

MODULATION OF PREY-CAPTURE BEHAVIOR IN THE PLETHODONTID SALAMANDER *ENSATINA ESCHSCHOLTZII*

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Summary

The hypothesis that salamander prey-capture behavior is highly stereotyped was tested in the plethodontid salamander *Ensatina eschscholtzii* using high-speed videography and kinematic analysis of feedings on two types of prey (waxworms and termites). The results show that *E. eschscholtzii* is capable of modulating the timing and magnitude of tongue and jaw movements in response to prey type. Feedings on waxworms, the larger prey, were characterized by shorter durations and higher velocities of tongue and jaw movements compared with feedings on termites, particularly in the latter portion of the feeding sequence (i.e. after prey contact). To test the hypothesis that sensory feedback through the tongue pad plays a role in modulating feeding movements in response to prey type,

the ramus lingualis of the glossopharyngeal nerve (cranial nerve IX), which is known to carry sensory information from the tongue pad in salamanders, was transected bilaterally. This experimental deafferentation of the tongue pad had no effect on the degree or direction of differences in feeding kinematics across prey type. These results refute the glossopharyngeal feedback hypothesis, but are consistent with the hypothesis that *E. eschscholtzii* responds more vigorously to larger prey by assessing prey size visually.

Key words: salamander, *Ensatina eschscholtzii*, prey capture, kinematics, feeding, sensory feedback, glossopharyngeal nerve, Plethodontidae.

Introduction

Terrestrial frogs and salamanders typically capture prey by tongue prehension, a behavior in which a sticky tongue is protracted onto the prey, adheres to it, and is drawn back into the mouth with the prey. Prey capture is performed extremely rapidly and, on the basis of the initial studies of a few taxa, such as the marine toad *Bufo marinus* (Gans and Gorniak, 1982) and the tiger salamander *Ambystoma tigrinum* (Larsen and Guthrie, 1975), this behavior was considered highly stereotyped, showing little variation within an individual in the timing of tongue and jaw movements. Later studies on additional taxa revealed variation in the prey-capture movements of frogs and suggested that the feeding of frogs was not as highly stereotyped as that of salamanders (Nishikawa and Cannatella, 1991; Reilly, 1995). However, studies of a wider range of salamander taxa, both terrestrial and aquatic, revealed more within-individual variation among salamanders than was previously suspected and demonstrated that variation in feeding movements is widespread among both salamanders and frogs (salamanders: Erdman and Cundall, 1984; Shaffer and Lauder, 1985; Larsen and Beneski, 1988; Miller and Larsen, 1990; Reilly and Lauder, 1989, 1992; Elwood and Cundall, 1994; Maglia and Pyles, 1995; frogs: Nishikawa and Cannatella, 1991; Deban and Nishikawa, 1992;

Nishikawa *et al.* 1992; Anderson, 1993; Ritter and Nishikawa, 1995).

Investigations into the causes of within-individual variation have shown that both frogs and salamanders can recognize features of prey visually, such as size and position, and can modulate their feeding movements in response to those features (Anderson, 1993; Maglia and Pyles, 1995). In addition, frogs have been shown to rely on sensory feedback from the tongue to coordinate and modulate tongue and jaw movements (Ritter and Nishikawa, 1995; Anderson and Nishikawa, 1996). In frogs, both visual assessment of prey and sensory feedback during feeding are involved in modulating feeding behavior (Ewert and Burghagen, 1979; Nishikawa *et al.* 1992), but in salamanders, only visual assessment of prey has been demonstrated (Roth, 1987). Nonetheless, salamanders, like frogs, possess sensory structures in the tongue pad that are innervated by the ramus lingualis of the glossopharyngeal nerve (cranial nerve IX). The ramus lingualis is entirely sensory, and the only known sensory nerve serving the tongue pad in salamanders; other branches of the glossopharyngeal nerve contain motor components that innervate tongue protraction muscles (Wake *et al.* 1983). The presence of this sensory pathway suggests that salamanders may have the ability to use

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sensory information from the tongue to modulate feeding movements, as some frogs do. Salamander species that show clear modulation in feeding movements in response to an easily controlled variable, such as prey type, are ideal for determining whether sensory feedback from the tongue plays a role in controlling modulation.

In this study, the terrestrial, direct-developing, plethodontid salamander *Ensatina eschscholtzii* is shown to modulate its feeding behavior in response to prey type. This behavioral modulation is used in conjunction with deafferentation experiments to test the hypothesis that sensory feedback through the tongue pad plays a role in the modulation of feeding movements. First, I present the kinematics of *E. eschscholtzii* feeding on two types of prey, waxworms and termites, and compare statistically the differences among individuals and within individuals across prey type. Next, I examine the effects of surgical deafferentation of the tongue pad, by bilateral transection of the ramus lingualis of the glossopharyngeal nerve, on overall feeding kinematics as well as the effects of deafferentation on differences in feeding kinematics among individuals and across prey type. I discuss the variation of feeding movements in *E. eschscholtzii* and the roles of sensory feedback and visual assessment of the prey in comparison with other salamanders and with frogs. I consider the potential for sensory feedback in controlling feeding movements in amphibians. Finally, I emphasize the importance of eliciting as wide a range of behavior as possible in laboratory studies of amphibian feeding and motor control.

Materials and methods

All *Ensatina eschscholtzii* Gray, 1850 used in this study were collected from wild populations in California and housed in plastic containers on moist paper towels at 13–17 °C with a 12 h:12 h light:dark cycle. Salamanders were maintained on a diet of waxworms, crickets and termites. Twenty individuals that fed readily were used for initial feeding trials in which they were video-taped feeding on these same prey. Of these, four individuals, ranging in size from 6.2 to 6.7 cm snout–vent length, were selected for kinematic analysis and deafferentation experiments. These individuals were offered large prey (waxworms, mean mass 262 mg, mean length 2.1 cm) and small prey (termites, mean mass 2.9 mg, mean length 0.5 cm). These prey were chosen because of their availability and because they differ vastly in size. In addition, these prey are representative of natural prey taxa and fall within the size range of natural prey items for *E. eschscholtzii* and related species of similar size (Lynch, 1985). Three feeding trials for each of the four experimental animals were recorded on each of the two prey types, both before and after surgical deafferentation of the tongue pad, giving a total of 48 feeding trials. Analysis of the feeding trials was restricted to the prey-capture event, beginning with the start of mouth opening and ending with the completion of mouth closing.

Videography

Feeding behavior was video-taped at 180 and 300 fields s⁻¹ in lateral view with a Display Integration Technologies HSC 300 high-speed video camera with synchronized stroboscopic illumination. Salamanders were video-taped at 17 °C feeding unrestrained on a substratum of moist paper towel, against a background of 1 cm squares to provide scaling factors and correct aspect ratio. Prey were placed individually in front of the salamanders with forceps, such that they would crawl towards or past the salamander. Occasionally, the salamander had to be positioned in lateral view by strategic placement of the prey item, to which it would orient its head and body. Salamanders were first allowed to swallow the prey they captured before another prey item was offered. Only feeding trials in which the salamander's jaws and tongue were visible throughout the sequence and in which the salamander remained in lateral view were used for kinematic analysis.

Kinematic analysis

Video sequences were captured and analyzed using NIH Image version 1.59 and Microsoft Excel version 5.0 software running on an Apple Power Macintosh 8500/120 computer. The *x,y* coordinates of four points on the salamander were recorded from each field of the video sequence: (1) tip of upper jaw, (2) jaw joint, (3) tip of lower jaw and (4) tip of tongue, the point on the tongue farthest from the jaw joint (Fig. 1). The *x,y* coordinates of the prey item in the first field of the feeding sequence were also recorded. These *x,y* coordinate data were used to calculate kinematic variables that describe the timing and extent of movements of the body, head, tongue and jaws of the salamanders. Distances are calculated in centimeters and velocities are reported in cm s⁻¹. Duration and timing variables are reported in milliseconds relative to the start of mouth opening at time zero (i.e. the first video field in which the mouth was seen to open). Times were converted from frames to milliseconds by multiplying the frame of the event (or frames of the duration) by the time interval between frames, which was 3.33 ms for sequences

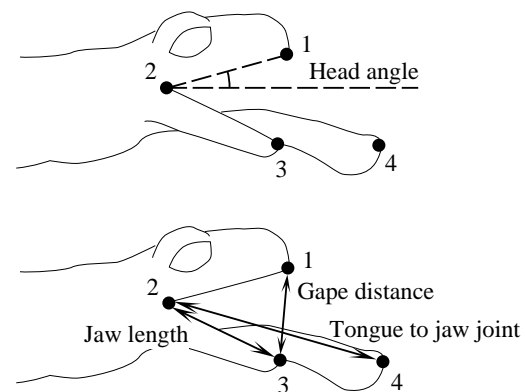


Fig. 1. Points used in the kinematic analysis: (1) upper jaw tip, (2) jaw joint, (3) lower jaw tip and (4) tongue tip. Head angle (upper diagram) and gape distance, jaw length and tongue to jaw joint (lower diagram) are explained in the text.

recorded at $300 \text{ fields s}^{-1}$ and 5.55 ms for sequences recorded at $180 \text{ fields s}^{-1}$.

