

## RATTLESNAKE STRIKE BEHAVIOR: KINEMATICS

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### Summary

The predatory behavior of rattlesnakes includes many distinctive preparatory phases leading to an extremely rapid strike, during which venom is injected. The rodent prey is then rapidly released, removing the snake's head from retaliation by the prey. The quick action of the venom makes possible the recovery of the dispatched prey during the ensuing poststrike period. The strike is usually completed in less than 0.5 s, placing a premium on an accurate strike that produces no significant errors in fang placement that could result in poor envenomation and subsequent loss of the prey. To clarify the basis for effective strike performance, we examined the basic kinematics of the rapid strike using high-speed film analysis. We scored numerous strike variables. Four major results were obtained. (1) Neurosensory control of the strike is based primarily upon sensory inputs *via* the eyes and facial pits to launch the strike, and upon tactile stimuli after contact. Correction for errors in targeting occurs not by a change in strike trajectory, but by fang repositioning after the jaws

have made contact with the prey. (2) The rattlesnake strike is based upon great versatility and variation in recruitment of body segments and body postures. (3) Forces generated during acceleration of the head are transferred to posterior body sections to decelerate the head before contact with the prey, thereby reducing impact forces upon the snake's jaws. (4) Body acceleration is based on two patterns of body displacement, one in which acute sections of the body open like a gate, the other in which body segments flow around postural curves similar to movements seen during locomotion. There is one major implication of these results: recruitment of body segments, launch postures and kinematic features of the strike may be quite varied from strike to strike, but the overall predatory success of each strike by a rattlesnake is very consistent.

Key words: rattlesnake strike, neurosensory control, kinematics, predatory behavior, *Crotalus viridis*.

### Introduction

The foraging behavior of rattlesnakes may include indirect opportunistic elements such as scavenging (Fitch, 1949; Gillingham and Baker, 1981; Hennessy and Owings, 1988) but, more commonly, foraging behavior is characterized by an envenomating strike (Klauber, 1956) of stalked prey. The strike may also be used during defensive behavior (e.g. Klauber, 1956), which includes some different behavioral elements (e.g. Gove, 1979) and different consequences (e.g. Russell, 1980; Kardong, 1986*b*; Hayes, 1991) from predatory strikes (Minton, 1969). The predatory behavior of rattlesnakes has generally been divided into phases, the number of which suits the research context. As few as three phases have been used explicitly or implicitly by some authors – prestrike, strike, poststrike (e.g. Chiszar *et al.* 1977) – and up to nine phases have been proposed by others (de Cock Buning, 1983). This predatory repertoire is preceded by behaviors that place the snake in locations where it is more likely to encounter prey (Duvall *et al.* 1985, 1990). In the present study, nine phases of the predatory behavior of rattlesnakes are recognized: placement, alertness, head turning, approach, preparation,

strike, re-approach, head searching and swallowing (after de Cock Buning, 1983; Hayes and Duvall, 1991). The result of this predatory behavior is determined by one critical phase, the strike itself, which may be extremely brief, lasting less than 0.5 s (Kardong, 1986*a*). During this brief instant, the head moves quickly to the prey, the fangs are erected and penetrate the prey, venom is injected, and the head of the snake is withdrawn. If fang placement is incorrect (Kardong, 1986*a*) or delivered to a less vulnerable location on the prey (Kardong, 1986*b*), or if venom quantity is too low (Hayes, 1991), then the prey may scamper beyond the recovery range of the snake, and that particular predatory episode may be unsuccessful (Hayes and Galusha, 1984; Kuhn *et al.* 1991; Chiszar *et al.* 1992).

Thus, clarification of the events during the strike is critical to understanding rattlesnake predatory behavior. Further, the sensory systems upon which predatory behavior is based change during the predatory episode (Kardong, 1992; Chiszar *et al.* 1977; Chiszar and Scudder, 1980). The strike itself represents the culmination of prestrike behavior modified by

the input from a multisensory system (Chiszar *et al.* 1977; Kardong, 1986b; Alving and Kardong, 1996; Haverly and Kardong, 1996) and an output that includes the rapid motor patterns of the strike. Although attempts to define these elements of the strike have been made previously (Van Riper, 1953) and a few recent reports are available (e.g. Janoo and Gasc, 1992), this central phase of predation has remained less well characterized than most other phases of snake hunting behavior, perhaps because of its very brief duration. We therefore carried out a careful analysis of the strike phase of the rattlesnake predatory behavior. The present study defines stages within the strike phase and characterizes kinematically some of the complex aspects of the accompanying motor patterns of the head, neck and body of the rattlesnake.

## Materials and methods

### Subjects

Qualitative and kinematic data were obtained from six adult northern Pacific rattlesnakes *Crotalus viridis oreganus* (Rafinesque) collected from Grant and Whitman Counties, Washington, USA, constituting a common laboratory colony kept in an isolated reptile room over a period of 5 years. Three of the snakes were defined (after Kardong, 1986b) as small (37.6–45.2 cm, snout–vent length, *SVL*) and the other three were large (52.8–68.3 cm *SVL*). All had been in captivity for over 6 months before predatory feeding trials were begun, a time of captivity which does not alter normal predatory behavior (Kardong, 1993; Alving and Kardong, 1994). The reptile room was kept warm all year (27–32 °C) and maintained on a 12 h:12 h, L:D cycle. Each snake was housed individually in a glass terrarium approximately 50 cm×50 cm×90 cm, and fed live and dead mice irregularly. Access to the room was limited to authorized personnel familiar with the experiments and safety procedures (Gans and Taub, 1964).

### Filming conditions

Using Eastman Ektachrome film type 7250, rattlesnakes were filmed individually at 500 frames s<sup>-1</sup> using a 16 mm Hycam high-speed camera with a timing light and illuminated by a pair of tungsten-filament photo flood lamps. The day before filming, each snake was placed on an aluminum table (25 cm×25 cm) with clear acrylic sides and a front-surfaced mirror tilted at 45° over the snake. This permitted filming of simultaneous lateral and dorsal views of the strike (Fig. 1A). The temperature within the acrylic enclosure was maintained between 29 and 32 °C. On the day of filming, a live mouse of known mass was placed behind a blind in front of the snake. The lights were turned on and the opaque partition separating mouse from snake was removed. If the snake showed an interest in the mouse, the camera was turned on and the ensuing strike filmed. Using such methods, 21 complete strike sequences were recorded. Frame-by-frame qualitative analysis of these sequences was carried out by projection with a Selecta-frame projector, and complex motions of the snakes were traced.

### Kinematic analysis

General methods follow those described elsewhere (Delheusy and Bels, 1992). The 16 mm filmed strike sequences were projected frame-by-frame to a digitizing table using a NAC ciné projector. During rapid parts of the strike, the sample rate between successive frames was 0.002 s, but this was less frequent as motion slowed. Taking advantage of distinct points on the head and of natural body coloration, points at kinematically active locations on the snake were digitized during each strike sequence. The same natural marks on the same snake were followed during different strikes. To standardize points between individual snakes, points at approximately similar body locations were chosen, including five points on the head at anatomically equivalent points (angle of jaws, tip of snout, tip of lower jaw, eye, fang tip) and, beginning above the cervical vertebrae, up to 20 points were chosen sequentially along the dorsum on the body at approximately 1 cm intervals. Lateral and ventral regions of the skin slip over underlying elements of the axial skeleton, but dissection confirms that the dorsal integument does not move relative to the underlying vertebrae because it is firmly attached to the neural spines. Although values are not reported here, the aluminum table upon which the snake was placed was a force platform with defined *x*-, *y*- and *z*-axes. From the dorsal film image, *x*- and *z*-coordinates were determined; from the lateral image, vertical (*y*)-coordinates were determined using the coordinates of the aluminum table as the inertial reference frame. Gape and body angles between these digitized points were calculated. The total gape angle was the angle between the jaws with the apex at the corner of the mouth. Each digitized body point served as the apex of a body angle; the next digitized points, anterior and posterior to this apex, were used to determine this angle. Occasionally, rattlesnakes may strike and hold prey, rather than releasing it, especially small prey (Kardong, 1986b). Our analysis was restricted to the more common strike behavior in which the snake released prey.

