

The functional morphology of hooding in cobras

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SUMMARY

Many snakes, particularly cobras, form as part of a defensive display, a hood, an active lateral expansion of their neck skin and underlying musculature and ribs. We identified muscle groups possibly involved in hooding based on their attachments on the specialized ribs of the neck. We then used a combination of morphology, kinematic analysis, morphometrics, electromyography and muscle stimulation to test hypotheses about the functional basis of hooding. We confirmed that hood protraction and erection is an active process that begins cranially and extends caudally, often in stages, through the combined action of several sets of muscles. One set of axial muscles (levator costae and supracostalis lateralis superior) coursing along a line of action to rib displacement are the prime erectors acting to lift the hood. However, a second set of muscles connecting ribs to skin primarily keep the skin taut, rather than to displace the ribs relative to the vertebrae. A third set of muscles coursing between ribs function primarily to transmit forces between adjacent ribs rather than to move ribs. The maintenance of the erect hood requires continued muscle activity. Hood relaxation is due to both active muscle contraction of a fourth set of axial muscles and to passive recoil events in the costovertebral ligaments. The shape of the fully erect hood is reflective of the morphometrics of the underlying ribs, while the duration and kinematics of hood erection and relaxation are related to the behavioral context of the display.

Key words: biomechanics, kinematics, snake.

INTRODUCTION

One of the most dramatic visual displays in snakes is hooding, wherein a length of the neck is flared laterally and compressed dorsoventrally, sometimes displaying distinctive surface patterns. In cobras, the prevalence of this behavior is widely discussed and illustrated in both technical and popular works. Given this, it is somewhat surprising that the functional basis of this behavior has never been detailed. The only study specifically addressing hooding was that of Russell and Home (Russell and Home, 1804), which concluded that, ‘The mechanism by which the Cobra de Capello...expands the skin of the neck...consists intirely of muscles.’ This early work was cited by some of the more influential treatise on snakes (e.g. Wall, 1921; FitzSimons, 1962) but most references to hooding simply assert that it is due to a displacement of the ribs.

Reviews of the vertebrae and ribs (Hoffstetter and Gasc, 1969) and axial muscle (Gasc, 1981) have not explored the functional basis of hooding. The axial musculature of snakes has been detailed by several workers (e.g. Auffenberg, 1962; Gasc, 1981) including Mosauer who described the axial musculature of many species including two cobras (Mosauer, 1935). None of these studies explored regional differences between the trunk and neck regions. The musculature of the neck region of *Vipera aspis* was detailed by Kramer (Kramer, 1977), and Ruben (Ruben, 1977) described general functional correlates with cervical morphology. Pregill offered a detailed description of the neck musculature of *Coluber constrictor* and explored the myological specializations associated with the first few ribs, and the general differences between the neck and the remainder of the body (Pregill, 1977).

Given these earlier descriptions, and general accuracy we found in these earlier anatomical descriptions, this contribution will not detail the morphology of the neck and or hood region. Rather our

purpose is to offer experimental evidence to establish the functional basis of hooding in cobras.

MATERIALS AND METHODS

Live animals

The six adult [snout–vent length (SVL) 1–1.5 m] cobras used for this study were obtained commercially (Glades Herp, Bushnell, FL, USA) and included three Egyptian (*Naja haje* Linnaeus 1758) and three Monocled (*Naja kaouthia* Lesson 1831) cobras. These snakes were maintained in individual terraria at temperatures of 27–31°C, with a 12 h:12 h light cycle, water *ad libitum* and a diet of pre-killed rodents. All maintenance and experimental use of these animals followed humane guidelines for reptiles and particularly for venomous snakes (Gans and Taub, 1964) (http://www.research.fsu.edu/acuc/policies_Guidelines/ASIH_HA_CC_GuidelinesAmphibians.pdf), and was approved by the Washburn University IACUC.

