 1). Maximum downward head rotation in the field prior to prey contact was −7.8°.

Jaw movements

Maximum gape occurred after the waxworm had been transported completely into the mouth and the tongue had almost returned to its resting position in the floor of the mouth (Fig. 2a). Maximum gape angle (65.7°) was reached 119 ms after the onset of mouth opening. The gape distance was 2.3 cm. The duration of mouth opening was 125 ms (Table 1).

The onset of mouth closing occurred 127 ms after the onset of mouth opening. The mouth was completely

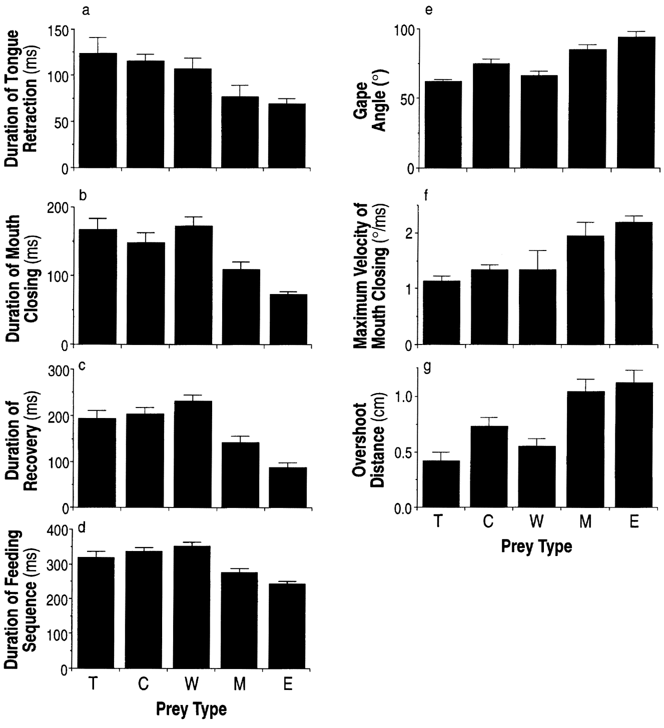

Fig. 4a–g Bar graphs showing the kinematic variables that are correlated significantly with prey mass: **a** duration of tongue retraction: **b** duration of mouth closing: **c** duration of recovery: **d** duration of feeding sequence: **e** maximum gape angle: **f** maximum velocity of mouth closing: and **g** overshoot distance. These variables were similar for earthworms and mice on the one hand, and for crickets, termites and waxworms on the other

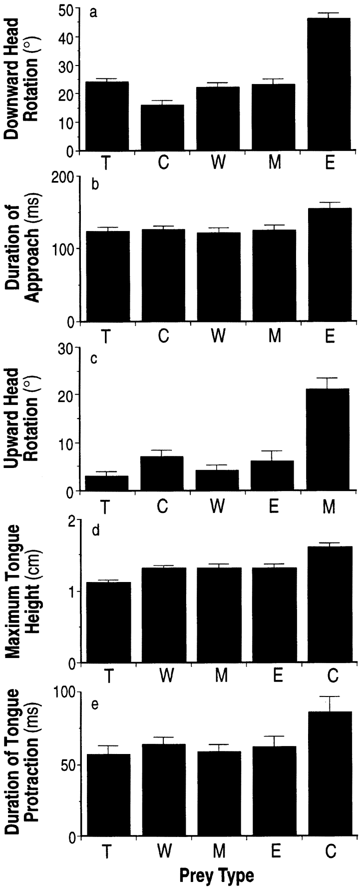

Fig. 5a–e Bar graphs showing the kinematic variables that were associated with other prey characteristics: **a** maximum downward head rotation and **b** duration of approach distinguished earthworms from all other prey types and were correlated significantly with prey length. Upward head rotation **c** distinguished mice from all other prey types and was correlated significantly with prey height; **d** maximum tongue height and **e** duration of tongue protraction were correlated positively with prey velocity. Duration of tongue protraction and tongue height distinguished crickets and were correlated significantly with the movement velocity of the prey

closed before the frogs returned to their original position (Fig. 2a). The frogs completed mouth closing on average 300 ms after the onset of mouth opening. The duration of mouth closing was 172 ms^{-1}. Maximum velocity of mouth opening was 2.1° ms^{-1} and maximum velocity of mouth closing was −1.3° ms^{-1}.