The times of 11 events were calculated: (1) time of first tongue visibility, the first video frame in which the tongue is visible in the mouth; (2) time of first forward movement, the frame in which the salamander first moves towards the prey; (3) time of prey contact, the frame in which the tongue first touches the prey; (4) time of maximum tongue reach, the frame in which the tongue is farthest from the jaw joint, (5) time of maximum gape, the frame in which the upper jaw tip and lower jaw tip are farthest apart; (6) time of maximum head angle, the frame in which the head is lifted the farthest from the initial vertical position; (7) time of maximum forward lunge, the frame in which the jaw joint is at its maximum forward excursion (i.e. towards the prey); (8) time of start of mouth closing, the frame in which the gape distance (distance calculations described below) begins to decrease for the last time; (9) time of start of tongue retraction, the frame in which tongue reach first begins its final decrease; (10) time of completion of tongue retraction, the frame in which the tongue is no longer visible; and (11) time of completion of mouth closing, the frame in which the gape last decreases. Timing variables 3–8 were included in the statistical analysis (see below and Table 1).

Six duration variables were calculated from the eleven timing variables: (1) duration of mouth closing, the time between the start of mouth closing and the completion of mouth closing; (2) duration of gape cycle, the time between the start of mouth opening at time zero and the completion of mouth closing; (3) duration of tongue protraction, the time between the frame of first tongue visibility and the frame of maximum tongue reach; (4) duration of tongue at target, the time between prey contact and the start of tongue retraction; (5) duration of tongue retraction, the time between the frame of maximum tongue reach and the completion of tongue retraction; and (6) duration of tongue cycle, the time between first tongue visibility and the completion of tongue retraction. All six duration variables were included in the statistical analysis.

Five distances and one angle (Fig. 1) were calculated from the coordinate data: (1) length of lower jaw; the distance between the jaw joint and the lower jaw tip; (2) gape distance, the distance between the upper jaw tip and the lower jaw tip; (3) tongue reach, the distance between the jaw joint and the tip of the tongue minus the length of the lower jaw; (4) forward lunge distance, the horizontal displacement of the jaw joint from the initial position; (5) initial prey distance, the distance from the lower jaw tip to the prey in the first frame of the sequence; and (6) head angle, the angle between a horizontal line and a line from the upper jaw tip to the jaw joint, normalized by subtracting the head angle in the first frame of the sequence. Maximum values of gape distance, tongue reach, forward lunge distance and head angle were included in the statistical analysis examining the effects of prey type and surgery.

Four velocities were calculated from the distance and timing

variables: (1) velocity of mouth opening, the maximum gape distance divided by the time of maximum gape (which equals the duration of mouth opening); (2) velocity of mouth closing, the maximum gape distance divided by the duration of mouth closing; (3) velocity of tongue protraction, maximum tongue reach divided by the duration of tongue protraction; and (4) velocity of tongue retraction, the maximum tongue reach divided by the duration of tongue retraction. All velocities were included in the statistical analysis.

Tongue deafferentation

Salamanders were anesthetized in 2% aqueous, buffered tricaine methanesulfonate (MS222) for 10–20 min. The salamander was placed under a dissecting microscope and the tongue was gently pulled from the mouth with blunt forceps. The ramus lingualis of the glossopharyngeal nerve (cranial nerve IX) could be seen running along the dorsal side of the tongue stalk, along the first ceratobranchial and lateral to the basibranchial, beyond which it enters the tongue pad (Fig. 2). A small incision was made in the transparent sheath surrounding the tongue stalk just dorsal to the ceratobranchial. The nerve and associated blood vessel were pulled through the incision. The nerve was teased away from the blood vessel and transected, and a small section of the nerve approximately 1–3 mm long was removed to retard regeneration. The nerve transection was performed bilaterally, and the tongue was then returned to the mouth. The salamander was returned to its cage and recovered from anesthesia within 1 h. Post-surgery feedings were recorded beginning the following day and were completed within a week of surgery. All animals fed readily

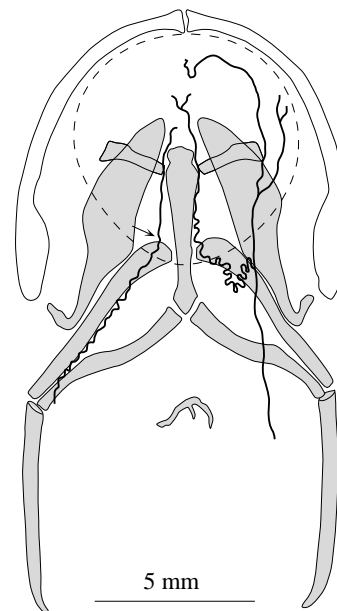


Fig. 2. Lower jaw and hyobranchial apparatus (shaded) of *Ensatina eschscholtzii* showing the ramus lingualis of the glossopharyngeal nerve (cranial nerve IX) on the left and the ramus hypoglossus of spinal nerves I and II on the right. The arrow indicates the approximate location of nerve transection, and the dashed line indicates the position of the tongue pad.

after surgery. After all post-surgery feeding trials had been completed, the animals were killed by over-anesthesia in MS222, and the nerve transections were confirmed by dissection.

Statistical analyses

Twenty kinematic variables (see Table 1) were used in five separate statistical comparisons, each an analysis of variance (ANOVA). To characterize adequately variation among individuals, between feedings on the two types of prey and across surgical treatment, the following ANOVAs were performed: (1) two-way ANOVA of all 24 normal feedings (before surgical treatment) examining the effects of prey, individual and individual \times prey interaction (see Table 1); (2) two-way ANOVA of all 24 post-surgery feedings examining the effects of prey, individual and individual \times prey interaction (see Table 2); (3) two-way ANOVA on all 24 feedings on waxworms examining the effects of individual, surgical treatment and individual \times treatment interaction (see Table 3); (4) two-way ANOVA on all 24 feedings on termites examining the effects of individual, treatment and individual \times treatment interaction (see Table 3); and (5) three-way ANOVA on all 48 feedings examining the effects of individual, prey, treatment and all interactions (see Table 4).

For each ANOVA, non-significant interaction terms were removed from the model on a variable-by-variable basis to increase statistical power. Individual was the random effect, and prey and surgical treatment were the fixed effects. In those analyses with significant interaction effects, the interaction mean square (individual \times prey or individual \times treatment) was used as the error term (denominator) to calculate the F -ratio for the fixed effect (Zar, 1996). Because 20 variables were compared in each statistical test, significance levels were adjusted to $P \leq 0.0025$ using the simultaneous Bonferroni correction for experiment-wide error (Sokal and Rohlf, 1995).

To determine which kinematic variables might be affected by the initial distance to the prey, least-squares regressions were performed for all 24 normal, pre-surgery trials on all 20 kinematic variables *versus* initial prey distance. In addition, to visualize the effects of prey type, surgical treatment and individual on overall feeding kinematics, a principal components analysis (PCA) was performed on all feeding trials and kinematic variables (on the entire data set of 48 trials). Unrotated factor scores for the first two principal components (PC1 and PC2) were calculated for each feeding trial and plotted against one another.

All statistical analyses were performed on an Apple Power Macintosh 8500/120 computer using StatView software version 4.5 and SuperANOVA software version 1.11.