Imaging

Individual cobras were placed on a table and the hooding kinematics were recorded using a TRV608 video camera (Sony, Tokyo, Japan) and a TroubleShooter 500S high-speed digital video camera (Fastec Imaging, San Diego, CA, USA) filming at 250 frames s⁻¹. One individual of each species was placed in a Plexiglas tube of adequate diameter to permit unencumbered hooding. The tubed snake was radiographed in the relaxed and hooded posture (and from both the dorsoventral and lateral perspective) using a General Electric MSI 850 unit (using Kodak T-mat L film exposed at 45 kV and 400 MA for 0.01 s; Fairfield, CT, USA). Following the functional analyses (see below) costovertebral joints from the hood and mid-trunk region were removed from euthanized specimens of each species and skeletonized using bacterial maceration. The cleaned

bones were dried, sputter coated with 15 Å of gold and the opposing articular surfaces were examined using a Hitachi S-570 scanning electron microscope (Lawrenceville, GA, USA). Upon completion of the functional analyses one individual of *N. haje* was euthanized, the viscera removed and the specimen posed in a hooding posture. The individual was pinned in this position and then fixed using 10% neutral buffered formalin (NBF). After fixation, the cobra was preserved in 70% ethanol and shipped to DigiMorph at the University of Texas at Austin where it was coated in lithium carbonate and scanned using high-resolution X-ray Computed Tomography (976 slices, each 0.1807 mm thick, with an interslice spacing of 0.1807 and a field resolution of 83 μm). This provided direct visual illustration of the underlying rib placement supporting the extended hood.

Histology

Following completion of the functional analyses (see below), blocks of tissue were removed from euthanized individuals of each species. Each block included two complete vertebrae and all surrounding tissue including the proximal quarter of the associated ribs; for comparison, similar tissue blocks were taken posterior to the hood from the mid-trunk region. The blocks were fixed in 10% NBF, decalcified in Cal-Ex (Fisher, Pittsburg, PA, USA), dehydrated through an ethanol series and Hemo-De (Fisher), and then embedded in Paraplast (Fisher). Each region was sectioned in both the frontal and transverse planes at 10 μm. Mounted sections were stained with Hematoxylin and Eosin, Milligan's trichrome and Verhoff's elastin stain. Staining procedures followed Humason (Humason, 1979) and Luna (Luna, 1968).

Rib morphometrics

Wall (Wall, 1921), and subsequent workers, have noted how the body shape changes during hooding. To quantify this we examined three preserved specimens of *N. kaouthia* (SVL=85, 91 and 102 cm). From each specimen the first 20 anterior ribs were removed as were 20 consecutive ribs centered at the mid-body. Each rib was manually stripped of muscle and air-dried. Once dried, the ribs were positioned in the same orientation on graph paper, and digital calipers (Mitutoyo 500-322, Aurora, IL, USA) were used to measure the span (proximal-to-distal tip) and the height (maximum perpendicular distance between the span and the body of the rib) of each rib. To eliminate artifacts due to size differences, mean span and height values were calculated for the 20 mid-body ribs (no individual rib varied from this mean by more than 5%), and we used these mean values as the basis for comparison with the ribs from the hood region.

Functional analyses

Four functional hypotheses were proposed guided by morphological dissection of the costal musculature with particular attention to the muscles' lines of action and by the observed displacement of the ribs during hooding (see below). The musculature acting on the ribs can be divided into four general groups (Fig. 1): muscles running between the rib tips and the skin, muscles running from rib to rib, muscles originating on vertebrae cranial to the rib of insertion (presumptive rib protractors), and muscles originating on vertebrae caudal to the rib of insertion (presumptive rib retractors). There are other muscles coursing between the ribs and the skin but none of these have a line of action that could produce the rib displacements observed during hooding (Fig. 2).

Hypothesis 1: our first functional hypothesis is that the rib-to-skin muscles act to move the skin along with the ribs, not erect the ribs. To test this hypothesis we experimented on three rib-to-skin