Tongue movements

The mouth opened and the tongue began to protract shortly after the forelimbs lost contact with the substrate (Fig. 2a). The frogs initially contacted the waxworms with the tongue. Prey contact occurred 40 ms after the onset of mouth opening. Completion of tongue protraction occurred 65 ms after mouth opening. Viewed from the front, the tongue resembles a suction cup with a depression in the middle surrounded by a thick ridge. The duration of tongue protraction was 63 ms. The duration of tongue at target was 32 ms. Maximum tongue height was 1.3 cm, and maximum tongue reach was 0.5 cm.

The waxworm adhered to the sticky tongue and the tongue was pulled back into the mouth, distally at first and later proximally (Fig. 2a). Onset of tongue retraction occurred 69 ms after the onset of mouth opening. The tongue completed its retraction into the floor of the mouth 176 ms after the onset of mouth opening. The duration of tongue retraction was 107 ms (Table 1).

Comparison of prey capture kinematics among prey types

As reported above, the kinematics of prey capture movements differs significantly among prey types. The following section describes specific differences between movements performed to capture waxworms and those performed for the other prey types. Kinematic variables are similar to those reported above for waxworm sequences, except where noted below.

Head and body movements

Position of the head relative to the horizon differed among prey types. Maximum downward head rotation was significantly greater in feeding sequences for earthworms than for the other types of prey (Table 1, Figs. 2, 3). A greater degree of upward head rotation was found in feeding sequences for mice than for any of the other four prey types (Table 1, Figs. 2, 3). In feeding sequences for earthworms, the frogs closed their mouths with the head in the downward position, whereas the head was rotated above the horizon when the frogs closed their mouths during feeding sequences for mice (Figs. 2, 3). When feeding on waxworms, crickets and termites, the head was level with the horizon when the frogs closed their mouths on the prey (Figs. 2, 3).

In the field prior to prey contact, the direction of head rotation differed significantly among feeding sequences for earthworms, waxworms and mice (ANOVA, ($F = 8.25$, $P = 0.011$). Post hoc tests showed significant differences between earthworms and mice and between waxworms and mice in the direction of head rotation. In the field before prey contact, the head was rotated upward to an angle of 6.9 ± 2.7° for mice, whereas for earthworms and waxworms the head was rotated downward to angles of −7.4 ± 1.6° and −7.8 ± 1.9°, respectively.

Distance to prey, lunge length and overshoot distance also differed among prey types. Distance to prey was significantly shorter in feeding sequences for termites than for waxworms, mice and crickets (Table 1). Feeding sequences for waxworms and earthworms had significantly shorter distances to prey than for mice, and earthworm sequences had significantly shorter distances to prey than sequences for crickets. Lunge length was significantly shorter for termites than for any of the other four prey types and significantly shorter in sequences for waxworms than for crickets and mice (Table 1). Overshoot distance was significantly greater in feeding sequences for mice and earthworms than it was for waxworms, termites and crickets and was greater for crickets than for termites (Table 1). The frogs had a significantly longer duration of recovery (Table 1) in feeding sequences for waxworms, crickets and termites than they did for earthworms and mice. The same pattern was observed for duration of the feeding sequence (Table 1).

Jaw movements

Maximum gape angle was significantly smaller in feeding sequences for waxworms and termites than for earthworms and mice (Table 1, Figs. 2, 3). When feeding on crickets, the frogs exhibited a significantly smaller maximum gape angle than when feeding on earthworms. Gape distance was significantly smaller in feeding sequences for termites than for all other prey types, and was significantly smaller for waxworms than for crickets and mice (Table 1, Figs. 2, 3).

Duration of mouth closing was significantly longer in feeding sequences for waxworms and termites than for earthworms and mice and significantly longer in sequences for crickets than in sequences for earthworms (Table 1, Fig. 3). The maximum velocity of mouth closing was significantly greater in feeding sequences for earthworms than it was for waxworms, crickets and termites and was significantly greater for mice than it was for waxworms and termites (Table 1).

For waxworms, crickets and termites, the prey item was transported to the esophagus before the mouth closed, whereas the prey item protruded from the mouth upon mouth closure in feeding sequences for earthworms and mice, and several transport cycles were required for deglutition (Fig. 2). In feeding sequences for waxworms, crickets and termites, the frogs closed their mouths as they were returning to their original position

(Fig. 2, 3). When feeding on earthworms and mice, the frogs first closed their mouths on the prey item, then began to return to their original position (Figs. 2, 3). Thus, the mouth closed on larger prey items before body recovery, whereas the mouth closed on smaller prey items during body recovery.

Tongue movements

For all five prey types, the tongue makes the first contact with the prey. Only duration of tongue at target differed among the prey types (Table 1). It was significantly longer in feeding sequences for termites and earthworms than for waxworms, crickets and mice. Tongue height was greater and duration of tongue protraction was longer in sequences for crickets, although the difference was not significant after the sequential Bonferroni correction (Table 1).

