

Viper Fangs: Functional Limitations of Extreme Teeth*

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ABSTRACT

The fangs of vipers are extremely long, rotating, hollow teeth. Analysis of video records of more than 750 strikes recorded at 60 or 250 frames per second for 285 individuals representing 86 species in 31 genera shows that vipers reposition fangs after initial contact with prey in more than a third of the strikes. Repositioning resulted when fangs missed prey entirely or hit prey regions that did not permit adequate penetration. The prevalence of repositioning, even among species that normally release prey, suggests strong selective pressure for rapid neuromotor response to fang placement error. The rapidity of repositioning suggests the existence of (a) fine-scale sensory detection of fang penetration depth, (b) rapid modulation of contraction of antagonistic muscles, and (c) possibly neurological modifications to shorten transmission time between sensory input and motor output. Extreme fang length has apparently coevolved with extreme functions.

Introduction

The origins of most extreme structures, such as the fangs of vipers, remain evolutionary puzzles (West-Eberhard 2003). Vipers are a clade of snakes including about 250 recognized species, most of which are characterized by having very long tubular fangs. The clade is distributed worldwide except for Australia, Antarctica, and most of the northern regions of North America and Eurasia (Pough et al. 2004). Most species are terrestrial or arboreal, although a few species are semifossorial (Young and Morain 2003), and one is semiaquatic (Greene 1992). They vary in body form, but all have relatively large triangular heads containing venom glands located between the eye and the jaw joint. Most species are ambush predators that rely on being cryptic or on caudal luring to bring prey

close enough to catch (Greene 1997). Vipers collectively prey on a wide diversity of vertebrate and invertebrate animals, although individual species typically eat relatively few prey types, and most species feed predominantly on small endotherms.

Vipers not only possess an extreme structure—very long fangs—they also perform an extreme function—very rapid injection of venom. Their fangs are so long that the bone that bears them must be rotated backward to fit the fang into the closed mouth, a feat permitted by remarkably mobile connections between the upper jaws and the braincase (Kardong 1974; Kardong et al. 1986; Cundall 2002). Recent studies of fang use (Kardong 1986; Janoo and Gasc 1992; Kardong and Bels 1998; Young et al. 2001*b*) included observations of strikes in which fang position was changed after initial contact with the prey. Previous accounts have neither considered fang repositioning as a potential correlate of the extraordinary shape and size of the fangs nor considered what repositioning tells us about potential neural control of motor events. This article deals with the timing of fang repositioning and what timing might tell us about the neuromechanics (Nishikawa et al. 2007) of fang placement.

Events Leading to Fang Repositioning

Mitchell (1861) remarked on the various problems rattlesnakes experience in envenomating prey, including failure to reach the prey, failure to penetrate tough skin, hitting the prey with the front of the fang (causing it to fold backward before it can be embedded), and embedding only a single fang (resulting in twisting the head to embed the other fang). High-speed recording technology has allowed us to see these events in much greater detail.

It is useful to divide instances of fang repositioning on the basis of whether the snake contacts its prey. Of these two options, strikes that do not contact the prey also fall into two basic kinds: one in which the snake's head simply does not reach the prey (short strike) and one in which the strike reaches the level of the prey but either it is misdirected or the prey moves before the snake's head reaches it.

A qualitatively different type of miss event is one in which missing the prey results in contact with an unyielding object in the environment. In the lab, snakes striking in an enclosed filming arena with solid walls sometimes hit the wall behind the prey. The timing of the snake's responses to these events may reveal more precise timing measures than do corrections in strikes made to prey with fur and flexible body surfaces. However, the latter reveal more about the functional relevance of corrections in the context of the anatomy of both the predator and the prey.

Of strikes that contact the prey, the following events have been seen. First, neither fang is embedded because (*a*) both

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fangs hit the prey and are folded backward as the snake's head is passing over the prey or (b) the prey is small and passes between both fangs. Second, only one fang is embedded (unilateral strike of Young et al. 2001b). Third, one or both fangs hit the prey but (a) only one or (b) neither penetrates prey tissues deeply enough for venom injection. All of these events are typically followed by repositioning of one or both fangs, and if the latter, right and left fangs are repositioned sequentially, not synchronously.

General Questions

Most of the current literature on striking in vipers suggests that strikes in which both fangs fail to penetrate the prey are relatively rare occurrences. However, the unilateral strikes analyzed by Young et al. (2001b) constituted about a third of analyzed strikes. The sample of strikes analyzed here, which may approximate a random sample more closely than those selected by Young et al. (2001b) for measurements of gape and fang movement, provides a basis for estimating the frequency of strikes ending in some kind of error. Further, the comparative data given here provide an estimate of whether there might be any relationship between frequency of repositioning and phylogeny.

The extreme length of fangs in vipers is linked to their function (Mitchell 1861; Klauber 1939). Quantitative analysis of fang form and size of representative vipers (Klauber 1939; Ernst 1982a, 1982b) provides a preliminary assessment of how the form of the fang might relate to errors. Relating fang features to associated skull elements also may begin to unravel the variations acted on by selection during the evolution of the viper envenomating apparatus. These features have been explored previously by Dullemeijer (1959), Brattstrom (1964), Kardong (1980, 1982), Savitzky (1980), Jackson (2003), and others.

Repositioning movements take time to complete, time that is added to the time needed to perform the movements of a "normal" strike. The use of fang repositioning suggests that completing envenomation is more strongly selected than is releasing prey without or with only partial envenomation. If so, then selection should also have favored shortening the duration of repositioning. This article explores the hypothesis that the extreme length of the fang, in combination with the selection of vertebrate prey, coevolved with the physiological capability to rapidly change fang placement.

Material and Methods

Recording Methods

The timing of striking events was analyzed from records for 755 strikes recorded from a variety of vipers (Table 1) between 1998 and 2007. Most of the snakes were maintained in major zoo collections and recorded under approved zoo Institutional Animal Care and Use Committee (IACUC) research protocols during periodic visits to the zoos (see "Acknowledgments"). Repeated records of strikes by individual snakes were gained from a relatively small number of vipers maintained at Lehigh University under approved Lehigh IACUC protocols (DR-01

and renewals, 07-56). Snakes were kept in individual cages, provided water ad lib., and fed live or dead (killed) mice or rats at irregular intervals.

Methods of recording were similar to those described for booids by Cundall and Deufel (1999) and Cundall et al. (2007). To gain adequate resolution of individual video frames on playback, strikes were illuminated either by a single Smith-Victor 600-W photoflood lamp for 60 frames per second (fps; analogue video records made with a Panasonic AG-456 camcorder) or by two NRG Versalite 150-W lamps for 250 fps (digital video recorded with a RedLake MotionMeter). A total of 371 strikes were recorded at 60 fps and 386 at 250 fps. Exposure times for both cameras were 1/1,000 s, which reduces blurring of the snake's head in frames showing peak velocities to the point where fang position and gape size can be seen. Files stored in the MotionMeter were digitized with Interview software using various playback rates, most at 10 fps, downloaded onto an Apple iBook G3, and transferred for analysis to an iMac G5.

Timing of Fang Movements

Strikes were analyzed by measuring times between events to the nearest frame. To determine the delay to initiate fang repositioning in strikes recorded at 60 fps, I counted the number of frames (playback on a Panasonic AG-1970 VCR at 60 fps) between the end of fang penetration and initiation of fang repositioning and converted the result to milliseconds. In 250-fps records, I measured time (in 4-ms intervals) between the initiation of fang repositioning and both initial prey contact (usually made by the mandible) and first fang contact. Apart from providing a measure of the minimum times for the mechanical expression of a reflex response, these data also allowed determination of relative numbers of repositioning events in different clades (subfamilies, genera, species).

All strikes were analyzed for distance to prey and for timing of specific events from the first movement of the strike to (a) depression of anterior lower labial scales, (b) lower jaw depression, (c) head movement toward prey, (d) end of extension phase, (e) first contact with prey, and (f) first fang contact with prey. In addition, the duration of fang protraction during repositioning was measured from the beginning of repositioning movement. For all snakes that released prey (Deufel and Cundall 2006), bite duration was measured from the point of fang contact to the initiation of release (usually seen as movement of the mandibles or braincase away from the prey), and release duration was measured from the beginning of release to maximum gape.