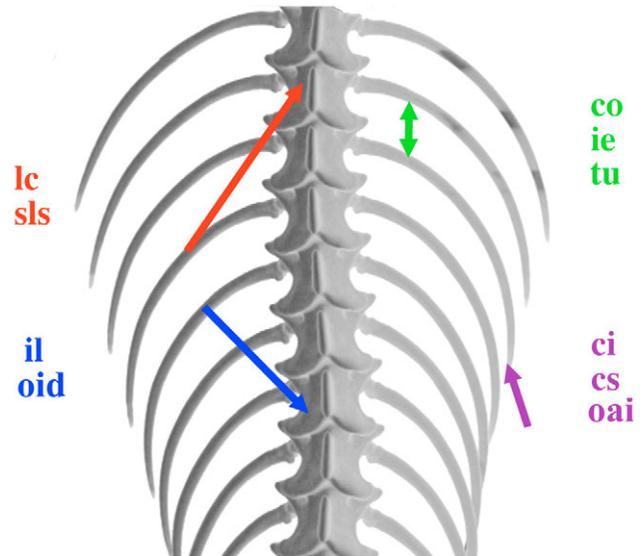


Fig. 1. The four general groups of costal muscles indicated diagrammatically. Red – hood erectors; blue – hood retractors; green – muscles spanning from rib to rib; purple – muscles spanning from the ribs to the skin. Muscle abbreviations: ci – costocutaneus inferior; co – costovertebrocostalis; cs – costocutaneus superior; ie – intercostalis externus; il – iliocostalis; lc – levator costae; oai – obliquus abdominus internus; oid – obliquus internus pars dorsalis; sls – supracostalis lateralis superior; tu – tuberculocostalis.

muscles: costocutaneus inferior (ci), costocutaneus superior (cs) and obliquus abdominus internus (oai) (Figs 1 and 2).

Hypothesis 2: the muscles coursing from rib to rib are incapable of producing rib erection; our second functional hypothesis is that the rib-to-rib muscles act to transmit forces acting on the cranial ribs to the more caudal ribs. To test this hypothesis, we experimentally tested three rib-to-rib muscles: costovertebrocostalis (co), intercostalis externus (ie) and tuberculocostalis (tu) (Figs 1 and 2).

Hypothesis 3: our third functional hypothesis relates to two of the presumptive rib protractor muscles, the levator costae (lc) and the supracostalis lateralis superior (sls). These two muscles have a line of action corresponding to the rib displacements observed during hooding, and therefore we hypothesize that they function in hood erection.

Hypothesis 4: finally, our fourth functional hypothesis concerns two of the presumptive rib retractor muscles, the iliocostalis (il) and obliquus internus pars dorsalis (oid). These two muscles span the caudal surface of the costovertebral joint and have lines of action that correspond to the displacement of the ribs during hood relaxation; accordingly we hypothesize that these two muscles function to relax or retract the hood. These specified functional hypotheses, and the possible roles of other costal musculature, were tested electromyographically during hood erection and relaxation.

Electromyography (EMG) was performed on all six individual cobras. The cobras were anesthetized with isoflurane, and small incisions were made on the dorsal and lateral surface of the neck in the region of the hood. Bipolar EMG leads, 2 m in length, were constructed from 0.05 mm-diameter stainless steel wire with nylon insulation (California Fine Wire, Grover Beach, CA, USA). Hypodermic needles were used to implant the leads ipsilaterally using a binocular dissecting microscope (Nikon, Melville, NY, USA); all implantation sites spanned a maximum of three vertebrae.

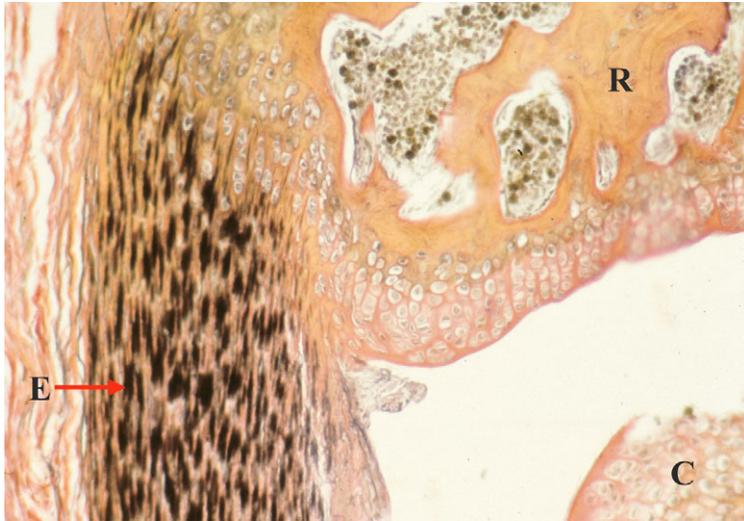


Fig. 4. Verhoeff's elasin-stained frontal section through the costovertebral joint. Note the abundance of elastin (E) in the ligament spanning the caudoventral surface between the rib (R) and vertebra (C).

depended upon individual cobra 'motivation' making the length of the hood phase quite variable and therefore making quantification of EMG durations impractical.