Tongue prehension was used to capture smaller prey types (i.e., crickets, termites and waxworms), whereas jaw prehension was used to capture larger prey types (i.e., earthworms and mice) (Fig. 2). Tongue prehension is characterized by reduced movements of the head and body. The tongue, rather than the jaws, is used to capture the prey and transport it through the oral cavity. Jaw prehension is characterized by head and body movements of relatively large amplitude. In jaw prehension, the tongue first makes contact with the prey, but the head is rotated downward and the jaws close on the prey before it is transported into the oral cavity. A combination of jaw and tongue movements is used to transport the prey through the oral cavity to the esophagus, which is sometimes assisted by forelimb movements. When feeding on earthworms, the frogs rotate the head downward and pick the prey up with the jaws. When feeding on mice, the frogs continue to raise their heads after initial prey contact to aid in capture of these taller prey with their jaws.

Several kinematic variables are associated with the distinction between jaw versus tongue prehension, including: 1) the duration of tongue retraction, the duration of mouth closing, the duration of recovery, and the duration of the feeding sequence, all of which are longer for tongue prehension than for jaw prehension; 2) maximum gape angle, which is larger for jaw prehension than for tongue prehension; 3) maximum velocity of mouth closing, which is faster for jaw prehension; and 4) overshoot distance, which is larger for jaw prehension than for tongue prehension. The results of the discriminant function analyses support the idea that jaw prehension and tongue prehension represent alternative strategies for capturing prey of different sizes.

Discussion

There have been numerous studies of the visual cues used in prey recognition by toads, *Bufo bufo* [reviewed; Ewert (1987)] These studies measured the rates of orientation and snapping elicited by artificial, two-dimensional, prey-like stimuli that differed in shape, size and speed of movement. These studies showed that toads exhibit higher orienting rates for rectangular objects which move in a direction that is parallel to their long axis (i.e., worm orientation) than for similar objects that move perpendicular to their long axis (i.e., anti-worm orientation).

The results of the present study complement, rather than contradict, these previous studies. In the present study, our focus was on patterns of movement elicited by different types of real prey, rather than rates of orientation and snapping elicited by artificial stimuli. We did not attempt to compare rates of orientation or snapping among the different prey types. In fact, we selected the frog *Cyclorana novaehollandiae* specifically because it was observed to feed readily on a wide variety of different types of prey.

Extent of behavioral modulation in *C. novaehollandiae*

The first objective of this study was to investigate the extent to which feeding behavior is modulated by sensory information in *Cyclorana novaehollandiae*. Previous studies have characterized the feeding behavior of frogs as a fixed action pattern that is highly stereotyped (Ewert 1984). However, the present study shows that *C. novaehollandiae* exhibits five different behavior patterns when feeding on the five different prey types used in this study. The limit of versatility of prey capture behavior in *C. novaehollandiae* has not yet been reached and, because 12 of 19 kinematic variables differed among prey types and 12 kinematic variables varied systematically with prey characteristics, the repertoire of feeding behavior patterns exhibited by *C. novaehollandiae* could be larger than the five behavior patterns described in the present study. Thus, our study suggests that the repertoire of feeding behavior patterns exhibited by anurans may not be as limited or stereotyped as was previously believed (Ewert, 1987; p 337). Instead, it appears that feeding behavior is subject to modification through visual analysis of several characteristics of prey, including size, shape and speed of movement (see below).

Pattern of variation in kinematic variables across prey types

Numerous aspects of prey capture were related to specific features of the prey. Of 19 kinematic variables, 12 were correlated significantly with one, and only one, of the prey characteristics. The kinematic variables fell into four groups, each corresponding to a particular prey characteristic. In the first group, seven variables (duration of tongue retraction, duration of mouth closing, duration of recovery, duration of feeding sequence, maximum gape angle, maximum velocity of mouth closing and overshoot distance) were correlated significantly with prey mass (Figs. 4, 6). These variables were similar for earthworms and mice on the one hand, and for crickets, termites and waxworms on the other. In the second group, two variables (duration of approach and downward head rotation) were correlated significantly with prey length (Figs. 5, 6). These variables distinguished earthworms from all other prey types. In the third group, a single variable (i.e., upward head rotation) was correlated significantly with prey height (Figs. 5, 6) and distinguished mice from all other prey types. In the fourth group, duration of tongue protraction and tongue height were correlated significantly with the movement velocity of the prey (Figs. 5, 6) and distinguished crickets from the other prey types. Finally, although gape distance and duration of mouth opening were not correlated significantly with any of the prey characteristics, they distinguished termites from all other prey types (Table 1, Fig. 6).