One problem in analyzing fang use is determining whether fang repositioning movement results from an error or is simply one of a number of preprogrammed motor patterns. For example, a case where one fang hits the prey and one misses (unilateral strike of Young et al. 2001b) would superficially appear to be an error. But the snake might have anticipated that one fang would miss the prey before launching the strike. In that event, motor events typical of those occurring at normal prey contact with both fangs would not be expected. Normal

events at prey contact include not only closing the mouth but also partial retraction of both fangs. If the snake anticipated missing the prey with one fang, the anticipation might be reflected in the absence of retraction of the unembedded fang. If fang retraction occurs, the snake presumably did not anticipate missing the prey with that fang, and any repositioning movement to embed that fang counts as correction of an error.

In many strikes in which one or both fangs are moved after initial placement, the fangs have actually hit the prey somewhere, and the reasons for moving a fang are difficult to determine. In some cases, as when a fang hits the head of the prey, the fang may have hit bone, preventing the fang from penetrating deeply enough for subcutaneous injection of venom. Because the precise location of a fang tip in a prey item at the time of penetration is often impossible to determine with accuracy, I coded approximate sites of fang initial placement as miss (0), head (1), neck (2), shoulder (3), thorax posterior to the shoulder (4), abdomen (5), and pelvic area and thigh (6).

Strikes in which the snake either missed or failed to reach the prey provided useful measures of the degree to which strike movements are preprogrammed. These strikes were also analyzed and used to determine the time from strike initiation to mouth closing and the relationship between movement patterns of the mandibles and upper jaws. These strikes invariably showed corrective movements, but these were not keyed to the moment of prey contact. Relatively few missed strikes were recorded at 250 fps because the camera stores only 4 s of data, and missed strikes were frequently followed quickly by envenomating strikes, leaving inadequate time intervals to download the missed strike to the computer.

In addition to timing variables, strikes were coded using distance to the prey at strike initiation in snake head lengths (0, 0.5, 1.0, 1.5, 2, 3, 4, 5, 6, 7). This factor was used to evaluate the nature of timing decisions that could be made before the strike. Strikes recorded at 250 fps were also coded by which part of the head hit the prey first (lower jaw, upper jaw, both) to estimate how this factor might influence fang repositioning.

Strike-timing variables were analyzed with one-way ANOVA, and the combined effects of two or more variables were analyzed with ANCOVA using SPSS 14.2 for Windows. Prey distance at strike initiation, strike fate (miss, hit prey with no correction, or hit prey but with a repositioning movement of one or both fangs), prey contact type (released or not released), and specific contact points of right and left fangs were treated as fixed factors. Strikes were treated as individual stochastic events, and hence repeated-measures ANOVA was not used. ANOVAs were also used to test variable means for subfamilial and generic clades and to test specific factor effects on timing of fang repositioning. Differences among species are not explored here.

Anatomy

To test the notion that fangs, as extreme structures, might exhibit variations in those features critical to their function and,

furthermore, that variations of some features might be more closely linked to behavioral modifications, I measured fangs in dried skulls of representative viper species. Specifically, I measured lengths of ankylosed fangs only (from base at maxillary edge to tip, not from the distal edge of the venom entry lumen to the tip, as done by Klauber [1939] and Ernst [1982a, 1982b]) and the distance from fang tip to the proximal edge of the discharge orifice in skeletons of the genera listed in Table 2. Variation in discharge orifice position was examined in those species for which sample sizes >10 were available.

I also measured selected aspects of the skull, including braincase length from the median anterior edge of frontals to the median caudal edge of the atlantal crest, straight-line mandible length, ectopterygoid length, maxillary height, and fang curvature (angle between vectors drawn through the middle of the base and the tip of the fang). The independence of the behavioral and anatomical data sets constrains interpretations that require linking the two analyses.

Phylogenetic Comparisons

Tables 1 and 2 list the taxa for which data have been gained. Table 1 includes species for which only one strike from one individual is currently available because these data were included in the overall analysis and in comparisons of subfamilial (Crotalinae, Viperinae) characteristics. Similarly, Table 2 lists genera for which only one skull has been measured because these also were included in subfamilial comparisons. Phylogenetic comparisons were initially made between major clades (subfamilies). Statistical results were then examined to determine whether particular behavioral or morphological features were distributed throughout the clade or were expressed by only a few genera or species. Quantitative behavioral and morphological traits are given for genera where sample size warrants. Genera with sample sizes >10 were analyzed for potential differences in fang repositioning times (one-way ANOVA), potential correlates to fang repositioning (Pearson correlation), and potential size (growth) effects on skull measures using regressions of ratios. Lengths of skull elements and fangs were converted to ratios using mandible or braincase length as the denominator, and the distance of the proximal end of the discharge orifice from the fang tip was size adjusted by using fang length as the denominator. This article concentrates on functional characteristics that appear to be widespread among vipers.

Results

Fang Movements

Fang Use in the "Typical" Strike. The nature and timing of fang use during a predatory strike by a viper are shown in Figure 1, and its temporal features and critical functional attributes are summarized in Figure 2. Kinematic details in most strikes were similar to those quantified by Janoo and Gasc (1992), Kardong and Bels (1998), Young et al. (2001b), and LaDuc (2002). The strike begins with rapid acceleration of the viper's

Table 1: Viper strike records analyzed for corrections (number of corrections per record type per species)

Genus and Species	N	60 fps		250 fps	
		No. Records	No. Corrections	No. Records	No. Corrections
Causinae:					
<i>Causus defilippii</i>	2	5	2	0	0
Viperinae:					
<i>Atheris ceratophora</i>	2	0	0	2	1
<i>Atheris chlorechis</i>	3	10	6	3	1
<i>Atheris squamigera</i>	5	6	2	12	4
<i>Bitis arietans</i>	7	42	22	29	21
<i>Bitis gabonica</i>	4	0	0	5	5
<i>Bitis nasicornis</i>	1	20	5	3	2
<i>Cerastes cerastes</i>	6	5	4	9	5
<i>Daboia palaestinae</i>	1	2	1	0	0
<i>Daboia russelii</i>	1	1	1	1	1
<i>Echis carinatus</i>	8	0	0	15	7
<i>Eristicophis macmahonii</i>	4	0	0	6	5
<i>Macrovipera lebetina</i>	1	0	0	1	1
<i>Macrovipera mauritanica</i>	6	11	4	7	5
<i>Montivipera albizona</i>	3	0	0	7	1
<i>Montivipera bornmuelleri</i>	1	3	1	0	0
<i>Montivipera raddei</i>	8	2	1	7	3
<i>Montivipera wagneri</i>	8	2	2	6	5
<i>Montivipera xanthina</i>	3	1	0	3	1
<i>Vipera ammodytes</i>	1	0	0	2	1
<i>Vipera aspis</i>	4	0	0	4	1
<i>Vipera (Pelias) kaznakovi</i>	2	0	0	2	1
<i>Vipera (Acridophaga) lotievi</i>	2	0	0	4	0
<i>Vipera (Pelias) nikolskii</i>	1	0	0	2	1
<i>Vipera orlovi</i>	1	0	0	1	1
<i>Vipera transcaucasiana</i>	5	4	0	1	1
Crotalinae:					
<i>Agkistrodon bilineatus</i>	1	0	0	1	0
<i>Agkistrodon contortrix</i>	5	13	3	1	0
<i>Agkistrodon piscivorus</i>	5	22	2	8	1
<i>Agkistrodon taylori</i>	8	2	1	7	3
<i>Atropoides mexicanus</i>	2	0	0	40	26
<i>Atropoides nummifer</i>	2	0	0	2	2
<i>Bothriopsis bilineatus</i>	1	0	0	1	1
<i>Bothriopsis taeniatus</i>	1	0	0	1	0
<i>Bothriechis marchi</i>	1	0	0	1	1
<i>Bothriechis nigroviridis</i>	1	2	1	0	0
<i>Bothriechis schlegelii</i>	6	2	1	4	3
<i>Bothrops alternatus</i>	2	4	0	0	0
<i>Bothrops asper</i>	2	0	0	2	0
<i>Bothrops atrox</i>	1	0	0	1	1
<i>Bothrops caribbaeus</i>	2	1	0	4	3
<i>Bothrops mattagrossensis</i>	2	0	0	2	1
<i>Bothrops moojeni</i>	1	0	0	1	1
<i>Bothrops venezuelensis</i>	1	1	0	0	0
<i>Calloselasma rhodostoma</i>	2	0	0	2	1
<i>Crotalus abyssus</i>	4	2	1	4	0
<i>Crotalus adamanteus</i>	1	1	1	0	0
<i>Crotalus atrox</i>	3	43	8	21	4