During our analysis of kinematic data, we noted two patterns of body displacements. To illustrate these further, we carried out an analysis of displacement vectors on one strike sequence, and report it in Fig. 9.

### Variables

In addition to displacements of digitized points and angles derived from them, additional predatory variables related to the strike were scored using criteria discussed in detail elsewhere (Kardong, 1986b, 1992). *Time-to-death* is the time from the strike to the last muscular twitch of the envenomated mouse. *Site* is the location on the mouse where the fangs made contact: site 1 (head/shoulders), site 2 (mid-body), site 3 (rump). *Range* is the shortest distance (cm) from the snake's head to the closest part of the mouse (not including the tail) measured at the moment the strike was initiated. The mass of each mouse was also scored as one of two size classes, small (8–16 g) and large (20–27 g). Selection of these prey size ranges was based on previous behavioral work that found that, if prey size were significant, these size ranges would be sufficient to elicit modified snake behavior (Kardong, 1986b).

Twelve kinematic variables were scored, which describe jaw and body displacements. In their order of occurrence, they were as follows. Extend stage: (1) duration of extend stage, time (s) from when the head of the snake begins to accelerate to the instant of first contact with the prey; (2) time to maximum gape angle, time (s) from first acceleration of the head to the instant the jaws reach maximum gape angle; (3) maximum gape angle (degrees). Contact stage: (4) time in contact, the time (s) from first jaw contact until the instant the jaws lose contact with the prey; (5) time to minimum gape angle, the time (s) from first contact with the prey until the jaws reach minimum angle on the prey; (6) minimum angle (degrees). Release/retract stage: (7) duration of release/retract, the time (s) from the end of the contact stage until the body completes its withdrawal from the vicinity of the prey; (8) time to maximum gape angle, time (s) from first complete jaw disengagement until the point of maximum gape angle during release of prey; (9) maximum gape angle (degrees) achieved. Overall strike: (10) time between maximum gape angles (8–2), the time (s) elapsed between the point of maximum gape angle during the extend stage and the maximum gape angle during the release stage; (11) duration from extend to end of retract (1+4+7), time (s) from the first evidence of head acceleration until the body ceases motion at the end of the strike; (12) duration of jaw movement, time (s) from the first indication of jaw opening, through the contact stage until the jaws finally close at completion of the strike.

Additional postural variables were defined. To examine possible differences in kinematics between regions of the body, 'straight' and 'acute' regions of the body were recognized on the basis of body posture at the moment the strike was initiated. Digitized points at the sharpest bends in the body were considered to define the apices of acute angles; three or more points lying on a connecting line through them defined straight regions (Fig. 1A).

Upper jaw elevation and lower jaw depression contribute to the total gape angle. To determine the separate contribution of each, we measured the angle subtended by each relative to the cervical axis in 10 strike sequences in which the lateral view was especially favorable to such quantification. The dorsal neck region as viewed in lateral profile was used to define the long cervical axis at maximum gape (usually just before contact). A line parallel to the dorsal neck profile but passing through the jaw articulation (quadrato-mandibular joint) was used as the reference baseline from which maximum upper and lower gape angles were measured to determine the separate angle subtended by each (Fig. 1C).

To determine possible effects of body posture upon strike kinematics, two prestrike body postures were recognized, 'tight' and 'loose', position 1 and position 2, respectively (Fig. 1B). These were scored at the moment the strike was initiated. A tight posture had acute body curves (less than approximately  $120^\circ$ ); a loose posture had open body curves (greater than approximately  $120^\circ$ ) (Fig. 1B). Where postures were intermediate, that particular filmed sequence was not included in the analysis of the effects of body postures on

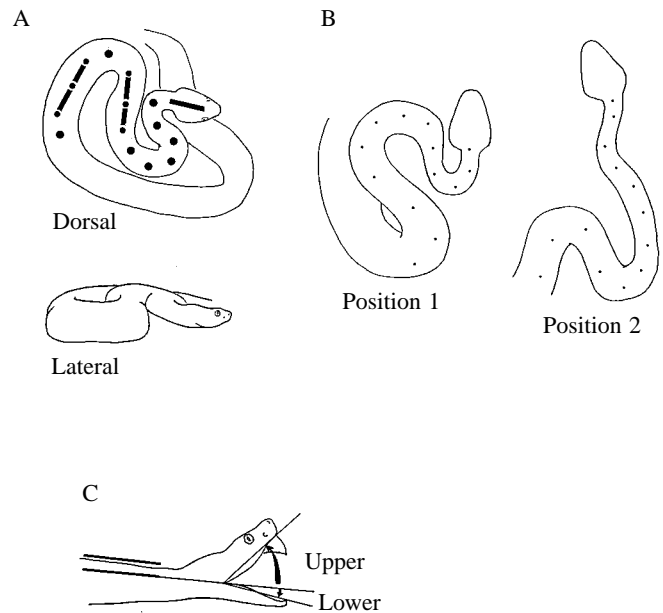


Fig. 1. Quantitative and behavioral variables measured. (A) Simultaneous dorsal and lateral views of the strike were filmed. Distinctive natural color points were digitized from the films. The digitized points were expressed as displacements in the  $x$  and  $z$  directions (dorsal view) and the  $x$  and  $y$  directions (lateral view). Angles between these points were determined. Straight lines (solid bars) and acute angles between points were identified at the beginning of the strike and the characteristic kinematic pattern of their displacements followed. (B) Two distinct postures at the time of initiation of the strike were defined. One with more acute, tight body angles (Position 1), the other with anterior body angles loose, more open and less acute (Position 2). (C) Separate upper and lower jaw gape angles were measured relative to a line passing through the angle of the jaws. Upper jaw elevation and lower jaw depression were determined at maximum opening by tracing, on an outline of the head, a reference line parallel with the dorsal neck so as to pass through the angle of the mouth. The jaw angles subtended above and below this reference line represented upper and lower jaw gape angles, respectively.

ensuing strike variables. This gave 15 strikes for analysis of the effects of body posture on kinematics and behavior.

#### Data analysis

All high-speed filming of rattlesnakes and analysis of data were carried out in one laboratory (K.V.K.); digitizing was performed on 16 mm films at the University of Liège (V.L.B.). The digitized data (displacements and angles) of body points were smoothed, and accelerations were calculated using equations of Lancos, a seven-point running average stepped along the displacement curve (see Alexander, 1983). Although absolute errors in maximum accelerations may arise (Harper and Blake, 1989*a,b*), our study used consistent methods to digitize, compute and compare in a relative way these kinematic features of the strike upon which the accelerations were based. Our conclusions do not depend upon absolute acceleration values, but are based upon relative accelerations calculated by these consistent methods.

Mean and standard error (S.E.M.) were calculated for jaw variables using snake SVL and mouse mass as selecting factors. Twelve kinematic variables were tested using a nested analysis of variance (ANOVA) (Statmost, DataMost Corp.). Each category of mouse was nested within each category of snake size (small *versus* large). A one-way ANOVA was used to compare the durations of the extend and retract stages of the strike, and the amplitude of gape angles before and after contact with the prey. A one-way analysis of variance was also used to test the effect of the distance (*range*) and the mass of the prey on the following kinematic variables; total duration of the jaw movement, the duration of the contact between the snake and the mouse after first jaw contact, and the duration of the extend stage. Finally, a one-way ANOVA was used to test the effect of *range* on *site* of the strike on the mouse. Multiple comparisons between kinematic variables were examined using Pearson correlations. Pairs correlated at  $r > 0.5$  were examined further using linear regression analysis at  $P < 0.05$  (StatMost).  $P < 0.05$  was considered to be statistically significant (Sokal and Rohlf, 1995).

## Results

### Feeding episode

As reviewed in the Introduction, the natural predatory behavior of a rattlesnake may include distinct behavioral patterns that precede the strike (prestrike) and several other patterns that follow (poststrike). Of these three general behavioral patterns, our analysis focused upon the very brief strike itself. The strike phase included the following four stages.