Each of these patterns represents a behavioral choice that appears to be made on the basis of prey characteristics (Fig. 6). For example, the frogs choose either jaw prehension or tongue prehension, depending on the mass of the prey. Likewise, the frogs choose whether or not to exhibit upward head rotation on the basis of prey height, and whether or not to exhibit downward head rotation on the basis of prey length (Fig. 6). The head is rotated upward for mice and downward for earthworms. The frogs also choose whether or not to exhibit increased tongue height on the basis of prey velocity (Fig. 6). For fast-moving prey, the tongue is protracted to a greater distance over a longer period of time (crickets), whereas for slow-moving prey, the tongue is protracted less far over a shorter period of time (waxworms and termites). Finally, if the frogs have decided to use tongue prehension to feed on slow moving prey, they next decide whether to exhibit a termite-type or a waxworm-type behavior pattern (Fig. 6). For termites, the gape distance was smaller and the duration of mouth opening was shorter than for any of the other prey types.

Alternative hypotheses for behavioral decision making

Two alternative hypotheses could account for the pattern of variation in kinematic variables across prey types in *C. novaehollandiae* (Fig. 6). The first hypothesis is that behavioral decision making is based on an analysis of all prey characteristics simultaneously, which is translated into features of the motor response in a non-hierarchical fashion. The second hypothesis is that behavioral decision making is hierarchical, in which case choices made earlier constrain which choices will be made later.

In this study, we found some evidence for a hierarchical pattern of decision making in *C. novaehollandiae* (Fig. 6). The first choice appears to be made between jaw versus tongue prehension on the basis of prey size (represented by mass in our analysis), with the frogs exhibiting jaw prehension for the larger, heavier

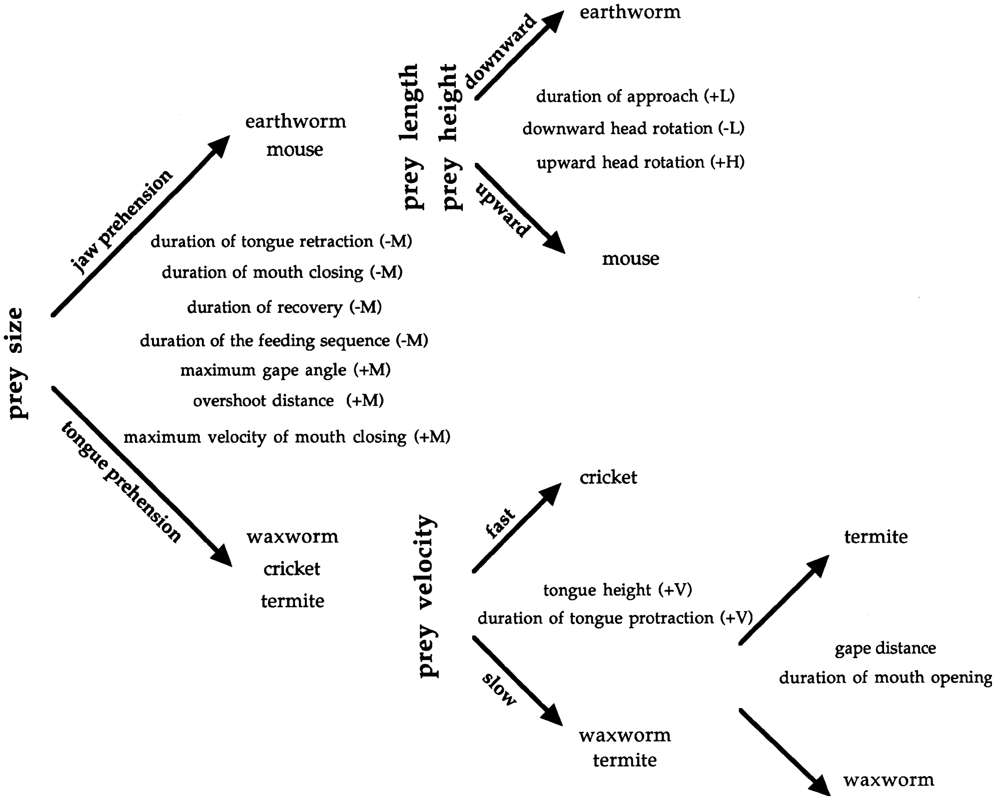

Fig. 6 A hierarchial hypothesis of behavioral decision making during feeding in *C. novaehollandiae* Letters (e.g., +*M*, −L) indicate significant correlations between prey characteristics and kinematic variables, as in Table 1. In this hypothesis, the frogs first choose between jaw prehension and tongue prehension based upon the size of the prey, as measured by mass. If the frogs have chosen jaw prehension, they next choose between downward and upward head rotation based on the length and height of the prey. If the frogs have chosen tongue prehension, they next choose between behavior for fast prey and slow prey. If the frogs have chosen slow prey behavior, they next choose between termite feeding behavior (decreased gape distance and duration of mouth opening) or waxworm feeding behavior