Table 1 (Continued)

Genus and Species	N	60 fps		250 fps	
		No. Records	No. Corrections	No. Records	No. Corrections
<i>Crotalus cerastes</i>	5	7	1	2	2
<i>Crotalus durissus</i>	5	0	0	5	3
<i>Crotalus horridus</i>	17	94	22	13	1
<i>Crotalus lepidus</i>	12	0	0	13	4
<i>Crotalus mitchellii</i>	5	1	0	4	3
<i>Crotalus molossus</i>	5	1	0	4	2
<i>Crotalus oreganus</i>	1	0	0	5	2
<i>Crotalus polystictus</i>	4	6	2	3	2
<i>Crotalus scutulatus</i>	2	0	0	7	4
<i>Crotalus simus</i>	1	0	0	1	1
<i>Crotalus tigris</i>	3	4	2	1	1
<i>Crotalus viridis</i>	1	0	0	7	3
<i>Cryptelytrops albilabris</i>	1	0	0	1	0
<i>Cryptelytrops fasciatus</i>	3	5	2	1	1
<i>Cryptelytrops insularis</i>	4	0	0	4	2
<i>Cryptelytrops kanburiensis</i>	1	0	0	1	0
<i>Deinagkistrodon acutus</i>	2	0	0	2	2
<i>Gloydus blomhoffi</i>	3	1	0	2	0
<i>Gloydus saxatilis</i>	2	7	0	1	1
<i>Gloydus ussuriensis</i>	2	0	0	4	0
<i>Lachesis muta</i>	8	3	1	6	4
<i>Lachesis stenophrys</i>	3	4	1	0	0
<i>Ophryacus melanurus</i>	1	0	0	2	0
<i>Ovophis monticola</i>	3	12	1	0	0
<i>Parias flavomaculatus</i>	6	6	0	6	4
<i>Porthidium ophryomegas</i>	4	1	0	15	4
<i>Protobothrops flavoviridis</i>	2	0	0	2	0
<i>Protobothrops jerdoni</i>	4	1	1	4	3
<i>Protobothrops mucrosquamatus</i>	3	0	0	4	2
<i>Protobothrops tokariensis</i>	3	0	0	5	2
<i>Sistrurus catenatus</i>	6	3	1	4	1
<i>Sistrurus miliarius</i>	3	0	0	3	1
<i>Trimeresurus borneensis</i>	5	1	1	4	2
<i>Trimeresurus puniceus</i>	1	0	0	1	1
<i>Trimeresurus trigonocephalus</i>	5	2	2	4	2
<i>Tropidolaemus wagleri</i>	3	0	0	3	2
<i>Viridovipera stejnegeri</i>	1	3	1	6	3
<i>Zhaovermia mangshanensis</i>	11	0	0	1	1
Total	285	369	109	386	188

Note. Total number of species = 86, total number of genera = 31.

head toward the prey (extend phase). During this phase, the mouth is opened by bilaterally synchronous depression of both mandibles and protraction of the right and left upper jaws, which erects the fangs and stretches the fang sheath. Vipers typically contact prey with the lower jaw first and close the mouth, driving both fangs into prey tissues (bite phase). Successful penetration of fangs causes the fang sheath to slide up the fang. Whether the snake's head is still moving forward at the moment of contact varies, as does the exact time when the mouth begins closing. In some strikes, the mouth begins closing

before the snake reaches the prey, but the bite phase begins only after the fangs penetrate prey tissues. After a variable period of time, some vipers rapidly open their mouth and release the prey, using maximal abductions of the upper jaws and mandibles to release their teeth and fangs from the surface of the prey (release phase), a phase that quickly leads into the withdrawal phase, in which the snake pulls its head away from the area occupied by the prey (Kardong and Bels 1998; Cundall 2002). This article deals almost exclusively with events of the bite phase, a phase traditionally typified as bilateral penetration

Table 2: Means \pm SD for fang length (FL), ectopterygoid length (EL), and maxilla height (MH) relative to the length of the mandible, distance of upper edge of the discharge orifice from the tip of the fang (DO) relative to fang length, and fang curvature (FC) in representative viperid genera

Subfamily and Genus	N	FL	DO	FC	EL	MH
Azemiopinae:						
<i>Azemiops</i>	1	.22	.22	135	.44	.17
Causinae:						
<i>Causus</i>	2	.13 \pm .01	.51 \pm .01	135 \pm 0	.38 \pm .02	.15 \pm .01
Viperinae:						
<i>Atheris</i>	10	.25 \pm .02	.29 \pm .08	125 \pm 15	.41 \pm .02	.23 \pm .01
<i>Bitis</i>	28	.29 \pm .04	.24 \pm .06	99 \pm 8	.47 \pm .03	.21 \pm .01
<i>Cerastes</i>	10	.21 \pm .01	.33 \pm .03	100 \pm 10	.41 \pm .02	.22 \pm .01
<i>Daboia</i>	4	.26 \pm .02	.31 \pm .05	111 \pm 15	.43 \pm .01	.21 \pm .01
<i>Echis</i>	1	.24	.38	150	.37	.23
<i>Macrovipera</i>	1	170	.41	.19
<i>Vipera</i>	7	.19 \pm .03	.35 \pm .06	117 \pm 18	.38 \pm .02	.20 \pm .01
Crotalinae:						
<i>Agkistrodon</i>	27	.21 \pm .01	.34 \pm .03	128 \pm 16	.37 \pm .02	.23 \pm .01
<i>Atropoides</i>	4	.26 \pm .01	.20 \pm .01	110 \pm 14	.47 \pm .01	.23 \pm .01
<i>Bothriechis</i>	5	.26 \pm .04	.28 \pm .05	119 \pm 17	.44 \pm .02	.24 \pm .01
<i>Bothriopsis</i>	2	.33 \pm .01	.27 \pm .01	150 \pm 14	.43 \pm 0	.23 \pm .01
<i>Bothrocophias</i>	1	.28	.12	110	.46	.22
<i>Bothrops</i>	13	.32 \pm .03	.24 \pm .02	127 \pm 19	.46 \pm .02	.22 \pm .01
<i>Cerrophidion</i>	2	.20 \pm .02	.31 \pm 0	123 \pm 18	.38 \pm .03	.22 \pm .01
<i>Crotalus</i>	68	.26 \pm .04	.32 \pm .05	108 \pm 16	.43 \pm .06	.24 \pm .03
<i>Deinagkistrodon</i>	2	.24 \pm .01	.27 \pm .01	122 \pm 10	.41 \pm .02	.23 \pm .01
<i>Gloydus</i>	3	.24 \pm .05	.25 \pm .05	112 \pm 23	.41 \pm .05	.21 \pm .01
<i>Lachesis</i>	4	.35 \pm .01	.19 \pm .03	140 \pm 14	.45 \pm .01	.23 \pm .01
<i>Ophryacus</i>	2	.24 \pm .01	.34 \pm .03	115 \pm 21	.46 \pm .01	.22 \pm .01
<i>Porthidium</i>	2	.29 \pm 0	.20 \pm .02	98 \pm 4	.45 \pm .02	.22 \pm 0
<i>Protobothrops</i>	2	.33 \pm 0	.25 \pm 0	145 \pm 7	.47 \pm .01	.21 \pm .01
<i>Sistrurus</i>	2	.24 \pm .01	.32 \pm .04	128 \pm 11	.44 \pm .01	.22 \pm 0
<i>Trimeresurus</i>	2	.20 \pm .01	.24 \pm .03	140 \pm 7	.48 \pm 0	.25 \pm 0
<i>Tropidolaemus</i>	1	.27	.18	135	.47	.24

Note. See text for explanation of measurements.

of fangs into prey tissues with bilaterally synchronous compression of the venom glands and ejection of venom from both fangs.