Following the EMG analyses the cobras were re-anesthetized. The EMG leads were again checked for placement, then removed and the same muscles exposed on the contralateral side (where the magneto-restrictive sensor was anchored). With the snakes under anesthesia the functional role of each muscle was confirmed using a custom-fabricated microstimulator to apply stimulation (generated by a GRASS S88 stimulator) to the surface of each muscle. The hood was manually placed in varying postures (i.e. relaxed, fully erect), and the impact of the muscle contraction documented through the output of the magneto-restrictive sensor. Upon completion of the stimulation trials the specimens were either euthanized for anatomical analyses (see above) or allowed to recover from the anesthesia and returned to home cages. Muscle nomenclature follows Gasc (Gasc, 1981) with the addition of oai from Mosaur (Mosaur, 1935). Developmentally, the snake neck represents a forward extension of the thorax (Cohn and Tickle, 1999). However, anatomically the anterior axial column exhibits distinct morphological features of a neck, especially in its musculature (Kardong, 1980; Pregill, 1977) and atlas-axis complex (Romer, 1976), providing us with the use of the term 'neck' to identify this anatomically distinctive region of the anterior snake axial column.

RESULTS

Morphology of the costovertebral joint

In the cranial portion of the hood, the entire articular surface of the rib is concave (Fig. 3A). A second, convex, articular surface expands in size with each successive rib of the hood (Fig. 3B). The diapophyses of the vertebrae in the cranial portion of the hood project laterally beyond the centrum and support a convex articular surface (Fig. 3C). Three trends are evident in the diapophyses along the length of the hood from anterior to posterior: (1) the extent of lateral projection is reduced; (2) the convexity of the articular surface becomes less pronounced; and (3) a second, concave, articular surface enlarges (Fig. 3D). All of the articular surfaces of the costovertebral joint are covered with hyaline cartilage. Two ligaments span the costovertebral joint, one on the craniodorsal surface and a larger one on the caudoventral surface. The ligament spanning the caudoventral surface of the joint includes an abundance of elastic connective tissue (Fig. 4).

Rib morphometrics

The first rib is borne on the 2nd vertebra caudal to the axis; it is the smallest of the anterior ribs having a span and height that is 53% and 22%, respectively, of the mean mid-trunk values. Successive ribs increase in span until the 7th or 8th rib that reaches a maximum span slightly greater (108%) than the mean mid-trunk value (Fig. 5). Caudal ribs of the hood gradually decrease in span until around the 19th rib (which has a mean span of 87% of the mid-trunk value) after which the ribs gradually increase to the mid-trunk value. Rib height increases rapidly from the 1st to the 4th rib, then more slowly to the 10th rib, which has a height equal to 79% of the mid-trunk value (Fig. 5). Little change in rib height is evident

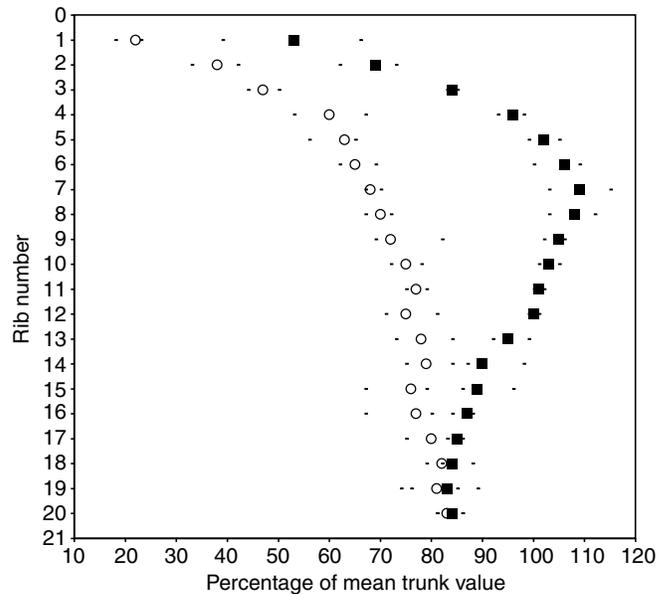


Fig. 5. Morphometrics of the ribs in the region of the hood. Note that rib span (filled squares) shows a distinct pattern through the hood, while rib height (open circles) changes more gradually over the course of the hood. Values given are the mean values from three specimens (expressed as the percentage of the respective mean trunk values) with the range indicated by the dashed marks.

between the 10th and 20th ribs of the hood, all of which are approximately 80% of the mean mid-trunk height.