prey types (i.e., earthworms and mice) and tongue prehension for the smaller, lighter prey (i.e., crickets, waxworms and termites). The choice between upward versus downward head rotation occurs only for larger prey within the jaw prehension category (Fig. 6), and not for smaller prey within the tongue prehension category. Likewise, the choice between slow versus fast moving prey and the choice between termite and waxworm occur only for smaller prey within the tongue prehension category, and not for larger prey within the jaw prehension category (Fig. 6).

The hierarchical hypothesis implies that the earliest choice (i.e., jaw versus tongue prehension) influences which choices will be made subsequently. For large prey, the subsequent choice appears to be made on the basis of prey shape (i.e, length and height), whereas for small prey the subsequent choice is made on the basis of prey velocity (Fig. 6). Likewise, the frogs appear to ignore both the shape of small prey and the velocity of large prey. For example, the velocity of movement is greatest for crickets (81 cm s^{-1}) and earthworms (16 cm s^{-1}) and smallest for mice (10 cm s^{-1}), waxworms (5 cm s^{-1}), and termites (5 cm s^{-1}). Although earthworms had the second highest velocity, the frogs showed no tendency to increase their tongue height for earthworms (Fig. 5). Further studies, in which artificial prey that are large and fast-moving are presented, could help to distinguish between the hierarchical and non-hierarchical hypotheses.

Only 3 of the 19 kinematic variables were inconsistent with the hierarchical hypothesis (Fig. 6). Duration of tongue at target was greater for earthworms and termites than it was for the other prey types, whereas distance to prey and lunge length were greater for crickets and mice than they were for the other prey types. Two variables (maximum tongue reach and maximum velocity of mouth opening) showed no differences among prey types.

The hierarchical hypothesis (Fig. 6) suggests, somewhat counterintuitively, that the frogs may plan the endpoint of the prey capture trajectory first, and subsequently fill in details of how they will reach that endpoint. For example, all of the kinematic variables associated with the earliest decision between tongue and jaw prehension (i.e., duration of tongue retraction, mouth closing, recovery, feeding sequence, maximum gape angle, overshoot distance and maximum velocity of mouth closing) occur late in the feeding sequence, whereas later decisions involve kinematic variables that occur earlier in the sequence, such as tongue height and duration of tongue protraction (Fig. 6).

Although the decisions concerning behavioral choice may be nested hierarchically, it is probable that they are made in a relatively brief period of time between when the frog first detects the prey and when mouth opening and tongue protraction are initiated. This time period corresponds to the orienting, approaching and fixating stages of Ewert (1987), or the preparatory (approach) phase of Gans and Gorniak (1982), and is of the order of 180 ms. The total time available for visual assessment of prey characteristics is probably on the order of at least 500 ms.

Mechanisms used to modulate feeding behavior

We next asked whether feeding kinematics changed as a purely biomechanical consequence of physical differences in prey characteristics (in the absence of behavioral compensation), or whether the frogs used sensory information about the prey to modulate feeding kinematics. A previous study of feeding kinematics in the treefrog *Pachymedusa dacnicolor* (a long tongued member of the family Hylidae) indicated that sensory information about the prey, rather than biomechanics, influenced feeding kinematics (Gray and Nishikawa 1995). Gray and Nishikawa (1995) compared successful captures (in which prey is contacted and adheres to the tongue) to misses (in which prey is neither contacted nor does it adhere to the tongue) and drops (in which prey is contacted but does not adhere to the tongue). The frogs received tactile information about the prey in captures and drops but not in misses, whereas biomechanical effects of the prey (due to adhesion on the tongue) were present in captures, but not in drops or misses. The results showed that the duration of the gape cycle was significantly longer during misses than it was during captures or drops, suggesting that tactile cues rather than biomechanics control gape cycle duration.