Critical elements of the strike-motor pattern, confirmed in all recorded strikes in the literature (*Crotalus viridis oreganus*: Kardong and Bels 1998; *Crotalus atrox*: Young et al. 2001b, 2003; LaDuc 2002) and in all of my data, are bilaterally synchronous opening and closing. What happens after closing begins varies considerably.

Preprogrammed Nature of Mouth Closing. A critical element in timing the beginning of fang repositioning is the neurological basis of jaw and fang movements at the point of prey contact. As has been stressed in previous work (e.g., Kardong and Bels 1998; Young et al. 2001b), vipers use limited gape when striking toward prey. This can be achieved only through modulation of abducting and adducting forces acting on the mandibles and

of protracting and retracting forces acting on the upper jaws, both of which collectively prevent the mouth from assuming the extreme excursions seen when the same snake either yawns or releases prey (Dullemeijer and Povel 1972; Young et al. 2001b; Cundall 2002). The last parts of the strike just before and immediately following contact with the prey are very fast. Kinematic evidence suggests that all motor events during this time interval are preprogrammed (Kardong and Bels 1998; Cundall et al. 2007). In 60 of the 371 strikes recorded at 60 fps and in 23 of 386 strikes recorded at 250 fps, the snake missed the prey (Fig. 3). In most of these missed strikes, the mouth begins closing symmetrically, and the fangs remain erect. The extent of closure varies, and the terminal parts of missed strikes can be highly variable. Mean time to peak gape was 80 ± 43 ms for 24 viperine missed strikes recorded at 60 fps and 54 ± 14 ms for 12 viperine missed strikes recorded at 250 fps. Equivalent times for crotaline missed strikes were $79 \pm$

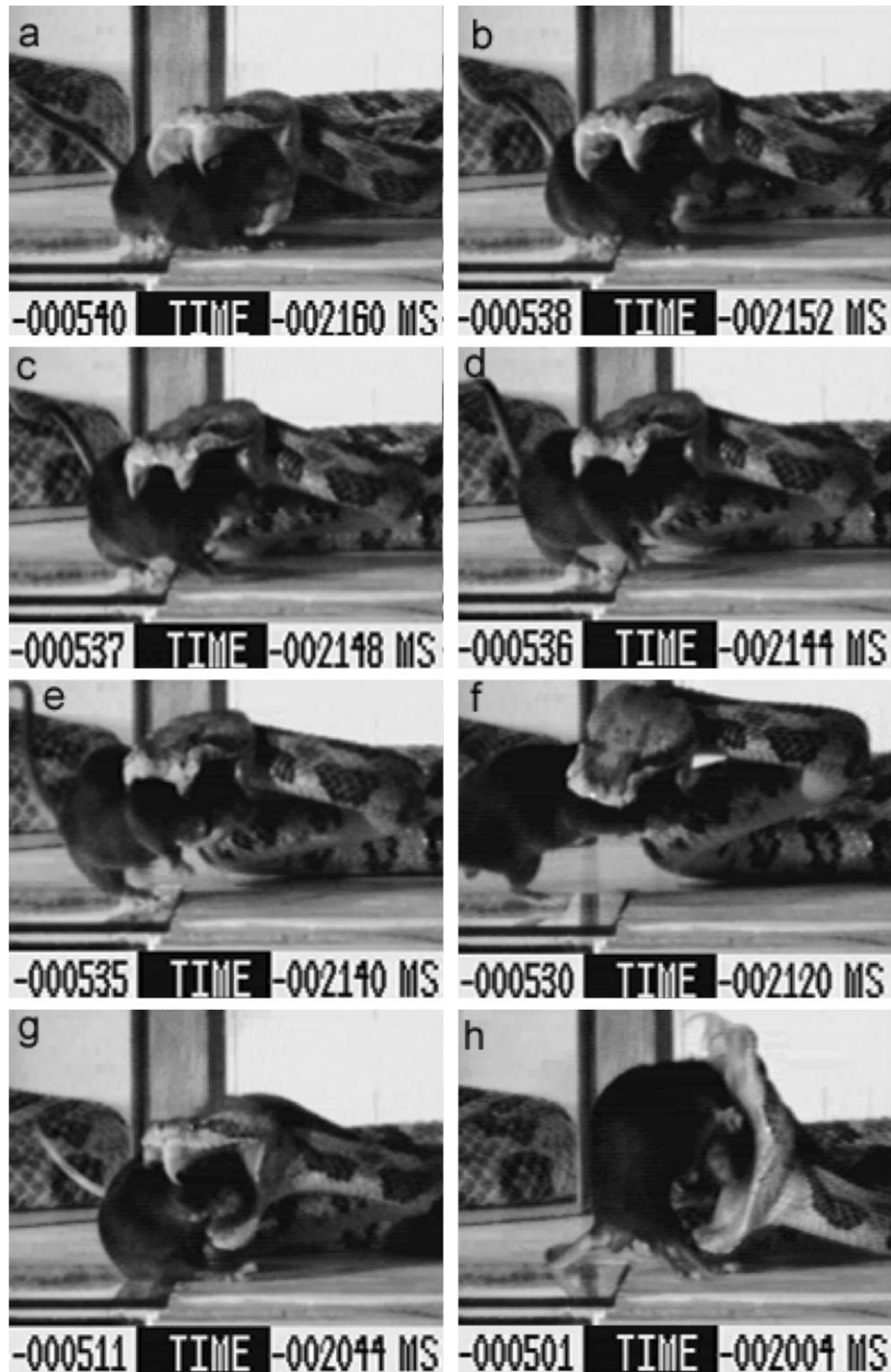


Figure 1. Fang use during a strike by an adult *Crotalus horridus* with no corrections or fang repositioning. In *a*, the mandible has already contacted the prey, and the upper jaws and fangs have just reached full protraction as elevation of the mandible has begun. Fangs contact the prey in *b* and begin penetration in *c*, and mouth closing continues in *d* and finishes in *e*. The bite phase is prolonged, and release begins at $-2,052$ ms, exposing the fangs in *g*, with maximum release gape being reached 48 ms later in *h*.

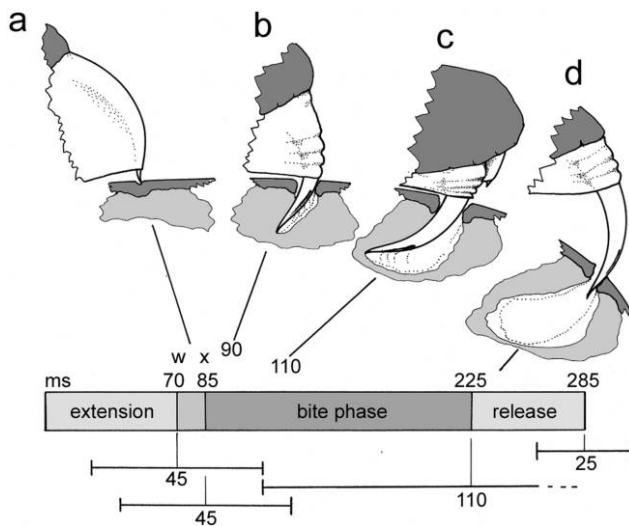


Figure 2. Diagrammatic summary of fang behavior during a “normal” viper strike in which prey are released. Numbers above the time bar are based on means for 111 strikes recorded at 250 fps and denote time to prey contact after first movement (w), time to fang contact (a ; x), time of initial fang penetration (b ; 90), and retraction of fang (c ; 110) lasting more than 100 ms, presumably accompanied by injection of venom during part or all of this phase. For most strikes, the presumption that venom injection occurred was confirmed by the behavior of the prey within seconds of the strike. However, the duration of venom injection could not be measured empirically and is inferred here solely from bite duration. Because fang tips in vipers have cutting edges on the rear surface (Klauber 1939; D. Cundall, personal observation), retraction of the fang potentially opens a space by slicing the prey’s tissues. The state shown in d occurs about 10 ms after the snake relaxes the bite to begin release at 225. Release involves rapid protraction of the upper jaw, often well beyond that seen during extension. The end of the release phase (285) is defined here as the point of maximum gape, although the snake’s jaws often lose contact with the prey before maximum gape is reached. Numbers and range bars below the shaded time bar represent 1 SD and derive from an analysis in which bite durations exceeding 600 ms were deleted.