Results

Normal prey-capture kinematics

Ensatina eschscholtzii used primarily tongue prehension to capture prey during the course of these experiments. During a

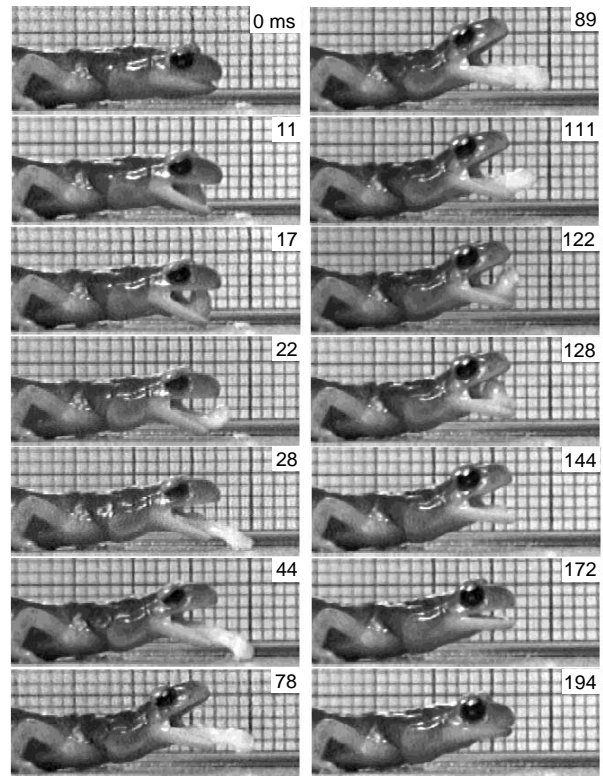


Fig. 3. Representative sequence of *Ensatina eschscholtzii* capturing a termite. The numbers represent time (in ms) from the start of mouth opening. Note the long duration of the sequence compared with that in Fig. 5.

typical feeding trial, the salamander orients to the prey, fixates the prey visually and then opens the mouth and protracts the tongue. The tongue contacts the prey and usually continues to extend following prey contact (Figs 3, 4). The tongue and adherent prey are then immediately retracted into the mouth and the mouth is closed. Mouth opening is accompanied by elevation of the head, and mouth closing is accompanied by depression of the head. Mouth opening and tongue protraction are sometimes accompanied by a forward lunge towards the prey. The eyes usually remain open for the duration of the prey-capture event. Tongue protraction occurs during mouth opening, and prey contact usually occurs in the video frame just before maximum tongue reach. Tongue retraction occurs during mouth opening, during mouth closing or during a plateau in gape distance. The gape profile consists of a period of mouth opening, a plateau that may or may not be present, and a period of mouth closing. An additional period of mouth opening may follow the plateau and is immediately followed by mouth closing. This second period of mouth opening coincides with tongue retraction and the passage of the prey into the mouth (Fig. 4).

Much of the variation in the extent and timing of movements of the head, jaws, tongue and body among trials and individuals was not correlated with any of the measured or controlled variables. Differences between feedings on different prey, however, were more consistent: feeding movements were

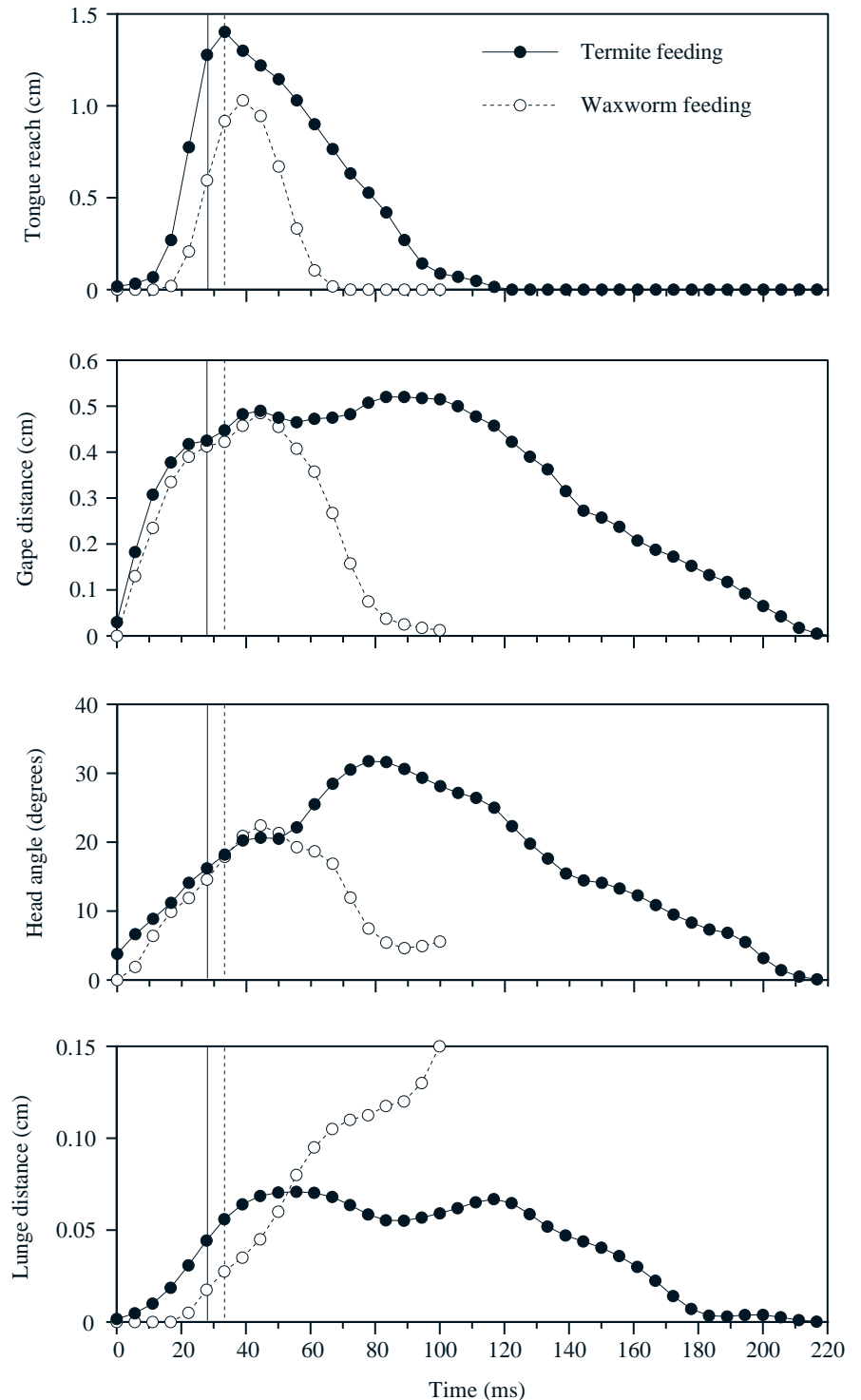


Fig. 4. Representative kinematic profiles of two prey-capture sequences of *Ensatina eschscholtzii* before tongue deafferentation. The termite feeding (filled circles) shows a long time course, asymmetrical shape of the tongue and gape profiles, and long duration of tongue retraction and mouth closing. The waxworm feeding (open circles) shows a short time course of movements and symmetrical tongue and gape profiles. The solid and dashed vertical lines indicate the time of prey contact for the termite feeding and the waxworm feeding, respectively. Note that the kinematic profiles of termite and waxworm feedings diverge strongly after prey contact.

performed more quickly with waxworm prey than with termite prey (Figs 3, 5).

Effect of initial prey distance

Four kinematic variables covaried to some extent with initial prey distance. Maximum tongue reach was the only variable to show a significant correlation with initial prey distance ($r=0.86$; $P<0.0001$); longer maximum tongue reach was

correlated with greater initial distance of the prey. Time to maximum tongue reach showed a slight, but non-significant, negative correlation ($r=0.52$; $P=0.009$), indicating that tongue protraction took longer in feeding trials in which the prey was more distant. Tongue protraction velocity showed a slight, but non-significant, positive correlation ($r=0.44$; $P=0.031$), suggesting that more distant prey elicited more rapid tongue protraction. Finally, tongue retraction velocity showed a slight

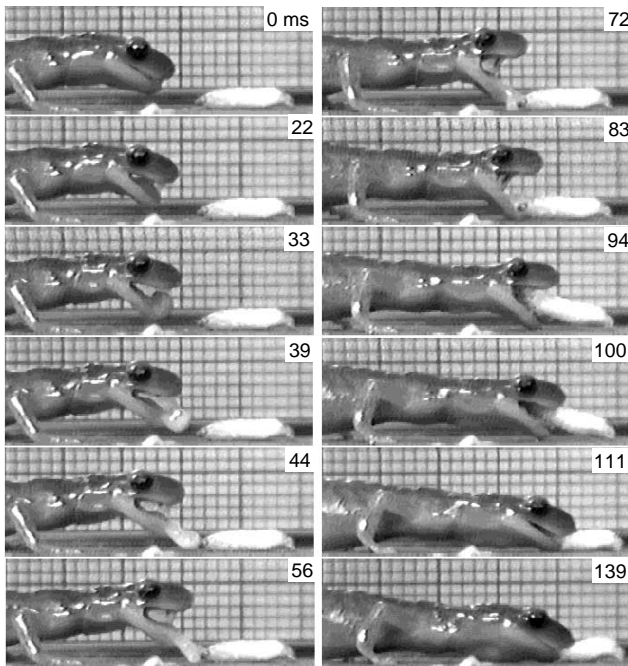


Fig. 5. Representative sequence of *Ensatina eschscholtzii* capturing a waxworm. The numbers represent time (in ms) from the start of mouth opening. Note the forward lunge and rapid time course compared with Fig. 3.

positive, but non-significant, correlation ($r=0.40$; $P=0.055$), indicating that more distant prey elicited slightly faster withdrawal of the tongue.