#### Extend stage

During the extend stage, rapid acceleration towards the prey was initiated. Body curves straightened and the head moved towards the prey. The jaws opened, and the fangs, riding upon the maxillary bone, rotated forward, becoming erect at the anterior roof of the mouth. Approximately the anterior one-third of the snake contributed to this forward extension. The remainder of the body did not move or change body angles and therefore established a relatively fixed set of coils without kinematic involvement in the strike, but which served as the base of support from which the anterior part of the body was launched.

The strike phase began from a body posture established in the preceding preparation or even earlier approach phases. During the preparation or approach phases, the snake drew closer to the prey, assuming a posture composed of lateral body curves. These curves often deepened (the angles became more acute), but the basic posture assumed upon approach to the prey and in preparation for the strike was the same posture from which the strike was launched during the extend stage.

#### Contact stage

Usually the lower jaw, but occasionally the upper jaw, was the first part of the approaching head to touch the prey and

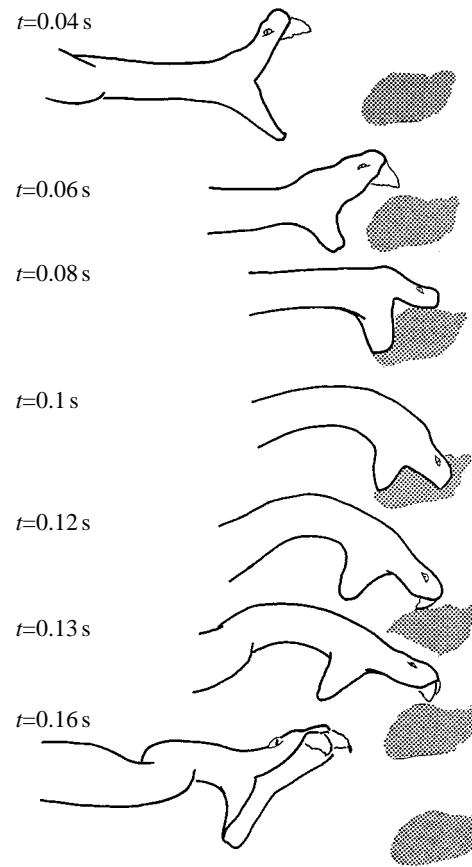


Fig. 2. Representative strike sequence. Tracings taken from high-speed film. The rattlesnake begins its strike at  $t=0$  s (not shown). It lifts up, forming an arch ( $t=0.06$  to  $t=0.1$  s), which drives the curved fangs into the prey. Jaw opening and retraction from the vicinity of the prey occurs at  $t=0.12$  to  $t=0.16$  s. The shaded area represents the prey.

marked the beginning of the contact stage. As the contact stage continued, the neck and anterior body of the snake arched upwards and forwards in a vertical plane, the jaws closed, and the erect fangs were rotated downwards into the prey. This downwards swing of the fangs occurred about an instantaneous point of rotation established within the neck. The formation of this cervical arch is illustrated clearly in lateral view tracings in Fig. 2. First contact with the prey was made at  $t=0.08$  s. Note that, at contact, the long axis of the cervical region in lateral profile is straight. Next, the upper jaws rotate downwards, driving the fangs into the prey, as the cervical region rises upwards, forming a distinct arch ( $t=0.08$ – $0.1$  s). Release begins ( $t=0.12$  s) and the head of the snake is withdrawn rapidly from the vicinity of the prey ( $t=0.13$ – $0.16$  s).

Occasionally a rattlesnake continued to hold the prey until dead, especially if the prey was small. However, in our filmed sequences using mice as prey, rattlesnakes usually quickly let go of large prey, making the overall contact stage very short ( $0.09 \pm 0.06$  s;  $N=5$ ). This was accomplished by lowering the arched cervical region, re-enlarging the gape and drawing the anterior body back into more acute angles, thereby lifting and

withdrawing the fangs away from the prey. When the jaws lost contact with the prey, the contact stage ended and the release stage began.

#### Release stage

Disengagement of the jaws from the prey marked the onset of this stage, and final closure of the jaws marked its end. Because the release stage largely involved the jaws, it included motor patterns initiated by jaw muscles. However, in these rattlesnakes, release was accompanied by the retract stage wherein the head was withdrawn from the vicinity of the prey. Therefore, release and retract activities were distinct, although often overlapping, stages.

#### Retract stage

Travel of the head in the horizontal direction towards the prey marked the extend stage. We defined the retract stage as the reversal of this displacement. Because the retract stage largely involved the body, it included motor patterns initiated by axial muscles. We noted the point within the strike when the braincase of the snake first began to move horizontally away from the prey as the time of onset of the retract stage. In two sequences, the jaws were opened wide to release the prey before evidence of head withdrawal from the prey was evident. However, usually ( $N=19$ ) the departure of the head from the vicinity of the prey was under way while the fangs were still engaged in the prey. Retraction of the head began with a decrease in the height of the arched neck and anterior body accompanied by a reformation of more acute angles within the rattlesnake's body. These postural changes decreased the distance between the head and the relatively fixed position of the mid and posterior parts of the snake's body. Therefore, as the jaws were next thrown open to release the prey, the head was already being retracted, thereby carrying the disengaging jaws away from the prey. As the retraction stage continued and the jaws were withdrawn further from the prey, the mouth began to close, usually completing its closure shortly before the retract stage ended. The retract stage ended when horizontal displacement of the head ceased.

The kinematic profiles that accompany these behavioral stages are illustrated in a series of selected points on a single rattlesnake during one representative strike in Fig. 3. Beginning with the onset of the strike, the total gape angle increased during the extend stage until the snake made contact with the prey; the gape decreased rapidly as the fangs penetrated the prey; the gape angle subsequently increased as the jaws began to disengage, until contact was lost, the mouse was released and the retraction stage withdrew the head from the vicinity of the prey. The displacements of one point on the head and three points on the body are shown above the gape during the same strike. The displacement of a point directly above the axis/atlas joint with the braincase has a relatively steep slope during the extend stage (Fig. 3). Successively more posterior points on the body exhibit successively decreased slopes in this strike sequence.

High-speed analysis of the strike revealed occasional, often

complex, modifications of the basic pattern: extend, contact, release/retract. In one such sequence, the snake failed to implant its fangs upon first contact, tried again and missed again, then turned, opened its jaws for a third time and successfully envenomated the mouse. Specifically, this snake, after initiation of the strike ( $t=0-0.024$  s), failed to implant its fangs successfully ( $t=0.06-0.08$  s) and became separated from the mouse ( $t=0.1$  s), which leaped upwards. The snake opened ( $t=0.12$  s) then closed ( $t=0.16$  s) its jaws, missing the mouse again. It then turned ( $t=0.22$  s), opened its jaws and approached the mouse for a third time ( $t=0.34$  s) to implant its fangs successfully. As the retract stage began ( $t=0.40$  s), the mouse bit the upper lip of the snake ( $t=0.50$  s), until the snake moved well away from the now envenomated mouse ( $t=0.52$  s).

In each of two other unusual sequences, the strike was wide of the prey, and only one fang initially penetrated. Immediately, each snake rotated its head around, re-erected the fang that failed to penetrate, and embedded it in the prey.