31 ms for 36 strikes at 60 fps and 87 ± 23 ms for eight strikes at 250 fps. The other three missed strikes at 250 fps involved contact with a solid object, and gape time could not be measured.

Incidence of Repositioning. The most common repositioning event in viper strikes is the movement of one or both fangs after initial fang contact with the prey. Of 755 strikes by all vipers, 294 (39%) involved fang movements after initial fang penetration. The different kinds of records give different results. The 60-fps records show fang repositioning in only 109 of 361 strikes (30%), whereas the 250-fps records show repositioning in 188 of 386 strikes (49%). The difference between the two types of records appears to be partly a function of sampling effects and the relative numbers of different taxa in each sample.

Young et al. (2001b) use the term “correction” to mean adjustment of strike trajectory, or “midstrike adjustment” in their terminology, an event that occurs before the snake’s head contacts the prey. Of all the strikes analyzed here, only one strike

(for *Vipera kaznakovi*) showed any evidence of a change in direction of the head during the extension phase of the strike, and that involved a change that began shortly after the head began moving forward. However, given the long duration of the extension phase of the strike, the correction actually could have been programmed.

In analyzing strikes by *C. atrox*, Young et al. (2001b) based their analysis on whether snakes hit the prey with one (unilateral; see also Fig. 4) or both (bilateral; Fig. 1) fangs. Their results show that 14 of 40 (35%) strikes were unilateral. Six of 14 unilateral strikes (43%) involved repositioning of the unembedded fang. However, a nearly equal percentage of bilateral strikes (42%, 11 of 26) showed fang repositioning. Here, 17% (62 of 376) of strikes recorded at 250 fps (10 strikes could not be scored for fang placement) were unilateral strikes, and of these, 65% (40) showed fang repositioning. Hence, 148 of 314 bilateral strikes (46%) recorded here involved fang repositioning. Given that this is nearly half of recorded strikes, the “traditional” view of the viper strike as one without fang repositioning does not describe half of the apparently normal behavior of viper fangs.

Timing of Repositioning. The mean time interval from contact with the prey to initiation of a repositioning movement is 29 ± 16 ms for 109 corrections in 371 strikes recorded at 60 fps. Because the temporal resolution of 60-fps records severely limits precision of start and stop times for events, the value of the estimate comes from the number of records on which it is based. For 250-fps records, differentiating between the time of first contact with the prey, usually by the mandible, and the time of fang contact showed that fang repositioning began 43 ± 16 ms after prey contact but only 30 ± 12 ms after fang contact (Table 3; Fig. 3). The minimum latency between fang contact and the beginning of fang repositioning movement is 4 ms, found in one strike of the viperine genus *Montivipera* and one strike each for the crotaline genera *Trimeresurus* and *Tropidolaemus*. More realistic minimum times are 16–20 ms recorded for 13 genera, although six genera have minimum times of 8–12 ms.

Bite Duration. Fang repositioning movements significantly increase bite duration, the time the snake remains in intimate contact with the prey. Of those strikes in which vipers released the prey without fang repositioning, bite duration was 140 ± 104 ms ($N = 111$), whereas strikes involving fang repositioning had bite durations of 185 ± 119 ms ($N = 85$; $F_{1,194} = 8.06$, $P < 0.01$). Before calculating the F value, 12 strikes were deleted in which repositioning occurred and prey were ultimately released but only after being held for more than 600 ms.

Prey Release. Initiation times for fang repositioning are significantly shorter in strikes in which prey are released than in those in which prey are held. Ignoring effects of phylogeny, in 74 strikes by vipers that released prey, time to initiate fang repositioning was 42 ± 16 ms from prey contact and 29 ± 12 ms from fang contact. These times were significantly shorter

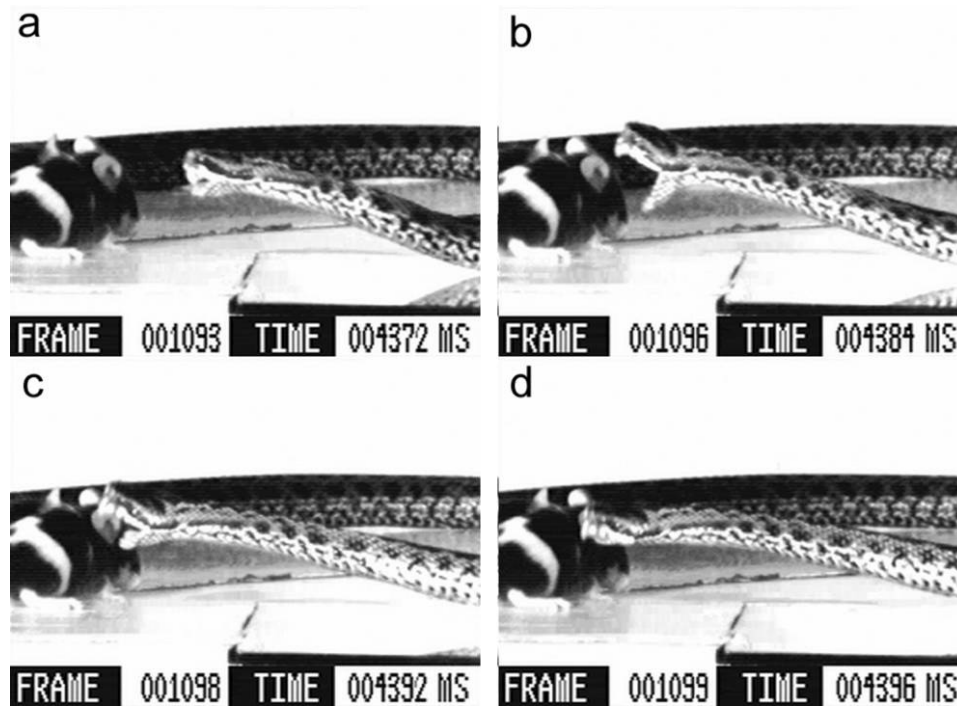


Figure 3. Missed strike by a *Vipera lotievi*. Snake's head is in the process of moving toward the prey in *a*, which shows retraction of the lower labials and the beginning of lower jaw opening. The snake reaches peak gape in *b* and, immediately following, begins closing the mouth, which is half closed in *c* and almost fully closed in *d*, with the fangs still erect and the snake's head a few millimeters short of the prey.

than those expressed in 114 (for prey contact)/113 (for fang contact) strikes by vipers that held on to prey (respectively, 48 ± 20 [$F_{1,186} = 5.8$, $P = 0.02$]; 36 ± 20 [$F_{1,184} = 7.1$, $P < 0.01$]).

Fang Contact Site and Repositioning. Where the fangs hit the prey might influence the probability that fangs would be repositioned or the duration of repositioning. Comparing contact sites in 250-fps strikes with no repositioning to those showing fang repositioning showed no significant differences in frequencies of fang placement at different regions of the prey's body except for fang misses, for which repositioning events significantly outnumbered absence of repositioning. For those strikes in which fang repositioning did occur, the time taken to move the fang to a new site did not differ significantly among the seven fang placement categories (right fang: $F_{6,173} = 0.95$, $P = 0.46$; left fang: $F_{6,173} = 0.65$, $P = 0.69$). Average time from beginning of repositioning to peak protraction was 49 ± 22 ms ($N = 180$).

Prey Distance. As shown in Figure 5, although the incidence of fang repositioning and the distribution of strikes are skewed slightly to shorter distances, there was no significant effect of prey distance on incidence of fang repositioning ($F_{9,376} = 1.76$, $P = 0.08$).

Phylogeny. The subfamilies of vipers do not differ in the timing of most major events or in the relative incidence of fang re-

positioning, which occurs in 56% of viperine strikes and 46% of crotaline strikes. For example, mean time to initiate head movement is 5 ms for both, mean time to first contact with prey is 66 ms for viperines and 75 ms for crotalines ($F_{1,370} = 3.42$, $P = 0.07$), mean time to first fang contact is 79 ms for viperines and 88 ms for crotalines ($F_{1,370} = 3.15$, $P = 0.08$), time from prey contact to initiation of repositioning is 47 ms in viperines and 45 ms in crotalines ($F_{1,184} = 0.65$, $P = 0.42$), and time to peak gape during prey release is 62 ms for both. Viperines initiate labial ($F_{1,361} = 10.2$, $P < 0.01$) and jaw ($F_{1,371} = 14.0$, $P < 0.01$) depression about 10 ms faster than crotalines. The 10-ms difference between viperines and crotalines for early strike events might have some phylogenetic significance, but given relatively small sample sizes of both taxa and individuals, the difference is more likely to reflect a sampling artifact. In those strikes ending in release of prey, viperines have slightly but not significantly longer bite durations (viperines: 175 ± 121 ms; crotalines: 151 ± 108 ms; $F_{1,194} = 1.9$, $P = 0.17$).