Termite captures versus waxworm captures

The kinematic profiles of termite captures are qualitatively different from those of waxworm captures. Tongue and jaw movements during waxworm captures produce nearly symmetrical kinematic profiles, while those of termite captures produce skewed, asymmetrical profiles (Fig. 4). Termite and waxworm captures show similar tongue protraction and mouth opening durations and velocities, but termite captures show greater durations of tongue retraction and mouth closing and a lower velocity of tongue retraction. Also, the time course of termite captures is much longer than that of waxworm captures. Waxworm feedings appear to be performed more vigorously, in general, than termite feedings.

One of 20 kinematic variables shows significant variation among individuals in the two-way ANOVA at the Bonferroni-corrected significance level of $P \leq 0.0025$: time of start of mouth closing ($F=6.91$, $P=0.0025$). Five kinematic variables show significant differences across prey type, including four duration measures that are significantly greater in termite captures than in waxworm captures: duration of mouth closing ($F=16.02$, $P=0.0008$), duration of gape cycle ($F=35.47$, $P=0.0001$), duration of tongue retraction ($F=22.27$, $P=0.0001$) and duration of tongue cycle ($F=21.98$, $P=0.0002$). The

Table 1. Kinematic variables comparing normal termite and waxworm feedings and two-way ANOVA testing effects of individual and prey

Variable	Termite		Waxworm		Individual <i>F</i> -ratio	Prey <i>F</i> -ratio	Individual \times Prey <i>F</i> -ratio
	Mean	S.E.M.	Mean	S.E.M.			
Time of prey contact (ms)	25.7	1.4	24.7	1.3	2.19	0.35	0.98
Time of maximum tongue reach (ms)	29.5	1.7	31.7	2.2	2.94	0.79	2.29
Time of maximum gape (ms)	61.8	10.9	46.6	2.2	4.29	2.72	2.26
Time of maximum head angle (ms)	77.1	9.4	46.9	6.0	3.63	9.99	1.43
Time of maximum forward lunge (ms)	54.5	4.9	60.0	9.0	0.46	0.27	5.22
Time of start of mouth closing (ms)	81.8	13.6	50.2	2.7	6.91*	9.36	4.89
Duration of mouth closing (ms)	107.7	12.9	44.2	7.8	0.29	16.02*	0.43
Duration of gape cycle (ms)	205.5	17.1	97.6	7.9	1.63	35.47*	0.74
Duration of tongue protraction (ms)	14.8	2.4	16.6	2.0	1.57	0.38	1.50
Duration of tongue at target (ms)	27.7	5.1	18.4	2.4	3.40	3.68	0.62
Duration of tongue retraction (ms)	77.9	11.6	24.2	1.5	1.47	22.27*	1.66
Duration of tongue cycle (ms)	116.6	14.3	52.2	3.0	1.94	21.98*	1.24
Velocity of mouth opening (cm s^{-1})	15.9	2.5	15.8	1.0	3.71	0.002	1.07
Velocity of mouth closing (cm s^{-1})	8.3	1.3	24.8	6.0	0.94	7.23	0.90
Velocity of tongue protraction (cm s^{-1})	80.5	9.8	58.3	9.5	0.67	2.55	3.05
Velocity of tongue retraction (cm s^{-1})	17.3	3.3	34.2	4.0	5.84	17.58*	1.79
Maximum gape distance (cm)	0.74	0.02	0.72	0.03	6.03	0.62	2.23
Maximum tongue reach (cm)	1.00	0.09	0.80	0.09	3.89	3.36	2.91
Maximum head angle (degrees)	29	2	25	2	0.15	1.91	0.69
Maximum forward lunge (cm)	0.20	0.02	0.27	0.06	0.39	1.15	0.55

$N=4$ individuals, with three feedings on each prey per individual, giving a total of 24 feeding trials.

*Significant at $P \leq 0.0025$, after simultaneous Bonferroni adjustments.

velocity of tongue retraction ($F=17.58$, $P=0.0005$) is significantly greater in waxworm captures than in termite captures (Table 1). The time of start of mouth closing and the velocity of mouth closing show non-significant effects of prey type. Waxworm captures showed slightly greater forward lunging than termite captures, although this effect was not significant (Fig. 4; Table 1). No measures of the magnitude of movements showed a significant effect of individual or prey. In general, the kinematic variables show that termite captures are characterized by longer durations and lower velocities of movements than waxworm feedings. No kinematic variables show significant individual \times prey interaction effects, indicating that individuals responded similarly to differences in prey.

Waxworm versus termite captures after tongue deafferentation

Qualitatively, prey capture behavior was unaffected by bilateral deafferentation of the tongue pad. Qualitative differences in the kinematic profiles of termite and waxworm captures persist after surgical treatment. Termite captures show asymmetrical tongue and gape profiles with long time courses, and waxworm captures show symmetrical or nearly symmetrical tongue and gape profiles with short time courses (Fig. 6). The animals responded to the two prey as they did before surgery: waxworms were attacked more vigorously than termites on average.

Following surgical treatment, a two-way ANOVA reveals significant variation among individuals in one kinematic variable: time of maximum head angle ($F=9.80$, $P=0.0004$). Velocity of tongue retraction shows a non-significant individual effect (Table 2). Ten kinematic variables show significant differences due to prey type: time of maximum gape ($F=12.93$, $P=0.0019$), time of maximum head angle ($F=56.49$, $P=0.0001$), time of start of mouth closing ($F=16.26$, $P=0.0007$), duration of mouth closing ($F=74.84$, $P=0.0001$), duration of gape cycle ($F=91.03$, $P=0.0001$), duration of tongue retraction ($F=23.15$, $P=0.0001$), duration of tongue cycle ($F=36.37$, $P=0.0001$), velocity of mouth opening ($F=12.53$, $P=0.0022$), velocity of mouth closing ($F=42.79$, $P=0.0001$) and velocity of tongue retraction ($F=12.84$, $P=0.0020$). Without exception, these variables characterize termite feedings as having later times of events, longer durations of movements and lower velocities of movements than waxworm feedings. One variable showed a significant individual \times prey interaction effect: time of prey contact ($F=9.42$, $P=0.0008$). No measures of the magnitudes of movements were significantly affected by prey type or individual.