In the present study, we investigated whether the frogs used visual or tactile information to modulate feeding behavior in response to prey characteristics, or whether purely physical differences among prey types affected feeding behavior. If significant differences among prey types in the mean values of a kinematic variable are evident prior to prey contact, then the kinematic variable must be modulated on the basis of visual information about the prey, because neither tactile information nor biomechanical effects are present before contact is made with the prey. If significant differences are evident only after prey contact, then the kinematic variable may be influenced either by tactile cues or biomechanical effects as well as by visual information about the prey. Biomechanical effects were examined by determining whether the differences in behavior among prey types were in the direction predicted on the basis of physical differences among the prey types. For example, the duration of tongue retraction should be longer for a massive prey such as a newborn mouse than for a lighter prey such as a termite so long as the frogs do not compensate for the mass of the prey. If they do compensate, then there is an interaction between biomechanical effects and sensory modulation, and the duration of tongue retraction may be similar for the two types of prey. We looked specifically for biomechanical effects in which there was no compensation, so that the difference in feeding kinematics should be in the direction predicted by the physical characteristics of the prey.

In cases for which there was evidence of compensation, we asked which sensory modality (visual versus tactile) was used to modulate feeding kinematics.

We found no evidence that the differences in behavior among prey types resulted purely from biomechanical effects of the prey. In every case, behavioral differences (if present) were in the direction opposite that predicted for purely biomechanical effects. For example, duration of tongue retraction, duration of feeding sequence and duration of recovery should be shorter for lighter prey types. However, all three duration variables were longer for lighter prey. In addition, when feeding on mice, the upper jaw continued to rise after prey contact. If this were a purely biomechanical effect, then the heavier mouse should have pulled the upper jaw downward. In no case was the difference in behavior among the prey types in the direction expected to result from physical differences among the prey (with no behavioral compensation).

The majority of the behavioral decision steps in the hierarchical model (Fig. 6) appear to be made on the basis of a visual analysis of prey characteristics. First, the decision to use tongue prehension versus jaw prehension appears to be associated with a visual assessment of prey characteristics. In *Rana pipens*, the decision to use jaw prehension versus tongue prehension is based on a visual analysis of prey length (Anderson and Brandt 1993; Anderson and Nishikawa, 1996). When the frogs were offered pieces of earthworm that ranged in size from 1.5 cm (i.e., the size of waxworms) to 4.5 cm (i.e., the size of whose earthworms), they always exhibited tongue prehension when feeding on 1.5-cm pieces of earthworm and always exhibited jaw prehension when feeding on pieces that were 2.0 cm and larger. Thus, although these prey types have the same smell, texture, colour and pattern of movement, and although they differ by only 0.5 cm in length, they elicit distinctly different behavior patterns.

In the present study, a series of prey types was used that differed in many characteristics, including size shape and speed of movement. We correlated kinematic variables with prey characteristics, rather than systematically varying each characteristic experimentally, as was done by Anderson and Nishikawa (1996). Although the latter approach is the stronger, it is important to note that possible confounding effects of analyzing physical characteristics across prey types should have tended to obscure patterns, whereas the patterns of correlation that we describe were uniformly strong (all $r > 0.9$). Also, it is important to note that the results obtained by Anderson and Nishikawa (1996), in which the effect of prey length on feeding kinematics was studied systematically in *Rana pipiens* using pieces of earthworms, are entirely consistent with those of the present study. It is possible that other cues, not measured in the present study, may also have contributed to the observed pattern of behavioral modulation.

The fact that feeding kinematics diverges early in the movement sequence when *R. pipiens* feeds on waxworms versus earthworms also suggests that visual information about the prey is used to choose between jaw prehension and tongue prehension (C.W. Anderson and K.C. Nishikawa, unpubl. obs.). *Rana pipiens* rotates the head downward significantly less for 1.5 than for 2.0 cm and larger pieces of earthworm. In the field before mouth opening, a significant difference in downward head rotation was already apparent between 1.5 and 2.0 cm pieces of earthworm, suggesting that the decision to use tongue versus jaw prehension was made before the movement was executed. The results of the present study suggest that the decision to exhibit downward versus upward head rotation is also visually guided and planned in advance. In the field before prey contact, a significant difference in head rotation was already apparent between sequences for earthworms and mice in *C. novaehollandiae*.

Whereas the decision to exhibit jaw prehension versus tongue prehension and the decision to use upward versus downward head rotation appear to be based on a visual analysis of prey characteristics, the decision to exhibit behavior for fast or slow prey and the decision to exhibit termite-like or waxworm-like behavior may result from either visual analysis or tactile cues. Duration of tongue protraction and tongue height are greater for fast-moving prey (i.e., crickets) than for slow-moving prey. These differences could be due either to a visual analysis of the movement velocity of the prey or to differences in tactile cues from the struggling prey once contact has been made between prey and tongue. The greatest increase in tongue height occurs after prey contact, which supports the tactile hypothesis. In fishes, it has also been hypothesized that information about the movement velocity of the prey results in modulation of feeding behavior (Liem 1978; Lauder 1981). However, the sensory modalities that are used remain unknown.