Among those genera with sample sizes large enough for comparison, Bonferroni and Student-Newman-Keuls post hoc tests show that only *Trimeresurus* had significantly shorter intervals (15 ± 7 ms) between fang contact and initiation of fang repositioning than three genera with long intervals: *Atropoides* (34 ± 13), *Bitis* (34 ± 12), and *Porthidium* (41 ± 5). The remaining seven genera tested (*Agkistrodon*, *Atheris*, *Crotalus*, *Echis*, *Montivipera*, *Protobothrops*, *Vipera*) did not differ significantly from the other four. On the basis of these figures,



Figure 4. Strike with fang repositioning by a *Crotalus atrox*. In *a*, the snake has already contacted the prey with its lower jaw, and the left fang may be in contact, but the right fang tip is visible. Slight retraction of the right fang in *b* and *c* reveals more of the snake's eye and shows that this fang is not embedded. The snake begins rotating its braincase dorsally and to its left in *d* as the right fang begins protraction that continues in *e* until full protraction and full right gape is reached and the fang is brought down on the surface of the prey in *f*.

the notion that genera characterized by prolonged prey holding or absence of prey release might have slower fang repositioning is not supported.

Anatomy

Fang length relative to mandible length varies from 0.13 to 0.35 among the vipers measured (Table 2). Among the skulls I mea-

sured, the distance of the upper edge of the discharge orifice from the fang tip as a function of fang length (Fig. 7*a*) varied from 0.12 in *Bothrocophias* to 0.51 in *Causus* (see Table 2; Figs. 6*a*, 7*b*, 7*c*), with shorter fangs generally having relatively longer discharge openings. There is a significant inverse correlation between relative fang length and relative distance of the proximal end of the discharge orifice from the fang tip ($r = -0.55$, $P \leq 0.01$, $N = 194$). However, there is no relationship

Table 3: Mean \pm SD times and minimum times for beginning of corrective movements from initial contact with prey and from the time of fang contact for all vipers, subfamilies, and genera

Clade	N	From Prey Contact		From Fang Contact	
		Mean \pm SD	Minimum (N)	Mean \pm SD	Minimum (N)
Viperids	176	43 \pm 16	4 (1)	30 \pm 12	4 (3)
Viperines	66	42 \pm 15	4 (1)	30 \pm 13	4 (1)
Crotalines	110	44 \pm 16	8 (1)	30 \pm 12	4 (2)
Genera:					
<i>Atropoides</i>	28	48 \pm 18	16 (1)	34 \pm 13	12 (1)
<i>Bitis</i>	23	44 \pm 17	16 (2)	34 \pm 13	16 (2)
<i>Crotalus</i>	31	39 \pm 13	12 (1)	29 \pm 10	8 (2)
<i>Montivipera</i>	10	35 \pm 14	4 (1)	25 \pm 11	4 (1)

Note. Sample sizes were 10 or more, based on 250-fps records.

between fang length and fang curvature among the viper skulls tested. Overall, fangs, as extreme structures, display wide variations in relative length, curvature, and the position of the proximal edge of the discharge orifice (Fig. 7). Data for the family as a whole are best fit by a cubic polynomial distribution ($r^2 = 0.314$) that suggests that caudines fall at one extreme of the viper fang morph, having very short fangs with very long discharge orifices extending half way up the fang (Figs. 6a, 7b). The downward curve at the other end of the distribution suggests that in some genera with long fangs (*Lachesis*, *Bitis*), the proximal edge of the discharge orifice is relatively more distal than in other vipers (Fig. 7c). The linear regression for the same data yields an $r^2 = 0.304$. Data for fangs of the genus *Crotalus* come closer to fitting a linear distribution (Fig. 6b).

Discussion

Behavior

The Ubiquity of Fang Repositioning. Fang repositioning occurred in nearly half the strikes recorded at 250 fps and in all of the genera for which more than a few records were obtained. The proportion of strikes in which repositioning occurred is similar among viperines and crotalines and appears to have little relationship to obvious physical features, such as prey distance, that might affect prestrike programming of motor events occurring through contact with the prey. Although proportionately fewer strikes recorded at 60 fps ended in repositioning of fangs, the behavior still commonly occurred. Most importantly, repositioning of fangs also occurred in strikes recorded in the field (Cundall and Beaupre 2001). My data are similar to those of Young et al. (2001b, 2003), who also found relatively high incidences of placement errors and repositioning in predatory strikes to live prey. The widespread but irregular and unpredictable appearance of repositioning among nearly all vipers suggests that the behavior is related to stochastic properties of the strike and intimately linked to aspects of fang function.

Extreme Fangs and Extreme Functions. The extreme length of viper fangs is coupled with the propensity of vipers to prey on

other vertebrates, particularly frogs, lizards, and small mammals (e.g., Greene 1997; Martins et al. 2002). Although somewhat simplified, Figure 8 shows one of the potential problems of using fangs to inject venom into other vertebrates, namely, fang contact with unyielding subcutaneous skeletal elements. This problem is compounded by the nature of the fang and the relationship of the discharge orifice to the fang tip (Fig. 7b). Because the fang functions as a hypodermic needle, its function would be greatly enhanced if the outlet for venom, the discharge orifice, lay at the tip of the fang, as it does in a hypodermic needle. The properties of dentine and enamel and the mode of development of fangs (Bogert 1943; Jackson 2002) evidently prevented this design from ever appearing among vipers. Nevertheless, this aspect of fang design displays considerable variation.

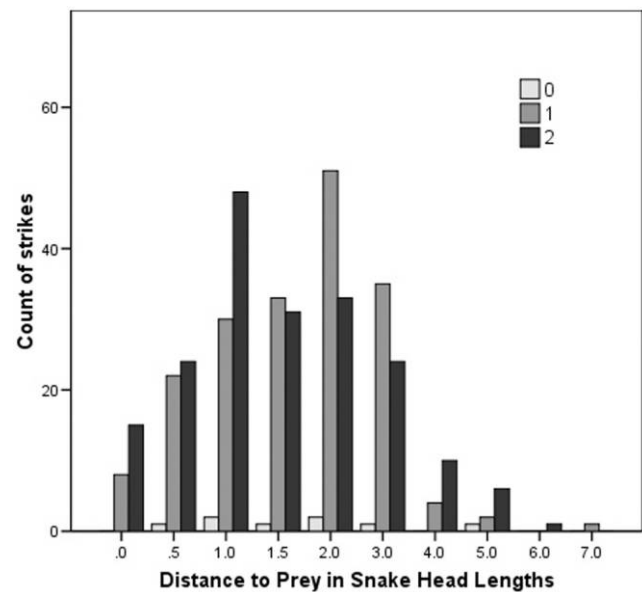


Figure 5. Relative distribution of strikes that missed prey (0), had no repositioning of fangs (1), or had one or both fangs repositioned (2) by distance to prey at the beginning of the strike for all 250-fps records ($N = 386$).