A two-way ANOVA was performed on feedings of each prey type to test the effects of individual and surgical treatment (i.e. glossopharyngeal transection) (Table 3). An individual \times treatment interaction effect was seen in one variable: time to maximum tongue reach ($F=7.66$, $P=0.0021$) for waxworm

Table 2. Kinematic variables comparing termite and waxworm feedings after bilateral tongue deafferentation and two-way ANOVA testing effects of individual and prey

Variable	Termite		Waxworm		Individual <i>F</i> -ratio	Prey <i>F</i> -ratio	Individual \times Prey <i>F</i> -ratio
	Mean	S.E.M.	Mean	S.E.M.			
Time of prey contact (ms)	26.5	1.6	23.1	1.7	1.01	0.47	9.42*
Time of maximum tongue reach (ms)	33.8	3.4	30.2	2.1	1.44	0.83	4.24
Time of maximum gape (ms)	82.0	10.0	47.7	4.0	3.02	12.93*	5.99
Time of maximum head angle (ms)	89.4	5.1	51.8	5.4	9.80*	56.49*	0.47
Time of maximum forward lunge (ms)	61.4	14.8	62.3	5.3	2.26	0.004	0.74
Time of start of mouth closing (ms)	92.8	10.8	56.1	4.3	5.61	16.26*	3.88
Duration of mouth closing (ms)	128.1	10.8	37.4	4.4	2.71	74.84*	1.44
Duration of gape cycle (ms)	224.2	14.8	96.2	6.4	4.20	91.03*	6.24
Duration of tongue protraction (ms)	19.0	2.9	15.7	2.1	0.05	0.70	0.60
Duration of tongue at target (ms)	25.5	4.4	19.0	2.1	3.09	2.31	1.60
Duration of tongue retraction (ms)	77.1	11.6	27.0	5.7	4.98	23.15*	2.47
Duration of tongue cycle (ms)	114.4	11.4	54.9	6.1	6.31	36.37*	4.05
Velocity of mouth opening (cm s^{-1})	10.8	1.0	15.2	1.3	5.72	12.53*	1.90
Velocity of mouth closing (cm s^{-1})	6.6	0.5	20.9	2.7	5.34	42.79*	4.16
Velocity of tongue protraction (cm s^{-1})	66.2	11.8	64.2	11.3	0.07	0.01	0.99
Velocity of tongue retraction (cm s^{-1})	16.9	3.0	38.5	7.1	5.56	12.84*	2.23
Maximum gape distance (cm)	0.79	0.02	0.68	0.03	2.83	11.79	6.79
Maximum tongue reach (cm)	0.99	0.10	0.77	0.07	1.81	3.54	0.68
Maximum head angle (degrees)	36	4	30	2	1.48	2.83	0.34
Maximum forward lunge (cm)	0.14	0.03	0.35	0.07	0.43	7.31	0.44

$N=4$ individuals, with three feedings on each prey per individual, giving a total of 24 post-deafferentation feeding trials.

*Significant at $P \leq 0.0025$, after simultaneous Bonferroni adjustments.

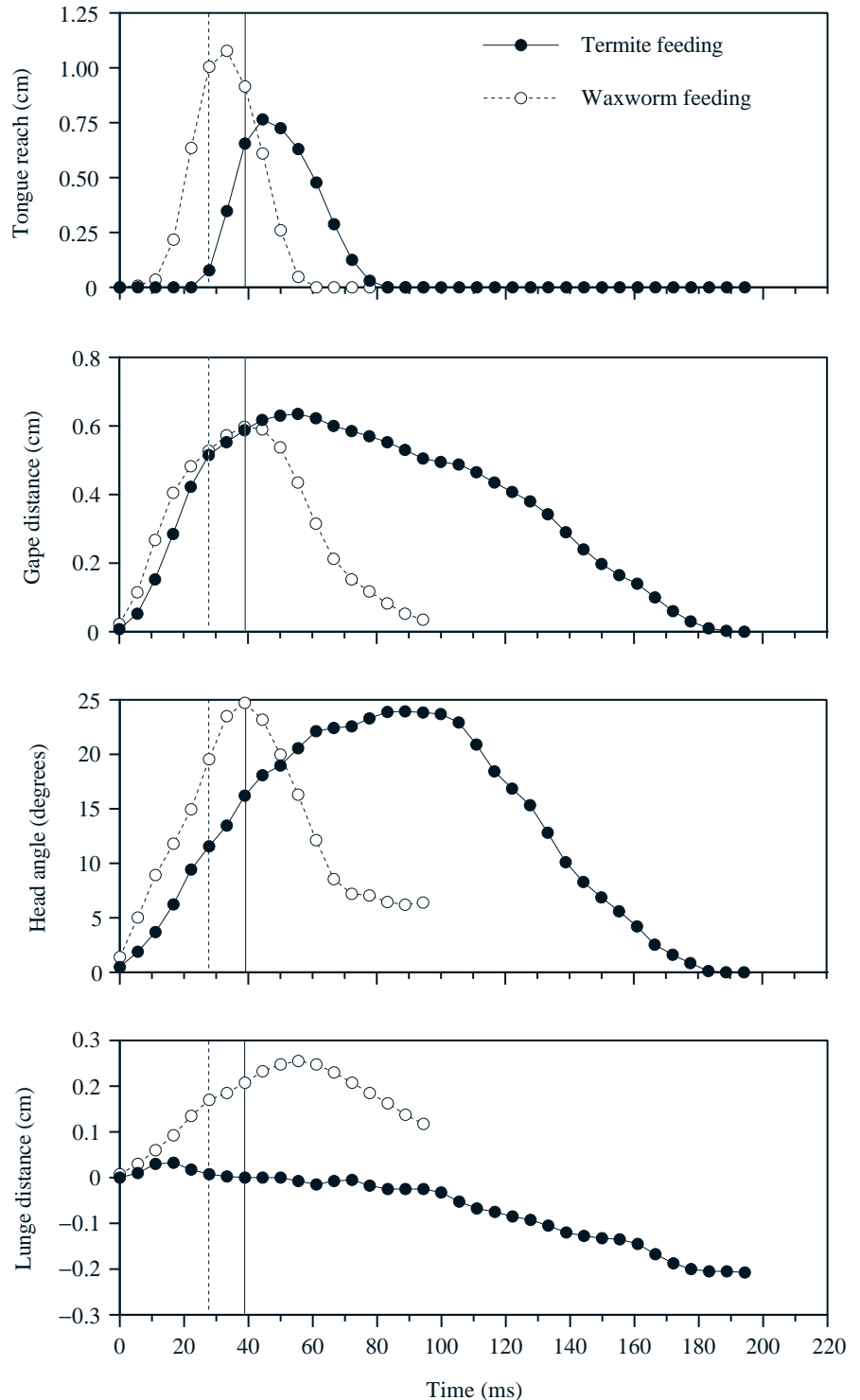


Fig. 6. Representative kinematic profiles of two prey-capture sequences of *Ensatina eschscholtzii* after bilateral tongue deafferentation. The termite feeding (filled circles) shows the persistence after deafferentation of a long time course, asymmetrical tongue and gape profiles, and long duration of tongue retraction and mouth closing. The waxworm feeding (open circles) shows the persistence of a short time course, symmetrical tongue and gape profiles, and short duration of tongue retraction and mouth closing. The solid and dashed vertical lines indicate the time of prey contact for the termite feeding and the waxworm feeding respectively. Note that the kinematic profiles diverge after prey contact in much the same way as before surgery (Fig. 4).

feedings. No significant effects of surgical treatment are observed in any variable among either termite or waxworm captures. Among termite captures, a significant effect of individual was observed in time of prey contact ($F=9.23$, $P=0.0006$), time of maximum gape ($F=9.36$, $P=0.0005$), time of start of mouth closing ($F=11.45$, $P=0.0002$), velocity of tongue retraction ($F=10.10$, $P=0.0003$) and maximum gape distance ($F=7.76$, $P=0.001$). Among waxworm captures, as for

termite captures, a significant individual effect was seen in time of start of mouth closing ($F=18.36$, $P=0.0001$), velocity of tongue retraction ($F=7.15$, $P=0.0021$) and maximum gape distance ($F=9.64$, $P=0.0004$).

A three-way ANOVA performed on the entire data set of 48 trials shows neither significant second-order interaction (individual \times treatment \times prey) effects nor significant individual \times treatment or treatment \times prey interaction effects.