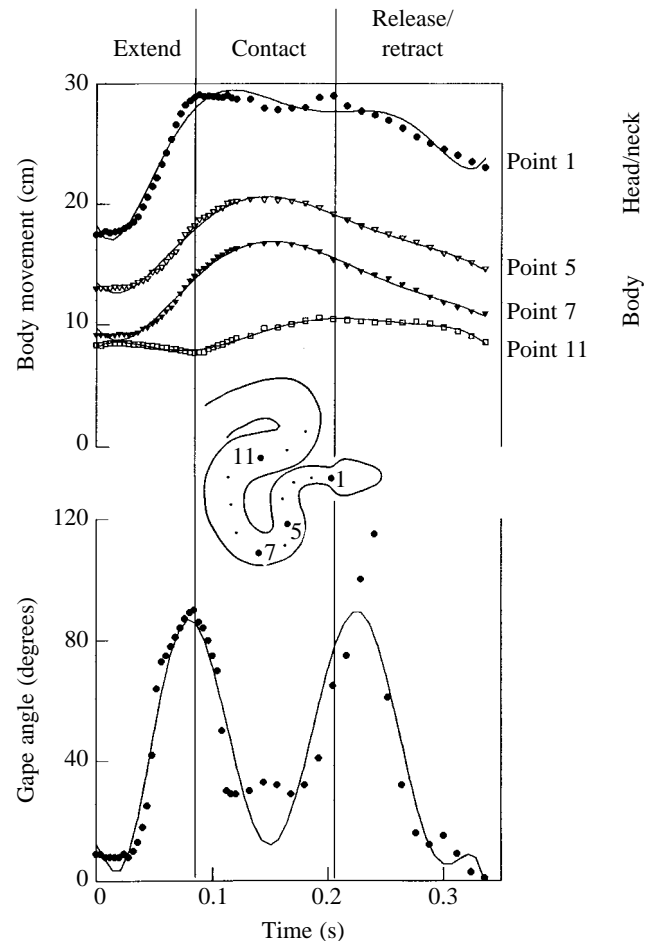


Fig. 3. Representative kinematic profiles of the extend, contact and release/retract stages of the strike phase. Body displacements in the  $x$  direction (towards the prey) are shown for a point situated approximately over the atlas/axis vertebrae and three other successive points on the body, indicated on the silhouette. The corresponding total gape angle, measured in lateral view, is shown below.

*Strike variables*

Means of kinematic variables are summarized in Table 1, for large and small snakes with all prey, as well as for large and small prey with all snakes.

To examine the possible effects of snake size and of mouse size on these variables, these data were analyzed using ANOVA, and the  $F$ -values are given in Table 2. Neither snake size nor mouse size had any statistically significant effect on these 12 kinematic jaw variables (Table 2).

Significantly correlated pairs of kinematic variables ( $r>0.5$ ) are presented in Table 3 together with the  $F$ -value of the interaction. The duration of the extend stage is correlated with the time to maximum gape angle ( $F=132.1$ ). During the contact stage, the time that the jaws remain in contact with the prey is correlated with the time required to reach the maximum gape angle during the preceding extend stage; the time to reach the maximum gape angle and the duration of the preceding extend stage are correlated with the time to reach the minimum gape angle upon contact. The duration of the release/retract stage, the time to reach maximum gape angle and the maximum gape angle during this stage are correlated with several variables of the preceding extend and contact stages. The overall strike is correlated with selected variables in all three stages.

Generally, the fangs made contact with *site 1* on the mouse, head/shoulders (71.4%, 15/21). However, as the *range* increased, there was a significant increase in bites to other parts of the mouse ( $F_{1,18}=5.8$ ,  $P<0.03$ ). With increasing *range*, the duration of the extend stage increased significantly as well ( $F_{1,16}=29.4$ ,  $P<0.001$ , Fig. 4). The maximum gape angle was significantly smaller and its duration was significantly shorter

during the extend stage than during the retract stage (gape angle:  $F_{1,33}=71.4$ ,  $P<0.001$ ; duration:  $F_{1,33}=30.2$ ,  $P<0.001$ , Fig. 4). However, we found no significant interaction between snake size or mouse size and the jaw gape angles (extend, retract), the duration of stages (extend, retract) or the duration of contact with the prey (Table 2).

In one small snake, sufficient numbers of trials in both body positions were obtained to allow a comparison of strike postures (tight and loose) for all kinematic variables using one-way ANOVA. Two out of 12 kinematic variables were significantly correlated with strike posture. Strikes beginning from tight postures (position 1) took significantly longer ( $F_{1,8}=5.4$ ,  $P<0.05$ ) to reach the prey (extend: duration of extend stage) and significantly longer ( $F_{1,8}=9.9$ ,  $P<0.05$ ) to achieve jaw closure on the prey (contact: time to minimum gape angle).

*Strike kinematics**Gape and body displacements*

Kinematic profiles from one snake during five different strikes are shown in Fig. 5. The kinematic profiles from two other snakes were also examined. The same basic pattern is evident in all records: gape increased until reaching maximum gape angle, then gape angle decreased rapidly during closure onto the prey. However, variation in timing and slope occur between strikes by the same snake (Fig. 5) and between different individuals.

During the extend stage, lower jaw depression and upper jaw elevation contributed differently to total gape angle. Upper and lower gape angles (Fig. 1C) were expressed as percentages of the total gape angle. During the extend stage, the upper jaw

Table 1. Summary statistics for 12 variables during extend, contact and release/retract stages as well as for the overall strike phase for strikes by small and large snakes and for small and large mice

Variable	Snake		Mouse	
	Small (N=14)	Large (N=6)	Small (N=13)	Large (N=7)
<b>Extend stage</b>				
Duration of extend stage (s)	0.043±0.009	0.033±0.012	0.043±0.009	0.033±0.012
Time to maximum gape angle (s)	0.034±0.006	0.032±0.008	0.037±0.006	0.029±0.008
Maximum gape angle (degrees)	88.7±4.4	87.5±5.8	82.2±4.4	94±5.8
<b>Contact stage</b>				
Time in contact (s)	0.200±0.047	0.094±0.061	0.168±0.047	0.126±0.061
Time to minimum angle (s)	0.070±0.011	0.078±0.014	0.072±0.011	0.076±0.014
Minimum gape angle (degrees)	39.5±12.8	40.7±16.8	45.7±12.8	34.5±16.8
<b>Release/retract stage</b>				
Duration of release/retract (s)	0.107±0.021	0.108±0.028	0.103±0.022	0.113±0.028
Time to maximum angle (s)	0.268±0.053	0.153±0.070	0.245±0.054	0.177±0.070
Maximum gape angle (degrees)	133.8±8.9	142.5±11.6	135.2±8.9	140.5±11.6
<b>Overall strike</b>				
Time between maximum gape angles (s)	0.233±0.051	0.121±0.066	0.148±0.066	0.207±0.051
Duration from extend to end of retract (s)	0.352±0.059	0.233±0.077	0.325±0.059	0.260±0.077
Duration of jaw movement (s)	0.411±0.062	0.267±0.080	0.360±0.062	0.318±0.080

Values are means ± S.E.M.  
Small mice weigh <16 g; large mice weigh >20 g.

Table 2. Results of ANOVA on the effects of snake size and mouse size on the strike during extend, contact and release/retracts stages and the overall strike of a rattlesnake

Variable	Snake size (1,1)	Mouse size within snake size (1,16)
Extend stage		
Duration of extend stage (s)	2.53	1.12
Time to maximum gape angle (s)	0.75	0.09
Maximum gape angle (degrees)	1.52	0.66
Contact stage		
Time in contact (s)	1.59	0.78
Time to minimum gape angle (s)	2.77	0.14
Minimum gape angle (degrees)	0.94	0.47
Release/retract stage		
Duration of release/retract (s)	0.20	0.49
Time to maximum gape angle (s)	0.06	0.03
Maximum gape angle (degrees)	0.01	1.99
Overall strike		
Time between maximum gape angle (s)	2.98	1.05
Duration from extend to end of retract stage (s)	2.37	1.51
Duration of jaw movement (s)	2.44	1.15

Values are *F*-values.  
Degrees of freedom are given in parentheses.

described a significantly greater angle (59%) than did the lower jaw (41%) ( $F_{1,22}=6.8$ ,  $P<0.02$ ).

In ten strikes ( $N=3$ ), accelerations were compared at approximately 2 cm distances along the kinematically active region of the body, beginning with the segment including the cervical vertebrae. In 80% (33/41 segments), the more anterior segment reached peak acceleration before the next adjacent posterior segment. Acceleration usually began in more anterior sections of the body and proceeded posteriorly in temporal sequence. Most (66%, 46/70) of the body segments reached peak acceleration before the jaws made first contact with the prey.

#### Body displacements

Movement of body segments during the strike was examined in several ways. First, a comparison was made of body angle changes during the strike. 'Acute' body sections (Fig. 6A) exhibited greater angular changes than did body sections along 'straight' locations (Fig. 6C). The angle of the most anterior acute body segments changed from approximately 120° to 175° (Fig. 6A). More posteriorly, body segments also established large angles. Body sections along straight sections of the body showed comparatively little change in angle (Fig. 6C), and in some cases the angles actually declined. In all snakes, the greatest displacement of the body tended to occur at locations where the body was already acutely curved when the strike was initiated, with less displacement occurring within body regions between acute bends (Fig. 6B,D).