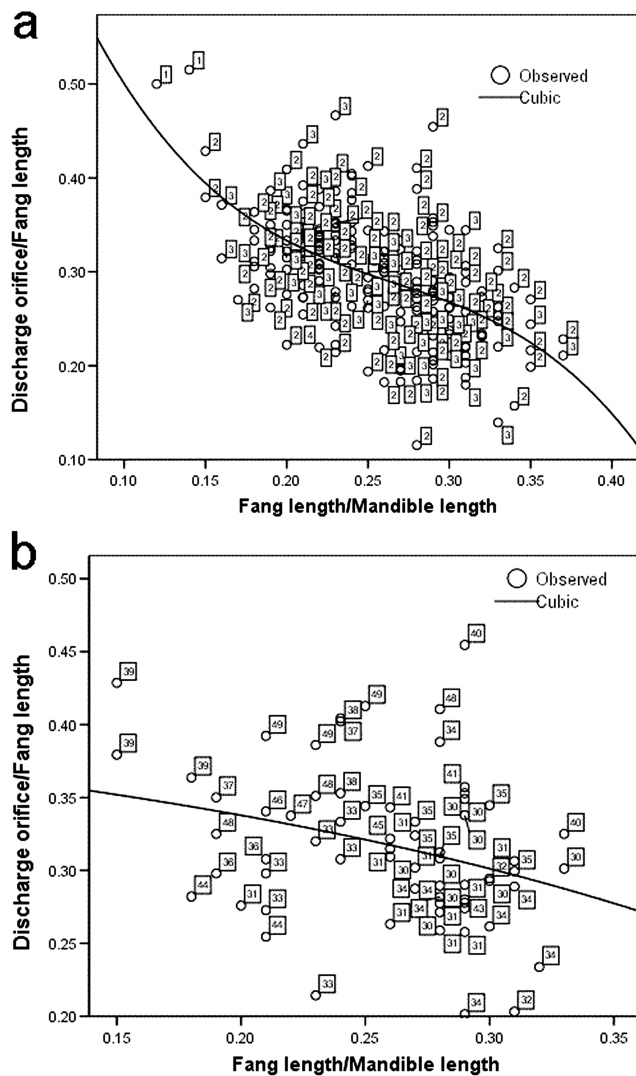


Figure 6. *a*, Relative distance of the proximal edge of the venom discharge orifice from the fang tip compared with relative fang length (as a function of mandible length) in all viper skulls measured. Case numbers: 1 = causers, 2 = crotalines, 3 = viperines, 4 = *Azemiops*. R^2 values are low regardless of which fit is used. For the cubic polynomial fit shown, $R^2 = 0.314$. For the linear regression, $R^2 = 0.304$. *b*, Same fang relationships as in *a* but for species of *Crotalus*. Case numbers: 30 = *C. adamantus*, 31 = *C. atrox*, 32 = *C. basiliscus*, 33 = *C. cerastes*, 34 = *C. durissus*, 35 = *C. horridus*, 36 = *C. lepidus*, 37 = *C. mitchellii*, 38 = *C. oreganus*, 39 = *C. pricei*, 40 = *C. polystictus*, 41 = *C. ruber*, 42 = *C. scutelatus*, 43 = *C. simus*, 44 = *C. tigris*, 45 = *C. tortugensis*, 46 = *C. triseriatus*, 47 = *C. unicolor* (*durissus*), 48 = *C. viridis*, 49 = *C. willardi*.

Klauber (1939) provided measurements for species of *Crotalus* (see his Table 30), showing a range in the relative distance of the proximal edge of the discharge orifice from the fang tip, calculated from his columns (N [length of discharge orifice] + P [length from distal end of discharge orifice to fang tip])/ B [total straight-line fang length], from 0.11 in *Crotalus basiliscus* to 0.49 in *Crotalus triseriatus*—an extraordinary range if the feature is subject to similar selection pressures. My data for

Crotalus species (Fig. 6*b*) do not match the range of Klauber's data but follow their general trend. Jackson (2002) illustrates a developmental series of fangs from a single *Bitis* that shows differences similar to those among different species. Similarly, fang curvature varies considerably, as noted by various authors and both quantified and illustrated by Klauber (1939). Klauber astutely pointed out that more highly curved fangs might function better in slipping the fang under the skin for subcutaneous venom injection, whereas straighter fangs might serve to penetrate the body wall for intraperitoneal venom injection. What is clear from the behavioral data is that no fang is perfectly designed because its point of entry into the prey cannot be determined with sufficient accuracy to prevent periodic encounters such as those shown in Figures 4 and 8.

Vipers have evolved a number of solutions to the problem of fang placement errors. All appear to reflect extreme functions at one level or another. Young et al. (2001*a*, 2001*b*, 2003) showed that venom expulsion from unembedded fangs was rare but that venom was occasionally ejected from fangs as they were withdrawn from prey. Young and Zahn (2001) recorded venom flow in the venom duct both when the ipsilateral fang penetrated and when it did not. Surprisingly, in the latter cases, no venom emerged from the fang, suggesting that flow through the fang is regulated independently of flow from the venom gland, supporting the hypothesis of a critical intermediate reservoir (Young and Kardong 2007) and the role of peripheral resistance in venom flow (Young et al. 2002, 2003). Further, the fact that venom is typically not ejected from an unembedded fang when the contralateral fang is embedded shows that although all events through early mouth closing are likely to be feed-forward ones, unilateral regulation of venom expulsion may not be a function of gland constrictor muscles but of

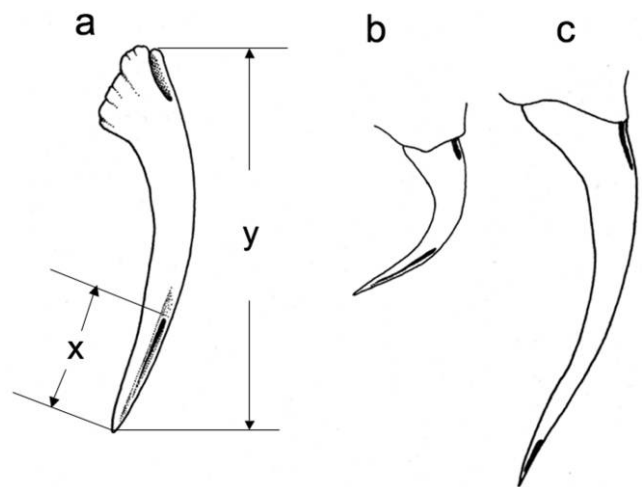


Figure 7. Viper fangs, showing (*a*) a fang from *Agkistrodon piscivorus* for which the measures for length of the proximal edge of the discharge orifice from the fang tip (x) and total length of the fang (y) are indicated. Variants in relative position of the discharge orifice and curvature of the fang are shown in *b* (characteristic of some *Causus* and *Vipera*) and *c* (characteristic of some *Bothrocophias*, *Lachesis*, *Bitis*, and *Crotalus*).

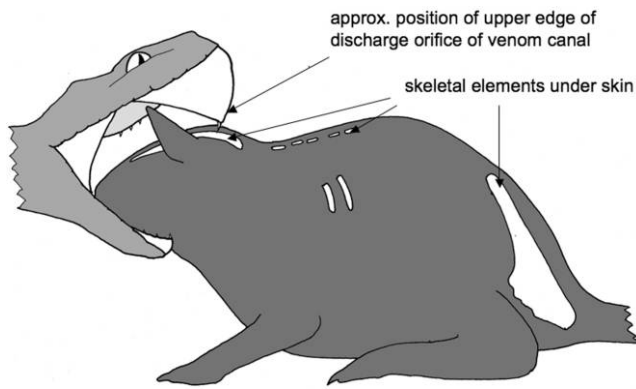


Figure 8. Model of fang-prey interactions at the point of fang contact. The stochastic nature of the strike results from the distribution of skeletal parts in the prey relative to the distance of the upper edge of the venom discharge orifice from the tip of the fang. The critical contribution of the fang sheath as a penetration detector is evident here, as it is in Figures 1 and 4.

peripheral regulators of venom flow lying somewhere between the duct and the discharge orifice of the fang. My data agree with all previous work in suggesting that venom expulsion begins only after fang entry.

Combining the critical flow data from Young and Zahn (2001) with all the other morphological and kinematic data produced by Young and colleagues (Young et al. 2000, 2001a, 2001b, 2002; Young and Morain 2003; Young and Kardong 2007) provides compelling support for the hypothesis that venom expulsion results from the fang sheath sliding upward (unplugging the discharge orifice) combined with entry of the discharge orifice into prey tissues having hydrostatic pressures lower than those in the venom duct and venom canal. The possible dependence of venom injection on sensory feedback may underlie the relatively long duration of the bite phase. Similarly, the repositioning movement of an unembedded fang or of one that has hit bone near the prey's skin surface can begin 8–20 ms after fang contact. The behavioral data suggest that sensory information used to cue fang movement arises from a number of sources, including the fang sheath.