Table 3. F-ratios of two-way ANOVAs testing effects of individual and surgical treatment for both waxworm and termite feedings

Variable	Individual		Treatment		Individual × Treatment	
	Termite	Waxworm	Termite	Waxworm	Termite	Waxworm
Time of prey contact	9.23*	0.16	0.27	0.48	1.00	4.00
Time of maximum tongue reach	3.14	0.21	0.16	0.06	1.75	7.66*
Time of maximum gape	9.36*	6.37	4.00	0.10	0.43	2.65
Time of maximum head angle	5.29	4.89	2.14	0.57	1.63	0.36
Time of maximum forward lunge	1.30	3.32	0.21	0.07	1.80	1.19
Time of start of mouth closing	11.45*	18.36*	0.98	4.45	1.29	6.29
Duration of mouth closing	1.47	2.09	1.57	0.67	0.33	0.33
Duration of gape cycle	5.97	3.37	1.15	0.03	0.16	0.23
Duration of tongue protraction	0.10	0.35	1.09	0.09	1.22	1.47
Duration of tongue at target	4.15	1.78	0.16	0.04	0.89	0.44
Duration of tongue retraction	4.72	5.36	0.004	0.35	0.68	3.01
Duration of tongue cycle	6.65	4.59	0.02	0.23	0.13	1.67
Velocity of mouth opening	3.70	5.97	4.91	0.020	1.04	1.91
Velocity of mouth closing	3.10	1.45	2.06	0.38	0.20	1.13
Velocity of tongue protraction	0.27	0.59	0.79	0.15	0.847	2.53
Velocity of tongue retraction	10.10*	7.15*	0.03	0.52	1.53	0.87
Maximum gape distance	7.76*	9.64*	4.42	1.73	2.77	0.62
Maximum tongue reach	5.58	1.23	0.02	0.07	1.63	0.93
Maximum head angle	0.51	2.88	2.72	3.74	0.40	0.11
Maximum forward lunge	1.66	0.52	2.80	0.64	0.41	0.23

N=4 individuals, with three pre- and three post-deafferentation feeding trials per individual on each prey type. Results are from two separate ANOVAs, one for each prey type testing for the effects of individual and surgery.

*Significant at $P \leq 0.0025$, after simultaneous Bonferroni adjustments.

Table 4. F-ratios of a single three-way ANOVA testing the effects of individual, surgical treatment and prey

Variable	Individual	Treatment	Prey	Individual × Prey	Individual × Treatment	Treatment × Prey
Time of prey contact	1.43	0.08	2.21	3.83	0.83	0.74
Time of maximum tongue reach	2.44	0.35	0.08	0.98	1.24	1.55
Time of maximum gape	10.54*	3.78	3.09	6.60*	0.08	2.97
Time of maximum head angle	8.78*	2.58	39.63*	1.39	1.20	0.50
Time of maximum forward lunge	2.48	0.27	0.13	1.22	0.87	0.07
Time of start of mouth closing	17.92*	2.20	5.75	6.28*	0.62	0.20
Duration of mouth closing	1.76	0.52	67.33*	1.30	0.34	2.11
Duration of gape cycle	5.43	0.64	118.11*	4.20	0.06	0.97
Duration of tongue protraction	0.38	0.44	0.08	0.04	0.80	0.99
Duration of tongue at target	5.83*	0.06	6.15	1.33	0.87	0.19
Duration of tongue retraction	4.87	0.02	45.37*	3.93	1.59	0.07
Duration of tongue cycle	6.79*	0.001	57.08*	4.52	0.60	0.10
Velocity of mouth opening	8.02*	4.67	2.75	0.35	0.31	2.86
Velocity of mouth closing	1.95	0.77	22.94*	1.12	0.98	0.11
Velocity of tongue protraction	0.17	0.15	1.24	0.64	0.43	0.79
Velocity of tongue retraction	11.43*	0.30	29.69*	2.63	0.51	0.50
Maximum gape distance	9.85*	0.04	1.87	6.30*	0.62	5.60
Maximum tongue reach	5.28	0.08	7.28	1.23	0.61	0.01
Maximum head angle	1.42	5.97	5.01	0.92	0.53	0.17
Maximum forward lunge	0.81	0.01	7.94	0.57	0.06	1.78

N=4 individuals, with three pre- and three post-deafferentation feedings per individual on each prey type, giving a total of 48 feeding trials.

*Significant at $P \leq 0.0025$, after simultaneous Bonferroni adjustments.

No significant effect of treatment was seen in any variable (Table 4). Three variables show significant individual × prey interaction effects: time of maximum gape ($F=6.6, P=0.001$),

time of start of mouth closing ($F=6.28, P=0.0014$) and maximum gape distance ($F=6.3, P=0.0014$). Significant effects of individual occur in time of maximum gape ($F=10.54$,

$P=0.0001$), time of maximum head angle ($F=8.78$, $P=0.0001$), time of start of mouth closing ($F=17.92$, $P=0.0001$), duration of tongue at target ($F=5.83$, $P=0.0020$), duration of tongue cycle ($F=6.79$, $P=0.0008$), velocity of mouth opening ($F=8.02$, $P=0.0002$), velocity of tongue retraction ($F=11.43$, $P=0.0001$) and maximum gape distance ($F=9.85$, $P=0.0001$). Seven variables show significant effects of prey: time of maximum head angle ($F=39.63$, $P=0.0001$), duration of mouth closing ($F=67.33$, $P=0.0001$), duration of gape cycle ($F=118.11$, $P=0.0001$), duration of tongue retraction ($F=45.37$, $P=0.0001$), duration of tongue cycle ($F=57.08$, $P=0.0001$), velocity of mouth closing ($F=22.94$, $P=0.0001$) and velocity of tongue retraction ($F=29.69$, $P=0.0001$). All kinematic variables displaying significant effects of prey show that termite captures have a later occurrence of events, longer durations of movements and lower velocities of movements than waxworm captures, repeating the general effects seen in the other ANOVAs.

Overall variation among feeding trials

The factor loadings of the PCA show that positive values on PC1 reflect late occurrence of kinematic events, long durations of tongue and jaw movements, short lunge distances and low velocities of jaw movements and tongue retraction. Negative values on PC1 represent early occurrence of events, short durations, long lunges and high velocities. Positive values on PC2 indicate primarily short duration of tongue protraction and high velocity of tongue protraction, while negative values represent long duration and low velocity of tongue protraction.

Termite and waxworm feedings differ primarily along PC1, but overlap on PC2, showing that termite feedings are of longer duration and lower velocity, in general, than waxworm feedings (Fig. 7A). Feedings before surgery overlap with feedings after surgery along both PC1 and PC2, indicating no effect of surgical treatment on feeding kinematics (Fig. 7B). Individual variation is apparent along both PC1 and PC2 for both prey types, although it is slight compared with the variation seen across prey type. Individuals 1 and 4 shows slightly lower values of PC1 than individuals 2 and 3 (Fig. 7C), indicating shorter durations and higher velocities in the feedings of these individuals. In addition, individual 3 shows the broadest range of values along PC1, indicating the most variable behavior among feeding trials. The differences seen in the PCA among individuals are reflected in the significant individual effect of some of the kinematic variables in the ANOVAs.

The PCA and ANOVAs taken together show that the type of prey, termite *versus* waxworm, influences many kinematic variables, especially the timing of tongue and jaw movements. Duration of mouth closing, duration of gape cycle, duration of tongue retraction, duration of tongue cycle and velocity of tongue retraction all differ significantly across prey type in all ANOVAs performed. The magnitude of movements was not affected by individual or prey type. The ANOVAs also show that surgical transection of the glossopharyngeal nerve has no

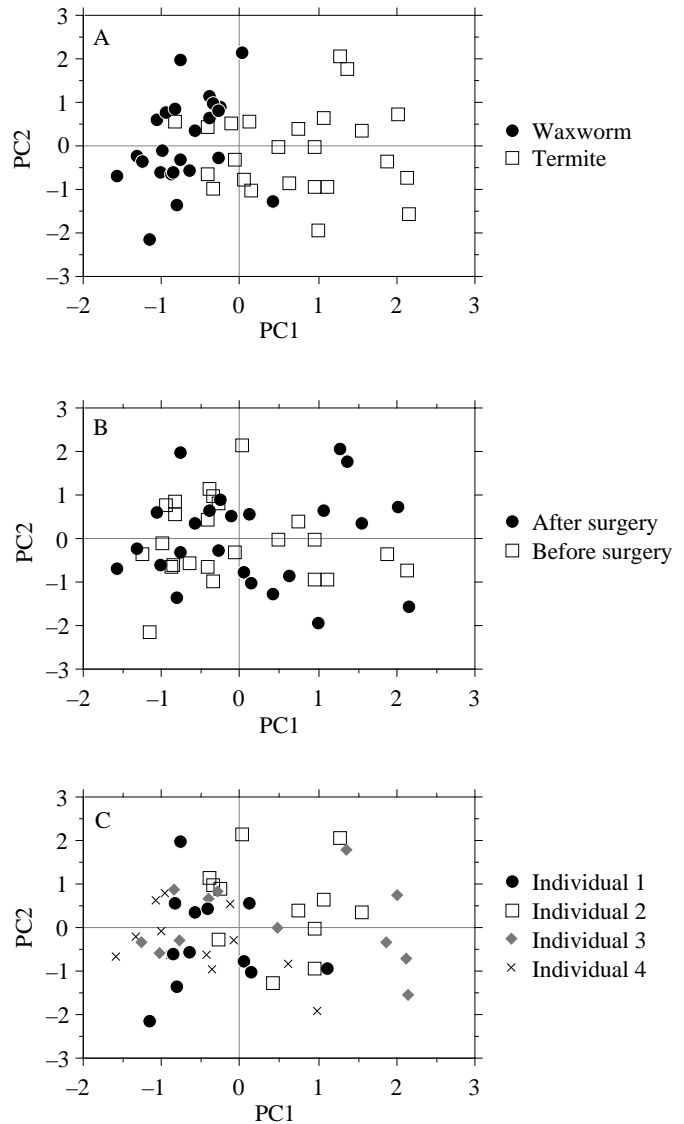


Fig. 7. Scatterplots of the first two principal components (PC1 and PC2) derived from all kinematic variables for all 48 feeding trials. Note the separation of feeding trials by different prey type (A), the broad overlap of pre- and post-surgery trials (B), and the relative positions and variation in the feedings of different individuals (C).

significant effect on feeding kinematics. This is the case among waxworm feedings, among termite feedings and among all feedings, as illustrated by the large overlap of pre- and post-surgery feeding trials in the PCA (Fig. 7).