Second, we also examined the recruitment of body segments

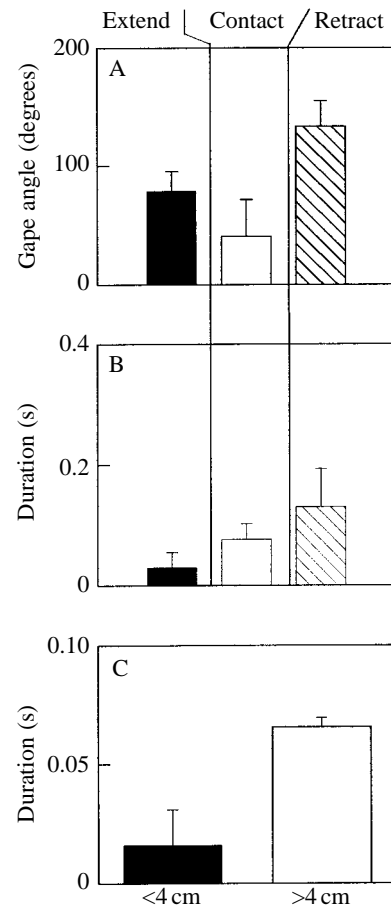


Fig. 4. Histogram of extend, contact and retract stages. (A) Maximum gape angle during the extend and retract stages, and minimum gape angle during the contact stage (close). (B) Duration of maximum (extend, retract) or minimum (contact) gape angle. (C) Duration of the extend stage for snake-to mouse range of less than 4 cm and greater than 4 cm. Values are means + S.E.M.,  $N=18$ .

during a strike sequence. In Fig. 7, the angular changes at 10 body points at approximately 1.5–2.0 cm intervals are ordered using the time during the extend stage of the strike when each section reached its maximum angle of opening. Some angles increased and others decreased during the extend stage. Note that the order of maximum angular change did not follow a strict linear series, anterior to posterior. Segments 2 and 4 reached maximum first, then segment 5 followed by segments 3, 6, 11, 9, 7, 8 and finally 10.

In one small (Fig. 8A) and one large (Fig. 8B) snake, the recruitment of individual body points was compared between two strikes. The chosen points were the same on both snakes. Note that at some points, a particular body angle increased in one strike, but decreased in the other. The extent of angular change about the same body point could also be quite different between the two strikes of one individual. Occasionally, a body segment exhibited no angular change and therefore added no component of displacement to the overall extension of the body.

Table 3. Significantly correlated (Pearson correlations) pairs of strike variables

STAGE: kinematic variable 1	STAGE: kinematic variable 2	F-value
EXTEND: duration of extend stage (s)	EXTEND: time to maximum gape angle (s)	132.1*
CONTACT: time in contact (s)	EXTEND: time to maximum gape angle (s)	4.98*
CONTACT: time to minimum gape angle (s)	EXTEND: time to maximum gape angle (s)	32.6*
	EXTEND: duration of extend stage (s)	30.9*
RELEASE/RETRACT: duration of release/retract (s)	EXTEND: maximum gape angle (degrees)	7.3*
RELEASE/RETRACT: time to maximum gape angle (s)	EXTEND: duration of extend stage (s)	7.1*
	EXTEND: time to maximum gape angle (s)	7.2*
	CONTACT: time in contact (s)	611.7*
RELEASE/RETRACT: maximum gape angle (degrees)	EXTEND: maximum gape angle (degrees)	5.5*
	CONTACT: time in contact (s)	7.62*
	RELEASE/RETRACT: time to maximum gape angle (s)	6.5*
	OVERALL: time between maximum gapes (s)	7.4*
OVERALL: time between maximum gape angles (s)	EXTEND: duration of extend stage (s)	4.9*
	EXTEND: time to maximum gape angle (s)	4.8*
	CONTACT: time in contact (s)	812.9*
	RELEASE/RETRACT: time to maximum gape angle (s)	1910.1*
	RELEASE/RETRACT: maximum gape angle (degrees)	7.4*
	OVERALL: duration of jaw movement (s)	142.9*
OVERALL: duration from extend to end of retract stage (s)	EXTEND: duration of extend stage (s)	6.62*
	EXTEND: time to maximum gape angle (s)	6.1*
	EXTEND: maximum gape angle (degrees)	5.8*
	CONTACT: time in contact (s)	144.7*
	CONTACT: minimum gape angle (degrees)	5.1*
	RELEASE/RETRACT: duration of release/retract (s)	10.9*
	RELEASE/RETRACT: time to maximum gape angle (s)	190.9*
	OVERALL: Duration of jaw movement (s)	443.5*
OVERALL: duration of jaw movement (s)	EXTEND: duration of extend stage (s)	6.8*
	EXTEND: time to maximum gape angle (s)	6.1*
	CONTACT: time in contact (s)	149.7*
	CONTACT: minimum gape angle (degrees)	4.6*
	RELEASE/RETRACT: duration of release/retract (s)	7.9*
	RELEASE/RETRACT: time to maximum gape angle (s)	155.1*

\*Significant at  $P < 0.05$ .

Correlation coefficients are greater than 0.5.

Third, during initial analysis of the kinematic data, we noted, in addition to simple straightening of body angles, a second pattern of body segment displacement. Occasionally body segments 'flowed' around body curves. This feature of body movement is illustrated with displacement vectors for one strike sequence (Fig. 9A), and defined points are followed around acute body curves during a strike (Fig. 9B). In Fig. 9A, 13 resultant displacement vectors on the body are plotted at an instant early in the extend phase ( $t=0.03$  s) and at the moment of contact ( $t=0.12$  s). Note that early in the strike only the first seven body points were kinematically active. However, at contact, 12 points were active, while point 13 (and all points posterior to it) remained fixed. Displacement vectors were short initially, with some directed actually away from the line of travel of the head. Later, most anterior vectors were large and more in line with the direction of head travel, although

points 11 and 12 were not so aligned with the direction of head displacement. In Fig. 9B, points 5, 6, 7 and 8 are illustrated as they move around the bend in the body from the early extend stage ( $t=0.03$  s) to the instant of contact ( $t=0.12$  s). Note, for example, that initially point 6 is to the left of the line between the point of contact and the center of the postural curve, subtending an angle of  $13^\circ$ . However, upon contact, point 6 has rotated around this postural curve and moved forward to a more advanced point, having described an angle of  $89^\circ$  from its initial position.

## Discussion

### *Neurosensory control*

In only one out of 21 filmed sequences did the snake fail to implant its fangs during the initial strike. In this sequence, the



snake opened and closed its mouth a second time, before successfully engaging and envenomating the rodent on the third attempt, thereby adjusting for an inaccurate strike, where the fangs/jaws failed initially to make contact. At the end of the second jaw closure, this snake turned, reoriented itself to the adjacent prey and attacked a third time. This reoriented third attack seemed to represent a new, reinitiated strike. Therefore, an unsuccessful strike can be followed immediately by a readjusted subsequent strike, possibly returning to

visual/infrared cues or taking advantage of tactile cues from contact with the prey. Thus, this episode represents multiple strikes in rapid succession. Quick multiple strikes, continued until successful envenomation, represent one adjustment to an initial error in fang placement.