The function of behavioral modulation is to match feeding behavior with prey characteristics to ensure that a behavior pattern that is effective for catching a given prey type is executed. The different behavior patterns exhibited by *C. novaehollandiae* when feeding on the five prey types appear to be well suited for capturing the particular type of prey with which each is associated. For example, tongue prehension is only effective in capturing prey for which the force of adhesion between tongue and prey is greater than or equal to the gravitational force on the prey. Both earthworms and mice are too heavy to be captured effectively using tongue prehension. Therefore, the frogs use jaw prehension to catch them. Likewise, upward head rotation enables the frogs to engulf tall prey with the jaws. Upward head rotation was exhibited by *C. novaehollandiae* only when feeding on mice, which are the tallest prey. A third example is the increase in tongue height and the duration of tongue protraction exhibited when feeding on crickets. It appears that the increase in tongue height may increase the area of contact between the sticky tongue and the struggling cricket, thereby increasing the probability of successful prey capture.

We hypothesize that experience is important in matching particular characteristics of the prey with appropriate changes in feeding behavior. As yet, there is no evidence that modulation of feeding behavior in response to prey type is learned gradually during ontogeny in frogs. However, recent evidence demonstrates that adult toads learn new behavior patterns over relatively short time periods (Innocenti and Nishikawa 1995). In toads, bilateral transection of the hypoglossal nerves denervates the tongue protractor muscles. Following hypoglossal nerve transection, toads learn to increase head and jaw movements to compensate for the lack of tongue protraction. The toads learn the new motor task within as few as 44 trials over an 8-day period.

Although neither tactile cues nor biomechanical effects play prominent roles in modulating feeding behavior, either could be important in shaping the feeding behavior of newly metamorphosed frogs when they first encounter different prey types. The first time a frog encounters a particular prey type, it may use biomechanical effects and tactile information to detect errors and ineffeciencies in its prey capture strategy. Through trial and error, the frogs may learn which behavior patterns can be used most effectively to capture prey that differ in size, shape or velocity of movement.

Evolutionary considerations

The frog *Rana pipiens* possesses a long tongue, which is a derived characteristic of anurans (Nishikawa et al. 1992). Anderson (1993) hypothesized that *R. pipiens* uses a plesiomorphic behavior pattern (i.e., jaw prehension) to catch larger prey and that a new behavior pattern for catching smaller prey (i.e., tongue prehension) had evolved with the acquisition of a long tongue. In contrast to *R. pipiens, C. novaehollandiae* possesses a short tongue that can be protracted only 25% of lower jaw length. This is the plesiomorphic state of the feeding apparatus among frogs (Nishikawa et al. 1992). Like *R. pipiens*, however, *C. novaehollandiae* also modulates its feeding behavior in response to different prey types. The behavior patterns exhibited by *R. pipiens* and *C. novaehollandiae* when feeding on earthworms and waxworms are very similar. When feeding on earthworms, *C. novaehollandiae* lunges forward, arches its body, rotates its head downward and captures the prey using jaw prehension, just like *R. pipiens*. When feeding on waxworms, *C. novaehollandiae* captures the prey using tongue prehension. For both *R. pipiens* and *C. novaehollandiae*, downward head rotation was significantly greater when feeding on earthworms than when feeding on waxworms and duration of mouth closing was significantly shorter when feeding on earthworms than when feeding on waxworms. Thus, it appears that the ability to modulate feeding behavior in response to prey type is widespread among neobatrachian frogs. Preliminary data suggest that *Bombina orientalis* (Family Bombinatoridae), an archaeobatrachian frog, is also capable of modulating its feeding behavior in response to prey type (C. Valdez, unpubl. obs.). Thus, it is probable that the ability to modulate feeding behavior in response to prey type is a primitive characteristic of anurans.

In contrast to *C. novaehollandiae* and *R. pipiens*, some species of anurans appear to have reduced or lost the ability to modulate their feeding behavior in response to different types of prey. For example, the marine toad (*Bufo marinus*, Family Bufonidae) has only been observed to use tongue prehension to capture prey, although a number of prey types have been tested, including termites, waxworms, crickets and earthworms (K. Nishikawa, unpubl. obs.). As expected, capture success is very low when toads use tongue prehension to capture earthworms. In contrast, African treefrogs of the genus *Leptopelis* (family Hyperoliidae) have only been observed to use jaw prehension to capture prey, although waxworms, termites and earthworms have been offered.