Discussion

The results reported here have several implications for our understanding of salamander feeding behavior. First, *E. eschscholtzii* shows considerable variation in prey-capture kinematics and modulates its feeding movements depending on prey type, refuting previous conclusions that salamander feeding is highly stereotyped. Second, sensory feedback through the tongue pad is not responsible for modulating

feeding movements in *E. eschscholtzii*, in contrast to the condition in frogs. Finally, *E. eschscholtzii* is capable of assessing prey visually and responding differently depending on features of the prey, and is likely to be responding to differences in prey size.

The results of the statistical analyses of the kinematic data demonstrate that the prey-capture behavior of *E. eschscholtzii* shows considerable variation among individuals. The salamanders tested show individual tendencies in the mean values of movements during prey capture as well as in the overall variability of movements. In addition, the results indicate that *E. eschscholtzii* can modulate its prey-capture behavior depending on the type of prey. Waxworms (large prey) are drawn into the mouth more quickly than termites (small prey), and the overall duration of feedings on waxworms is shorter than for feedings on termites.

The possibility of passive biomechanical effects of prey mass producing the kinematic differences between waxworm and termite feedings can be ruled out. The direction of the differences in tongue retraction duration and velocity is the opposite of that expected if prey mass were influencing tongue retraction kinematics passively without compensation by the salamander. If heavier prey were drawn into the mouth with the same effort as lighter prey, one might expect slower tongue retraction on waxworm feedings compared with termite feedings. However, more massive prey are drawn into the mouth more rapidly, showing that the salamanders are modulating the force output of the tongue retractor muscles to compensate for the larger load.

More rapid tongue retraction is accompanied by faster mouth closing. The rapid tongue retraction and mouth closing contribute to the significant difference across prey type of the entire tongue cycle and gape cycle, both of which are of shorter duration in waxworm feedings. In addition, termite captures appear to show greater individual variation than waxworm feedings (Fig. 7A).

Hypotheses concerning the mechanism of modulation

Comparisons of feedings for the initial 24 feeding trials before surgery showed that events after prey contact differed significantly between feedings on different prey; for example, duration and velocity of tongue retraction (Fig. 4). Events before prey contact appeared to be unaffected; for example, duration and velocity of tongue protraction (Table 1). This pattern initially suggested that a tactile cue is responsible for the modulation of behavior after prey contact, and suggested the hypothesis that the salamanders were receiving information about the size of the prey through the tongue pad and were responding with more vigorous tongue retraction and mouth closing if the prey happened to be large. The ramus lingualis of the glossopharyngeal nerve (cranial nerve IX), which innervates the tongue pad in salamanders and other amphibians, is entirely sensory in salamanders and was hypothesized to be the route of sensory information concerning prey size. Other potential sources of sensory information about prey size, such as mechanoreceptors of the jaws or head, might

play a role in modulating feeding movements in response to loads placed on muscles and cannot be entirely ruled out. However, glossopharyngeal feedback is known to be involved in the tongue withdrawal reflex in the toad *Bufo japonicus* (Matsushima *et al.* 1988), so the hypothesis that *E. eschscholtzii* might possess a similar reflex seemed likely and is a good place to begin investigating the role of sensory feedback in salamander prey capture. Transection of the ramus lingualis was predicted to eliminate any sensory feedback through the tongue pad and thereby to reduce or eliminate the modulation of feeding movements after prey contact. An alternative hypothesis, that the salamanders are assessing the prey visually and are planning their movements on the basis of prey size before the onset of feeding movements (i.e. a 'feedforward' mechanism, *sensu* Pearson, 1993), is also consistent with the kinematic differences observed. In the case that glossopharyngeal nerve transection fails to reduce or abolish modulation of prey capture in response to prey type, the glossopharyngeal feedback hypothesis would be rejected and we would have to consider either an alternative hypothesis of sensory feedback by another route or a feedforward hypothesis based on visual assessment of the prey.

Modulation after tongue deafferentation

After nerve transection, kinematic variables differ in the same direction across prey type as before surgery (Table 2), demonstrating that surgery failed to eliminate modulation. In fact, more variables were significantly different across prey type after surgery than before surgery (time of maximum gape and time of maximum head angle, Table 2). These results may seem to suggest that deafferentation of the tongue pad increases the modulation of the prey-capture behavior. Comparisons within each prey type across treatment, however, reveal no effect of surgery in any kinematic variables, indicating that deafferentation of the tongue pad does not influence the kinematics of feedings on waxworm or termites (Table 3). In addition, comparisons across surgery among both waxworm and termite feedings taken together reveal no influence of treatment on feeding kinematics (Table 4). The PCA plot (Fig. 7B) shows that pre- and post-surgery feedings overlap considerably along both PC1 and PC2 and illustrates the absence of an effect of surgery. Thus, the hypothesis that sensory feedback through the tongue pad is responsible for modulation of feeding behavior on prey of different sizes is rejected.

Visual assessment of prey type

Of the two alternative hypotheses, the hypothesis that visual information is used to modulate feeding behavior is most likely in *E. eschscholtzii*. Salamanders, as well as frogs, are known to be able to distinguish among various parameters of visual stimuli, including shape, size, velocity and pattern of movement, and to show preferences for stimuli with certain combinations of parameters (see Roth, 1987, for a review). For example, the plethodontid salamander *Hydromantes italicus* strikes at stimuli within a broad range of sizes and movement

velocities, but prefers to strike at stimuli that fall within a relatively narrow range (Roth, 1976). The terrestrial salamander *Plethodon cinereus* uses visual encounters to specialize on large fruit flies when presented with a choice of large and small fruit flies after experience with both (Jaeger *et al.* 1982). In general, salamanders orient to and snap at large prey more frequently than small prey, up to a certain size which varies among species. Beyond that size, responsiveness decreases with increasing size (Roth, 1987). The *E. eschscholtzii* used in this study showed the same differential response to the two prey offered. They responded more frequently to waxworms than to termites, and a waxworm would often elicit a feeding response when a termite failed to attract the attention of the salamander. The results of this study demonstrate that the kinematics of the feeding response differ with prey size in the same way. Captures of large prey were performed more quickly than captures of small prey. Qualitatively, captures of waxworms appeared more vigorous than captures of termites. Thus, the preference for larger prey influences not only the responsiveness of the salamander in terms of whether or not it makes a feeding attempt, but also the degree to which it responds during a given feeding attempt. Larger prey may be worth not just more attention but also more effort. The preference for larger prey and the more vigorous feeding on waxworms are consistent with the hypothesis that visual assessment of prey size is responsible for the differences documented here in the feeding kinematics of *E. eschscholtzii*, rather than sensory feedback from the tongue pad through the glossopharyngeal nerve.

Variation and modulation in amphibian feeding behavior

The results of this study are in conflict with earlier reports that salamander feeding movements are highly stereotyped and are in accordance with recent studies that document variation and modulation of feeding movements in other salamander taxa.