Rapid Behaviors. The capacity for rapid responses to environmental irregularities must be a feature of most animal motor systems. However, most reflexes operate within physiological limits imposed by nerves and muscles and their particular functional constraints (Rome and Lindstedt 1997). Although some feeding movements are remarkably fast (e.g., Grobecker and Pietsch 1979; Alfaro and Herrel 2001; Alfaro 2002, 2003; Smith et al. 2002), most of these are feed-forward processes in which much of the sensory and motor processing was done tens or hundreds of milliseconds before the actual mechanical (kinematic) event (e.g., Deban and Dicke 1999, 2004). Kinematic responses of guinea fowl to hidden perturbations (a decrease in elevation of 8.5 cm concealed by tissue paper) on a runway during bipedal running (Daley and Biewener 2006) reveal some of the time constraints on a locomotion apparatus. In most

trials, the birds adjusted their stride by continued extension of the foot, resulting in minimal fall of the center of gravity of the body. However, when allowed visual recognition of the 8.5-cm drop, the birds stumbled, stopped, or fell in almost half the trials (Daley et al. 2006).

In a sense, the fang-repositioning problem is similar to a perturbation experiment in which the primary senses can play no or little role in the muscles' responses. The snake is dependent on some type of sensory feedback at the moment of fang entry because the precise position of the fang at penetration cannot be accurately predicted. In contrast to the guinea fowl running experiments, however, the snake cannot simply extend its fang movement pattern. If repositioning is needed, the snake must reverse a motor program that is in the process of closing the mouth and retracting the fangs. It is this aspect of the problem that suggests physiological capabilities temporally outside those of "normal" reflexes of the feeding apparatus. In humans, reflexive contraction of the masseter to prevent jaw drop during walking, running, or jumping takes approximately 40 ms after the initial movement of the jaw that stretches the masseter (Miles et al. 2003). Most of the delay occurs at the masseter (electromechanical coupling) following arrival of the signal at the motor endplate. Snakes are theoretically subject to similar constraints. Thus, the ability of some vipers to activate visible repositioning movement of the fangs within 12–20 ms (a conservative estimate) is a puzzle that cannot be accounted for by the shorter distances that information has to travel.

Missed Strikes

Two elements of mouth-closing behavior illustrate the complexity of the strike-motor program and the speed of reflexive movements that must be keyed to particular sensory events. Closing the mouth in swallowing is typically initiated by pterygoideus and lateral mandibular adductor activity (Cundall and Gans 1979), and in strikes that contact the prey, activation of essentially the same combined patterns of contraction must occur inasmuch as unilateral strikes are uniformly characterized by retraction of the unembedded fang, regardless of whether the mandible of that side contacts the prey. What this means is that the left and right pterygoideus muscles must fire synchronously, or close to it, during strikes that contact the prey. Sensory feedback from an unembedded fang in this situation can arise either from the fang sheath or from pterygoideus spindle or tendon organs.

However, in strikes that miss the prey completely, the fangs remain erect despite closing of the mouth. The only way this can occur is if the lateral adductors fire independently of the pterygoideus muscles because the latter cannot be contracting if the fangs remain erect (Cundall 1983). The data strongly suggest that pterygoideus activity during closing after prey contact is initiated by sensory feedback, and given the time frame of fang retraction, the logical sources of the sensory feedback lie either in the mouth lining, including the fang sheath, or in pterygoideus spindles and tendon organs.

The Fang Sheath

One reason for thinking that critical sensory feedback arises from the fang sheath is that fang contact without penetration, which might stimulate both tendon and spindle organs, rarely leads to fang retraction or venom ejection but frequently leads to repositioning.

However, when a fang hits bone before the discharge orifice is driven below the skin, is information from spindle and tendon organs integrated with that from fang sheath receptors? And what exactly are the fang sheath receptors? Given the extraordinary level of control that some vipers have over venom expulsion (Young et al. 2000, 2001a, 2003), it seems probable that the sheath is a critical receptor of information about fang penetration levels as well as possibly mediating venom flow (Young and Kardong 2007). We currently know too little of the neuroanatomy of this complex system to formulate decent hypotheses.

Behavior of Zoo Animals

Available evidence shows that the strike kinematics of long-term captives does not differ from the kinematics of individuals of the same species that had never experienced captivity and were recorded in the field (Cundall and Beaupre 2001). Captivity and captive propagation also appear to have no detectable effects on other aspects of predatory behavior, such as tongue flicking and strike-induced chemosensory searching (Chiszar et al. 1993). Given the nature of the problem, there are few alternatives to studying captive animals. My experience suggests that snakes are now maintained in many zoos under feeding regimes approximating natural conditions, a result due partly to productive interactions between academics and zoo professionals (Murphy 2007). However, captive vipers are rarely given prey they would normally take in the field. The long-term effects of captive feeding regimes and captive propagation on complex behaviors such as viper striking remain untested.

Anatomy

Vipers vary considerably in skull form (e.g., Dullemeijer 1959; Gloyd and Conant 1990; Campbell and Lamar 2004) and overall body proportions (Klauber 1938; Pough and Groves 1983) but share one functional characteristic: extraordinary maxillary rotation. Evolution might have acted to optimize the structural aspects of the fang and those parts of the skull critical to its movement, stabilizing linkage and fang design. Alternately, constraints imposed by the nature of materials and selection pressures arising from striking mechanics and the nature of prey may have driven divergent patterns of fang and skull form, potentially resulting in different linkage dynamics and fang behavior. Regardless of structural variations, however, the data given here suggest that most, perhaps all, vipers are constrained by prey variables that have driven a physiological solution that we can view either as superseding morphological solutions to unpredictability or as allowing morphological variations to con-

fer some functional advantages when envenomating specific kinds of prey. The methods used here and our limited knowledge of how most viper species envenomate prey in the field makes this latter possibility currently untestable. However, the extraordinary variation in fang form suggests that except at the extremes of the range, fang variations are accommodated by a physiological adaptation that permits rapid repositioning of fangs. Extremely long fangs challenge fang movement mechanics, and it may be this functional limitation that drove selection for more distal positioning of the discharge orifice.

Variations in fang form are similar to those seen in some other extreme forms, such as the canines of nimravid and felid sabertooth cats (Van Valkenburgh 2007) or the jaw forms of butterfly fish (Ferry-Graham et al. 2001). Whereas the use of canines in sabertooth cats remains unknown, the long-jawed extreme in butterfly fish allows greater jaw protrusion, which correlates with selection of more elusive prey. It seems possible that fang variation in vipers is similarly correlated to natural-history features. These will be difficult to unravel without natural-history data combined with laboratory records of feeding of different viper species on prey usually taken by those species. More data ultimately may reveal phylogenetic trends that can be related quantitatively to natural history or function, but none are obvious at the moment.

Linking the anatomical and functional analyses suggests another interpretation. Because virtually all clades repositioned fangs during some strikes, vipers may be examples of an evolutionary strategy in which an extreme structure—the fang and its associated support, linkage, and movement apparatus—all work as long as all parts fall within some finite limits. The critical limits to variation are not in form but in function. To function effectively, the “working” part of the system is primarily constrained by time, namely, the time taken to immobilize prey. As time to immobilize prey decreases, so does the probability that prey held in the mouth can damage the snake (Rowe and Owings 1990) or that prey released can move far from the snake (Hayes et al. 2002). It is this aspect of the system that appears to have generated the greatest selection pressures and to have experienced the greatest evolutionary modification. I suggest it has done so partly through structural and physiological mechanisms associated with transferring information from the fang to its control muscles. Although a key element of this problem is obviously the evolution of venom efficacy (e.g., Fry and Wüster 2004; Mackessy and Baxter 2006), the other part of the time-constraining process is injecting the venom into the prey. For vipers striking at relatively large and potentially dangerous prey, rapid achievement of effective fang placement underlies successful envenomation.

Summary

The viper strike cannot be viewed as stereotyped or preprogrammed. It cannot be stereotyped or preprogrammed because living prey, considered at structural and behavioral levels, generate stochastic events. Regardless of its aim, the snake cannot know exactly where each fang will hit until its fangs make

contact with the prey. Thus, although the terminal part of the extension phase may be preprogrammed, the strike as a whole cannot be. Our drive to generalize has misrepresented a fundamental feature of the viper strike, namely its ability to adjust to the stochastic nature of driving a venom-injecting tooth into a living, moving animal.

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