Displacement of the ribs during hooding

Comparing radiographs of cobras in the relaxed and hooded posture reveals that erection of the hood is accomplished by rotation of the ribs in both the frontal and transverse planes (Fig. 6). These rotations displace the distal tip of the ribs cranially (protraction) and dorsally (elevation); the angular magnitudes of these displacements are greatest in the cranial portion of the hood and decrease throughout the length of the hood. As the rib rotates in the transverse plane, the head of the rib displaces dorsally on the parapophysis (Fig. 7).

The video records revealed the temporal pattern of hooding to be highly variable. The expansion of the hood always begins cranially then spreads caudally. Often hood erection and relaxation occur in stages; the hood can be maintained in a partially erect or partially relaxed stage for extended periods (>10 min). Similarly, the hood can be maintained in a fully erect position for long periods; the tendency to maintain the erect hood is highly dependent on the visual stimulus provided but may be influenced by intra- and inter-specific variation. Analysis of the video records suggests that the hood can be fully erected in approximately 80 ms. Hood relaxation, which proceeded in the reverse order from hood erection, typically was a slower process lasting several minutes.

Electromyography

Electrical activity patterns, synchronized to videographic records of hood displacement, were recorded from every muscle examined in this study (Fig. 8). When the results from all of the EMG studies are integrated there is a clear temporal pattern. Bursts are recorded in the sls and lc shortly before erection of the hood (Fig. 9). Lower level electrical activity continues in these two muscles throughout the duration of hooding, and in the case of the sls, into the early portions of hood relaxation.

Concurrent with, or slightly (~25 ms) subsequent to, the initial displacement of the cranial ribs, low level electrical activity was recorded in the oai and costocutaneous (ci and cs). These muscles remained active – although at low levels and with occasional gaps of inactivity – as long as the ribs were expanded (Fig. 9). The co, ie and tu – all of which span from rib to rib – were active concurrent with rib displacement. Activity within the tu continued throughout hood relaxation (although at a reduced level) whereas activity in the other two muscles generally terminated once the hood was fully erect (Fig. 9).

The onset of hood relaxation is marked by the onset of electrical activation in the il and the oid (Fig. 9). This electrical activity begins at a low level but generally increases in amplitude when the hood is actively reducing in size. There was typically a bit of a temporal offset between these two muscles with both the onset and termination of the il delayed relative to the oid.

Muscle stimulation

Stimulation of the most cranial sls produced marked protraction and slight elevation in the first few cranial ribs (the exact number of ribs displaced depended on the site of muscle stimulation); stimulating the sls in more posterior portions of the hood produced less rib displacement (Fig. 10). Strong contraction in the cranial sls was enough to cause displacement in more caudal ribs but this displacement was not equivalent to that observed during true hooding. Stimulation of the lc produced elevation and slight protraction of the rib; the influence of this muscle appeared to be consistent throughout the length of the hood and – as with the sls