A second method of adjustment occurs during a single strike after contact with the prey. Because each fang rides on independently protractible jaws, a fang that misses the prey can be re-erected and penetrated, joining its partner in delivering venom. However, such head realignment and fang adjustment occurred only after contact with the prey. Unlike pythons (Frazzetta, 1966), we observed no abrupt change in the trajectory of the head of the snake during the extend stage of a strike. This suggests that, during a single strike, adjustments in response to prey evasive action or inaccurate targeting are made only during the contact stage, not during the extend stage. The strike of the rattlesnake is elicited primarily by visual and/or infrared information (de Cock Buning, 1983; Kardong, 1992). During the extend stage, the eyes and the heat-sensitive facial pits could potentially continue to monitor the displacement of the head along its trajectory towards the prey, but this seems unlikely. Elevation of the upper jaw carries these sensory organs upwards, directing them away from the prey and thereby obstructing their direct exposure to the prey. The presence of diffuse thermosensitive receptors in the oral epithelium (Dickman *et al.* 1987) raises the possibility that oral receptors may monitor prey position as the open jaws approach. However, all corrections observed in the present study occurred *after* the jaws had made contact with the prey. Therefore, tactile cues may be important not only in eliciting jaw closure and venom release, but they may also be the sensory modality responsible for stimulating final fang adjustment to prey position. This further suggests that, during the strike, there is a change from the visual/infrared information (eyes, facial pits) of the extension stage to the mechanical information (tactile) of the contact stage to guide the motor patterns used in envenomation.

The length of time that the jaws make contact with the prey is related to the problem of fang penetration (Kardong, 1986a) and not to the problem of venom metering (Hayes *et al.* 1995). It is conceivable that larger volumes of venom could be delivered by extending the time of jaw contact, thereby allowing more venom to flow into the prey. However, this apparently is not the basis for venom metering. Even when biting multiple times during a strike, the overall time of contact with the prey was brief (less than 1 s). Retaliation by rodents may include the use of their sharp incisor teeth to return a lacerating bite to the head of the snake (Radcliffe *et al.* 1980; Kardong, 1986b). The chances of injury from prey are reduced by the short times of contact and by drawing the head away completely from the prey during the retract stage. As reported by others (e.g. Hayes, 1991), we found no correlation between the time of jaw contact and successful envenomation (time-to-death). Rattlesnakes do exhibit control over the volume of venom injected, but this is delivered in one brief pulse (Kardong and Lavín-Murcio, 1993) and in

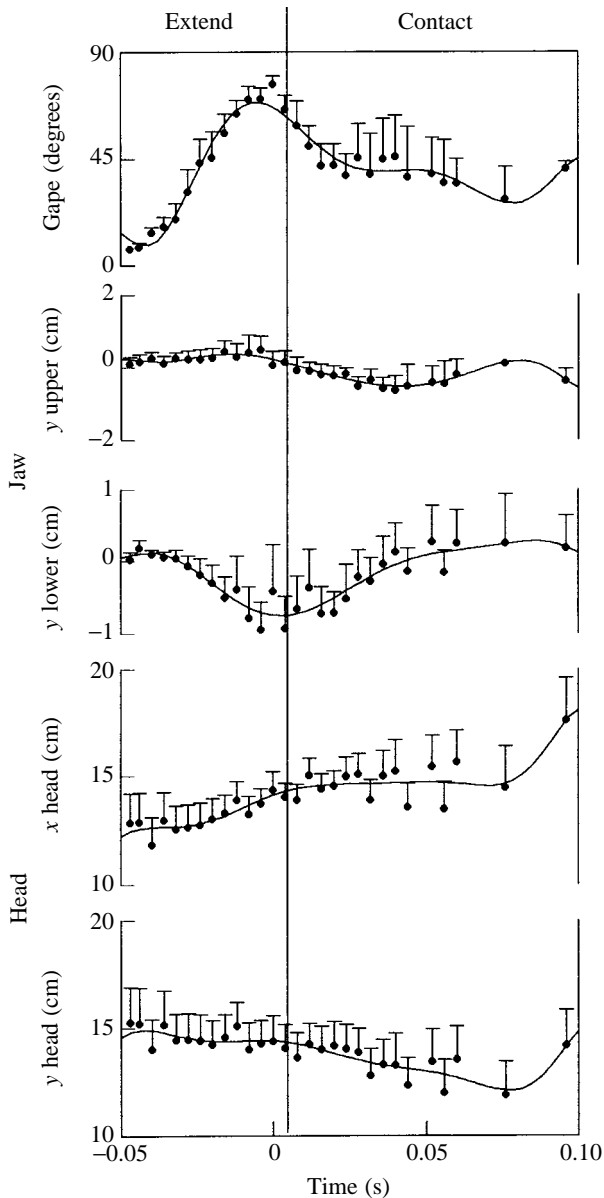


Fig. 5. Kinematic profile from one individual using the same digitized points during five strikes. In the upper panel, gape angle is plotted, below which are the corresponding vertical displacements of the upper and lower jaws, and the horizontal and vertical displacements of a fixed point on the head.  $t=0$  was standardized to the frame in which the jaws reached maximum total gape, and points before and after this are plotted. The mean (filled circle) and S.E.M. (vertical bar) are indicated.

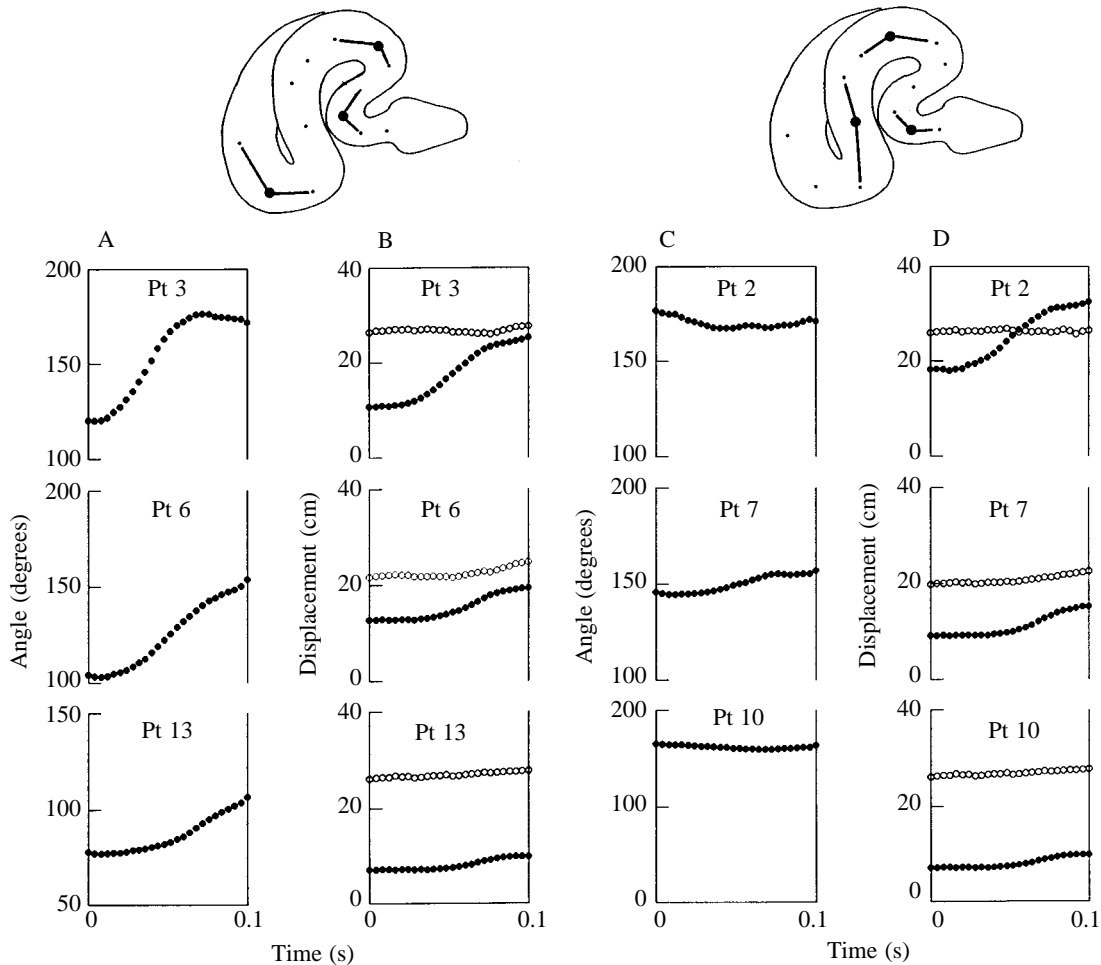


Fig. 6. Changes in body angle and the displacement of the numbered points shown in the silhouette during the extend stage of the strike of one snake. (A,B) Acute body sections. (A) Three points on the body were selected on the prestrike snake body that were the apices of acute body angles followed during the extend stage. (B) The displacements of the same point in the  $x$  (filled symbols) and  $z$  (open symbols) directions. (C,D) Straight body sections. Three points on the same snake were selected that were relatively straight in the prestrike posture, and their angles (C) and displacements (D) are plotted.

proportion to prey size (Hayes, 1991, 1995; Hayes *et al.* 1995). Our interpretation is that, upon contact with the prey, rattlesnakes move and adjust their fang placement until a successful envenomation of a predetermined volume is achieved. Depending upon prey evasive action and/or targeting errors, this may take variable amounts of time until fang penetration is completed. However, the mechanism producing larger releases of venom into prey is not dependent upon prolonging the time of contact *per se*.