The view that salamander feeding in general is highly stereotyped originates from studies on a few taxa of salamanders that show little within-individual variation: *Ambystoma tigrinum* (Larsen and Guthrie, 1975), *A. dumerilii*, *A. mexicanum*, *A. ordinarium* (Shaffer and Lauder, 1985) and *Bolitoglossa occidentalis* (Thexton *et al.* 1977). Comparisons of data from these taxa with anuran feeding kinematics suggested that salamander feeding is far more stereotyped than frog feeding (Nishikawa and Cannatella, 1991; Reilly, 1995). Recently, however, numerous studies of salamander feeding have revealed variation within individuals from a variety of salamander taxa, both terrestrial and aquatic (Erdman and Cundall, 1984; Larsen and Beneski, 1988; Miller and Larsen, 1990; Elwood and Cundall, 1994; Maglia and Pyles, 1995). The present study places *E. eschscholtzii* among those salamander taxa that have the capacity to modulate their feeding movements.

Variation in the kinematics of feeding among species of terrestrial salamanders has been documented in many groups, including salamandrids (Miller and Larsen, 1990),

plethodontids (Larsen *et al.* 1989), hynobiids (Larsen *et al.* 1996) and ambystomatids (Beneski *et al.* 1995). While variation among and within individuals has often been noted, it has been little studied, and the causes of the intraspecific variation have not been examined in detail. A few studies of intraspecific variation in both terrestrial and aquatic salamanders have focused on variation among feeding trials within individuals. These studies, discussed below, provide mixed results in terms of the degree of stereotypy or modulation within individuals of a species.

Among terrestrial salamanders, the plethodontid *Bolitoglossa occidentalis* shows variation in the duration and force of tongue contact with prey, both of which decrease with increasing prey distance (Thexton *et al.* 1977). Electromyographic (EMG) recordings revealed little modulation in the timing of activation of tongue protractor and retractor muscles, and stimulation experiments failed to find evidence for sensory feedback. *B. occidentalis* shows little capacity to modulate tongue movements, which are stereotyped owing to the specific arrangement of the hyolingual apparatus and its musculature (see Thexton *et al.* 1977, for a discussion of the morphology and biomechanics). In addition, the gape cycle of *B. occidentalis* is relatively stereotyped when feeding on a single prey type (Larsen *et al.* 1989).

Studies of another terrestrial plethodontid salamander produced different results. *Plethodon cinereus*, a close relative of *E. eschscholtzii*, was found to vary the timing and extent of body, tongue and jaw movements with prey type (Maglia and Pyles, 1995). Like *E. eschscholtzii*, *P. cinereus* completed prey capture more quickly on large prey (mealworms and crickets) than small prey (fruit fly adults and larvae) primarily because of faster movements in the latter portion of the feeding sequence. *P. cinereus* approached some prey more closely than others before initiating feeding (Maglia and Pyles, 1995), suggesting that it distinguishes prey by sight.

Variation of feeding kinematics was found among individuals and between two species of terrestrial *Hynobius*, but no within-individual variation was found among feedings on a single type of prey (Larsen *et al.* 1996). *H. nebulosus* was found to use the same feeding behavior, as judged qualitatively from standard video recordings, on prey that differed vastly in size and shape: mealworms and earthworms (Kuramoto and Aratani, 1984). The terrestrial ambystomatid *Ambystoma tigrinum* uses highly stereotyped tongue protraction movements. However, its close relative *A. macrodactylum* shows a greater repertoire of feeding behaviors and can vary the degree to which it protracts its tongue, sometimes forgoing tongue protraction to capture prey with the jaws (Larsen and Guthrie, 1975). The *E. eschscholtzii* used in this study modulated the degree of tongue protraction, and the use of jaw prehension was observed occasionally, but this variation did not partition by prey type.

The clearest example of modulation of prey-capture

behavior in salamanders is that seen in newts that feed both on land and in water. Newts use tongue protraction to capture prey on land and suction feeding to capture prey in water (Miller and Larsen, 1990). In addition, newts of the species *Paramesotriton hongkongensis* and *Cynops pyrrhogaster* vary the degree of tongue protraction during terrestrial feeding on a single prey type, from full protraction to no protraction whatsoever, and vary their gape cycles accordingly (Miller and Larsen, 1990).

Among aquatic salamanders, *Ambystoma mexicanum* shows stereotyped EMG patterns when feeding on a prey with different escape capabilities (Reilly and Lauder, 1989). In contrast, *Amphiuma tridactylum* and *Cryptobranchus alleganiensis* are known to show within-individual modulation of feeding behavior in which the relative timing of jaw and hyobranchial movements varies with prey type, and *C. alleganiensis* shows variable asymmetry of movements among feeding trials (Erdman and Cundall, 1984; Elwood and Cundall, 1994).

Among frogs, we see examples of species that show modulation as well as those that appear highly stereotyped. *Hemisis marmoratum* and *Rana pipiens* modulate their movements with prey type and prey position (Ritter and Nishikawa, 1995; Anderson, 1993), while *Bufo marinus* responds similarly to a variety of prey (Nishikawa *et al.* 1992). Visual assessment of prey parameters is known to occur among frogs (e.g. Ewert and Burghagen, 1979; Anderson and Nishikawa, 1996), and sensory feedback can be important in controlling feeding movements. The lingual withdrawal reflex in a variety of frogs relies on sensory feedback (Matsushima *et al.* 1988), and sensory feedback coordinates tongue and jaw movements in *R. pipiens* (Anderson and Nishikawa, 1996) and *B. marinus* (Nishikawa and Gans, 1992, 1996), and allows for controlled variation of these movements (i.e. modulation) in *Hemisis marmoratum* (Ritter and Nishikawa, 1995). A striking difference between the feeding of these last two taxa is that tongue protraction in *Bufo* is ballistic (i.e. protraction relies on momentum) and is much more rapid than tongue protraction in *Hemisis*, which is hydrostatic. The different roles of sensory feedback in these two systems may be explained in part by differences in the biomechanics and speed of movement.

Sensory feedback in salamander feeding

The functions of sensory feedback in frog feeding can be used to make predictions about the potential role of sensory feedback in salamanders. Salamanders such as bolitoglossine plethodontids which protract the tongue rapidly and ballistically, relying to some extent on momentum to carry the tongue to the prey, may lack the opportunity to make adjustments to tongue movements during the course of the behavior, so sensory feedback may play no role in modulating those movements as they occur. In addition, the constraints of the peripheral morphology may not permit a variety of responses to prey, even if the salamander recognizes the prey as different. *Bolitoglossa occidentalis* has extremely rapid

tongue protraction (approximately 7 ms), coordinates tongue movements biomechanically by the arrangement of the hyolingual apparatus, and shows no evidence of modulation or of sensory feedback controlling tongue movements (Thexton *et al.* 1977). Salamanders that have slower tongue protraction, with the biomechanical potential for controlling movement during the course of the behavior, might be expected to use sensory feedback to make adjustments to the trajectory of the tongue after the feeding behavior has been initiated. *E. eschscholtzii* also has rapid tongue protraction (7–40 ms), but can modulate its movements. This suggests that the biomechanical arrangement of the hyolingual apparatus permits control, but predicts that modulation *via* sensory feedback during the course of the behavior is unlikely, a prediction consistent with the results of the deafferentation experiments. Thus, in *E. eschscholtzii*, the pattern of movements in response to prey is largely determined before movement begins, based on visual assessment of the prey. Salamanders that feed relatively slowly and display modulation of behavior, such as some newts, possess the potential for a role of sensory feedback in the modulation of feeding behavior. Further, salamanders that feed rapidly but appear biomechanically capable of variation in movements, such as many suction-feeding salamanders, might represent a group in which sensory feedback may play a role in coordinating movements and reducing rather than increasing variation, as seen in *Bufo*.

Some salamanders appear to have stereotyped behavior, such as aquatic ambystomatid salamanders (Reilly and Lauder, 1989), but the growing number of studies in which variation and modulation are demonstrated suggests that taxa with highly stereotyped behavior may be unusual rather than the general rule. Apparent stereotypy may reflect real biological limits, but it may simply represent an artifact of the laboratory technique in which the subject is offered one prey type in a standardized manner. Many salamanders are clearly capable of responding in a variety of ways to encounters with prey and, to learn about how behavior is modulated, whether centrally or by peripheral feedback, it is necessary to place bounds on the entire behavioral repertoire of which a given taxon is capable (and likely to express in nature) rather than on the specific behaviors that we happen to observe in the laboratory under artificially limiting conditions. This necessitates an understanding of the natural history of the organism, especially its dietary breadth (Greene, 1986), and requires that we attempt to elicit as broad a range of natural behaviors as possible from the organism in the laboratory.

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