In conclusion, *Cyclorana* exhibits different feeding behavior patterns depending on the type of prey being captured. The differences in behavior observed when *Cyclorana* feeds on earthworms versus waxworms are very similar to the differences observed when *Rana pipiens* feeds on the same prey types (Anderson 1993). The extent to which the feeding behavior of frogs can be modulated by sensory input is greater than previously thought. The decisions regarding which feeding behavior patterns will be exhibited appear to be organized hierarchically, and are based primarily on visual analysis of prey characteristics rather than tactile cues or biomechanical effects. Tactile cues may be important for fine tuning of feeding behavior during the later phases of prey capture.

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References

Anderson CW (1993) The modulation of feeding behavior in response to prey type in the frog *Rana pipiens* J Exp Biol 179: 1–12

Anderson CW, Brandt T (1993) Sensory modalities that influence motor pattern choice in the leopard frog, *Rana pipiens,* Soc Neurosci Abstr 19: 1617

Anderson CW, Nishikawa KC (1996) The role of sensory information during motor program choice in frogs. J Comp Physiol A 179: 753–762

Deban SM, Nishikawa KC (1992) The kinematics of prey capture and the mechanism of tongue protraction in the green tree frog, *Hyla cinerea* J Exp Biol 170: 235–256

Ewert J-P (1984) Tectal mechanisms that underlie prey catching and avoidance behaviors in toads. In: Vanegas H (ed) Comparative neurology of optic tectum. Plenum Press, New York, pp 247–416

Ewert J-P (1987) Neuroethology of releasing mechanisms: Prey-catching in toads. Behav Brain Sci 10: 337–405

Ford LS, Cannatella DC (1993) The major clades of frogs. Herpetol Monogr 6: 118–131

Gans C, Gorniak GC (1982) Functional morphology of lingual protrusion in marine toads (*Bufo marinus*). Am J Anat 163: 195–222

Gorniak GC, Rosenberg HI, Gans C (1982) Mastication in the tuatara, *Sphenodon punctatus* (Reptilia: Rhynchocephalia): structure and activity of the motor system. J. Morphol 171: 321–353

Gray LA, Nishikawa KC (1995) Feeding kinematics of phyllomedusine tree frogs. J Exp Biol 198: 457–463

Hiiemae KW, Crompton AW (1985) Mastication, food transport and swallowing. In: Hildebrand M et al (eds) Functional vertebrate morphology. Harvard Univ Press, Cambridge, MA, pp 262–296

Honigmann H (1944) The visual preception of movements by toads. Proc R Soc London Ser B 132: 291–307

Innocenti CM, Nishikawa KC (1994) Motor learning in toads (*Bufo marinus*) following hypoglossal transection. Am Zool 34: 56A

Lauder GV (1981) Intraspecific functional repertories in the feeding mechanism of the characoid fishes *Lebiasina, Hoplias* and *Chalceus*. Copeia 1981: 154–168

Lauder GV (1983) Functional and morphological bases of trophic specialization in fishes. Science 219: 1235–1237

Liem KF (1978) Modulatory multiplicity in the functional repertoire of the feeding mechanism in cichlid fishes I. Piscivores. J Morphol 158: 323–360

Liem KF (1980) Adaptive significance of intra- and interspecific differences in feeding repertoires of cichlid fishes. Am Zool 20: 295–314

Nishikawa KC, Anderson CW, Deban SM, O'Reilly JC (1992) The evolution of neural circuits controlling feeding behavior in frogs. Brain Behav Evol 40: 125–140

Nishikawa KC, Roth G (1991) The mechanism of tongue protraction during prey capture in the frog *Discoglossus pictus*. J Exp Biol 159: 217–234

Rice WR (1989) Analyzing tables of statistical tests. Evolution 43: 223–225

Rossignol S, Lund JP, Drew T (1988) The role of sensory inputs in regulating patterns of rhythmical movements in higher vertebrates: a comparison between locomotion, respiration and mastication. In: Cohen AH et al (eds) Neural control of rhythmic movements in vertebrates. Wiley New York, pp 201–284

Valdez CM, Nishikawa KC (1993) Behavioral pattern differences in response to varying prey type in the Australian frog *Cyclorana novaehollandiae* Am Zool 33: 77A

Wainwright PC, Lauder GV (1986) Feeding biology of sunfishes: pattern of variation in the feeding mechanism. Zool J Linn Soc 88: 217–228

Weerasuriya A (1989) In search of the motor pattern generator for snapping in toads. In: Ewert JP, Arbib MA (eds) Visuomotor coordination: amphibians, comparisons, models and robots. Plenum Press, New York, pp 589–614