#### Strike kinematics

##### Kinematically active regions

When a rattlesnake strikes, over half of its body may participate, especially if the strike is defensive (Klauber, 1956; Russell, 1980). In the present study, in which the snakes were allowed to accommodate to a simulated ambush position, strikes included approximately the anterior one-third of the

body, the remainder of the body showing no appreciable change in posture. We therefore recognize a kinematically active region of the snake, the region exhibiting displacement and changes in posture, and a kinematically fixed region. Although it exhibits no displacement, the fixed body region establishes a secure purchase with the substratum from which the active region is extended towards the prey.

##### Neck arching

Rattlesnake fangs are long, curved teeth. If their tips strike the surface of the prey obliquely, then penetration of the integument becomes mechanically more difficult (Frazzetta, 1966). Rarely do erected fangs stab the prey (*sensu* Van Riper, 1953). Instead, the lower jaw usually makes contact first, then arching of the neck and anterior body drives the erected fangs into the prey with the aid of the accompanying jaw closure. During penetration, the fangs describe an arc with a center of rotation located approximately within the neck. We suggest

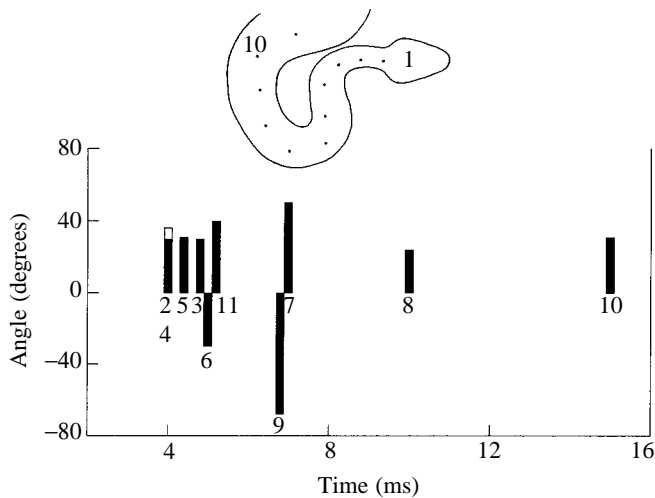


Fig. 7. Sequential change in angles within the body during the extend stage of the strike. Ten sequential points (1–10) on the body were selected (silhouette) as the apices of 10 corresponding angles and their change in degrees during the extend stage plotted. Angles that increased are given positive values, those that decreased are negative. The time during the strike that each angle reached its maximum is used to order the sequence.

that this displacement arc is coincident with the morphological arc of the fangs, thereby orienting the fang tip favorably to the surface of the prey and encouraging its passage through the pliable integument.

#### Feeding stages

In many derived snakes, the predatory strategy has changed from mechanical to chemical means for killing prey (Kardong and Lavín-Murcio, 1993). In colubrid snakes that use no venom, prey is subdued by constriction (Willard, 1977; Greene and Burghardt, 1978) or by the overpowering use of the jaws alone. Swallowing of the dispatched prey may proceed directly or the prey may be released and the snake searches for a new point on the prey to begin swallowing. Consequently, in many colubrid species, a distinct release stage is an obvious behavioral pattern included in their overall predatory behavior (Kardong, 1986c). However, in rattlesnakes, the release of prey following the strike is correlated with prey size (large prey tend to be released, Kardong, 1986b) and with prey type (elusive prey tend to be held, Hayes, 1991). When rattlesnakes release rodents, the release and retract stages overlap, with the retract stage beginning before the jaws are completely disengaged from the prey. Therefore, when disengaging from prey, these two stages are often coincident in rattlesnakes.

#### Strike variables

In general, the farther the snake is from the prey, the longer it takes for its fangs to reach the prey. This suggests that the snake does not make significant adjustments in its kinematics to compensate for the greater distance the head must travel to reach the prey.

#### Gape

During the strike phase, the jaw gape angle increases during the extend stage, decreases during fang penetration, then increases again during the retract stage before finally closing. The relative lengths of each stage are not fixed. If the prey is close to the snake, the extend stage is shorter than if the prey is positioned farther from the snake. The contact stage tends to be variable in length, possibly due to variation in adjustments of fang placement once contact has been made with the prey.

Upper jaw elevation contributes more than lower jaw depression to the overall gape. This supports the theoretical view (Frazzetta, 1983) that prehension of prey from the substratum limits the extent of lower jaw depression because the risk of collision with an obstructing object is increased if the lower jaws are depressed too far.

Mechanical injury may result if rodents inflict a bite on the attacking snake, and rattlesnakes are responsive to prey retaliation (Radcliffe *et al.* 1980; Kardong, 1986a). Cobras, which tend to hold prey, will often release a rodent if it delivers a bite to the snake's head (Kardong, 1982). Therefore, the greatest gape occurs during the release stage. This throws the jaws clear of the prey, contributes to fang withdrawal from the integument and helps to dislodge a clinging and biting rodent.

#### Force transfer

The kinematic patterns observed within the body of a striking rattlesnake imply force transfer between the body

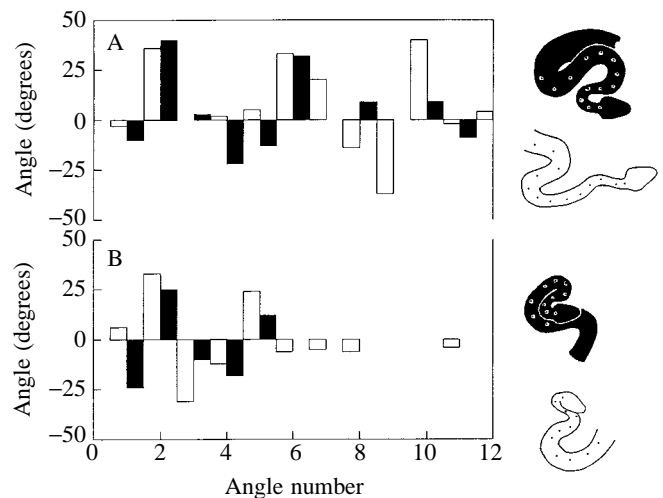


Fig. 8. Sequential change in body angles during the extend stage of two different strikes. Points were selected that formed the apices of 12 (A) or 11 (B) corresponding kinematically active angles and their change in degrees during the extend stage was plotted. Angles that increased are given positive values, those that decreased are negative. (A) For one individual, the same 12 body angles are plotted from two strikes (shown by dark and light bars) that differed on initial strike postures (dark and light silhouettes, respectively). Note that, between the two strikes, the same body point may exhibit quite different angular changes. (B) For a different individual, the sequential change in 11 body angles (silhouette) during the extend stage of two different strikes are plotted. Points are 1.5–2.0 cm apart.

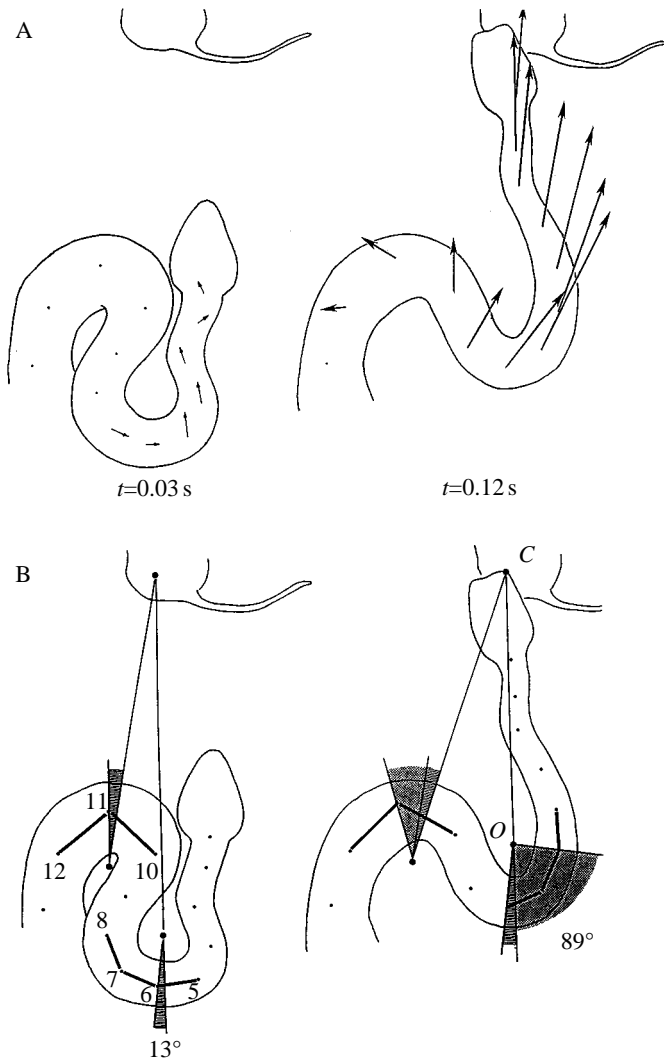


Fig. 9. Displacement of body sections during the strike. (A) Vector displacements of 13 body points during the extend state ( $t=0.03$  s) and at contact ( $t=0.12$  s). Arrow direction and length shows vector direction and magnitude of displacement. Vectors were calculated over 0.04 s. (B) Body displacement relative to postural curves. From the early onset of the extend state ( $t=0.03$  s) to contact stage ( $t=0.12$  s), two sets of adjacent points are followed: four anterior (5, 6, 7, 8) and three posterior (10, 11, 12). Both sets lie within the bend of a postural curve of the body when the strike begins. Note that the posterior set remains relatively fixed in position within this postural curve until contact, opening like a gate hinged at point 11. The anterior set of points, residing within the postural curve initially, have moved around this curve by the time of contact. The angle subtended by point 6, relative to the instantaneous center of the postural curve (point  $O$ ), is indicated. A line drawn from the eventual point of right fang contact ( $C$ ) through the center of radius of the body curve formed by these points ( $O$ ) helps to illustrate their movement.

segments as a mechanism to decelerate the head. Within the kinematically active region of the body, the more posterior sections may not reach peak accelerations until after the anterior body sections. In fact, most sections of the body

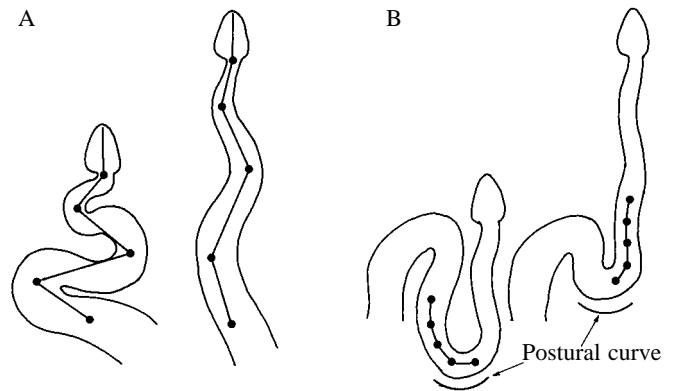


Fig. 10. Strike models. (A) Gate model. The body extends towards the prey when fixed points at acute body bends act like gate hinges, opening the body at each angle they define. (B) Tractor-tread model. The body flows through a postural curve, moving the section of body forward and extending the head towards the prey.

actually begin to decelerate before jaw contact. This reduces the forces that would otherwise be experienced by the jaws upon impact with the prey and thereby reduces the potential for mechanical injury resulting from collision with the prey.

The differential times of peak acceleration within the kinematically active region also suggest a mechanical strategy for distributing forces generated within the body. Anterior body sections tend to reach peak accelerations first, thereby bringing the jaws quickly into the immediate vicinity of the prey, where they close upon the prey before it can effectively evade the snake. However, dissipation of the accompanying forces may be accomplished by force transfer to more posterior sections of the body, as is suggested by their later attainment of peak accelerations. Therefore, the kinematically active region of the rattlesnake body is not analogous to a compressed, ideal spring wherein all bends contribute simultaneously to extension. Instead, the active region of the body exhibits differential displacement and timing of kinematic events.

#### Body displacements

Body segments forming more acute angles at the beginning of the strike undergo greater angular displacements than body segments at less acute postural locations (Figs 6, 10), i.e. displacements at the points of greatest body curvature contribute most to the forward extension of the head. The recruitment of a segment is not simply due to its linear position along the body (Figs 7, 8). Further, between strikes, any one segment may contribute in different ways (Fig. 8).

These kinematic features, together with behavioral modifications of the basic strike pattern, lead us to conclude that the rattlesnake strike is not a fixed pattern, but a general pattern adjusted to accommodate immediate circumstances.

#### Body posture

During the strike, extension of the body is accomplished by straightening of postural curves in the active region of the

body. The configuration of these curves apparently has no effect on the strike. These body curves are established when the snake settles into an ambush position. The use of locomotor undulations to reposition the snake before a strike has been noted in other species (Kardong, 1975) and reported previously for rattlesnakes (Kardong, 1986b). When a mouse approaches, the snake may slowly straighten these curves to bring its head closer to the mouse or these body curves may become more acute just before a strike is launched (Kardong, 1975, 1986b). Prior locomotor activity may define the posture and thus the kinematic requirements for an ensuing successful rattlesnake strike.

#### Strike model

Extension of the body, and thus the advance of the jaws towards the prey, is based on two patterns of body movement. The body curves may open like a gate (Figs 9, 10A) or body sections may flow through an established postural curve, like a tractor tread around a rim (Figs 9, 10B).

The tractor-tread pattern is similar to some modes of snake locomotion. Lateral body forces applied against a firm substratum return a reaction force contributing to forward locomotion. This point in the body often forms an identifiable bend in the body (Gray, 1946; Lissmann, 1950; Gray and Lissmann, 1950; Jayne, 1986) and these applied forces can be measured (Jayne, 1988; Gasc *et al.* 1989). Sections of the body 'flow' through this point, each in turn applying a force against the substratum. Unlike locomotion, the kinematically active region of the snake during a strike is not in contact with the substratum and so is not involved directly in force application against the ground. However, the displacement pattern of body segments, flowing around these postural curves, is similar to displacement patterns during sinusoidal locomotion. This suggests that the control of kinematic displacements of the body is based upon similar neuromuscular patterns.

During the rattlesnake strike, a kinematically active region produces acceleration of the head from a kinematically fixed base of support. Adjustments of the strike to compensate for initial errors in trajectory or evasive action of the prey are made after contact, not while the head is being projected towards the prey. The quantity of venom injected does not depend upon the time the jaws are engaged in the prey. All this suggests that neurosensory control of the strike is based initially on visual/infrared sensory inputs (eyes, facial pits) when launching the strike, but switches to tactile stimuli once physical contact is made with the prey.

The kinematics of the strike exhibit great versatility and adjustment to particular demands of successful predatory behavior. How a particular body region contributes kinematically to the strike is variable from strike to strike, yet the basic overall performance of the rattlesnakes remains relatively constant. Deceleration of anterior body sections before contact suggests that forces are transferred to posterior body sections to help decelerate the head before impact with the prey. Within the kinematically active region, acceleration is accomplished by two general patterns of body displacement.

One is similar to a gate, with body segments remaining fixed in relation to body curves. The other is similar to locomotion where body segments move around and through body curves.

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