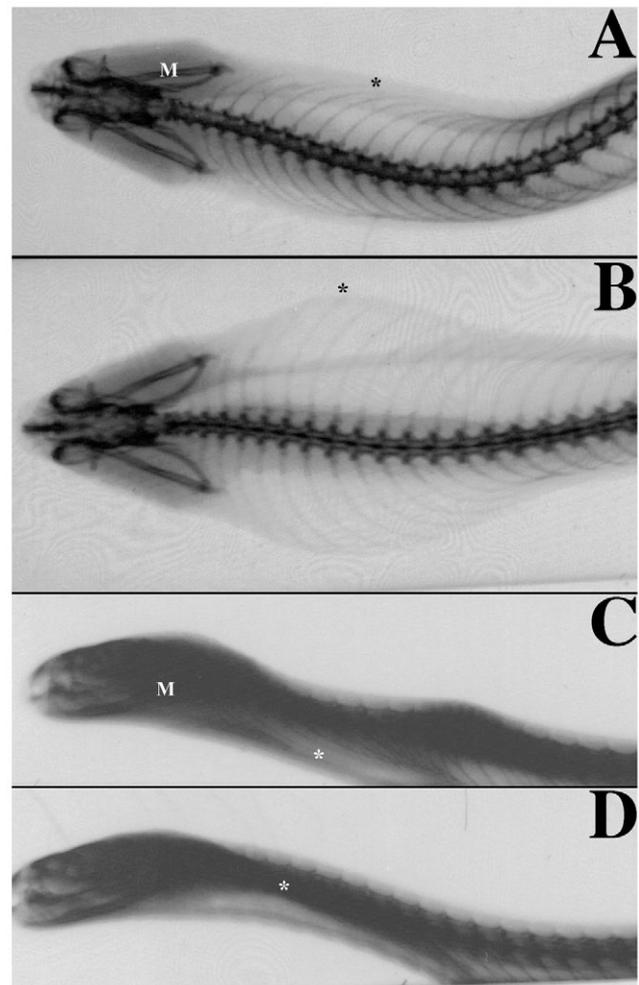


Fig. 6. Radiographs of *Naja kaouthia* in the relaxed (A,C) and hooded (B,D) posture showing the cranial and dorsal displacement of the ribs during hooding. The distal tip of the 6th rib has been marked by an asterisk (*) in each figure. M – mandible.

– when stimulated separately was incapable of producing a ‘typical’ hood.

Stimulation of the costocutaneous (ci or cs) and tu produced only modest displacements involving a slight shift and buckling of the scapulation and adduction of the adjacent ribs (respectively). Isolated stimulation of the il produced modest retraction of the corresponding rib. Stimulation of the oid resulted in distinct retraction of the rib and slight depression; as with the other separate muscle stimulations, these separate stimulations did not produce complete hood relaxation.

DISCUSSION

Functional morphology of hooding

The functional hypotheses were tested through a combination of EMG and muscle stimulation. We hypothesized that the muscles connecting the ribs to the skin [cs, ci and oai] function primarily to keep the skin taut, rather than to displace the ribs relative to the vertebrae. Experimental results corroborate this. Stimulation of these muscles caused limited superficial deformation of the skin but no noticeable deflection of the ribs. Further, the muscle activity patterns of three of these muscles (ci, cs and oai; see Fig. 9) do not



Fig. 7. Computed tomography (CT) image of *Naja haje* in the hooded posture; note how the ribs in the region of the hood are displaced dorsally on the parapophyses relative to those in the trunk region. From Kardong (Kardong, 2009); Digital Morphology, at http://digimorph.org/specimens/Naja_haje.

coincide with either hood erection or relaxation. Rather, the electrical activity is concentrated during the time when the hood is erect. This activity pattern is somewhat surprising for the *cs*, which shows morphological specializations in the cranial portion of the hood (covering the first four scutes). Since rib displacement begins in this region, tensile forces on the skin may be most important (in terms of coordinating erection of the entire hood). The signals recorded from these muscles were complicated by the fact that the cobras almost always hood while lifting the anterior portion of the trunk off of the substrate, sometimes in a nearly vertical orientation. As such, some of the muscle activity we observed may be associated with this change in posture rather than with hooding *per se*.

We hypothesized second that the muscles coursing between the ribs [*co*, *ie* and *tu*] function primarily to transmit forces between adjacent ribs, rather than to move the ribs relative to the vertebrae. This hypothesis was supported by the stimulation experiments (during which the intercostals gap was reduced, rather than the ribs displaced relative to the vertebrae) and by the electrical activity recorded from the *co*, *ie* and *tu*. The activity pattern of each muscle revealed that low-level activity might begin before hood erection, the maximum activity only occurred after the initiation of rib displacement (Fig. 9). These results may oversimplify the functional role of the *co*. This muscle originates as two heads; a medial head covering much of the ventral surface of the vertebra and the costovertebral joint, and a lateral head that originates on the proximal end of the rib (near the tubercle). Thus, one portion of this muscle spans the costovertebral joint, while the other portion does not. Only the lateral head of this muscle was implanted with electrodes during the current experiments.

The third hypothesis that the *lc* and *sls* are responsible for hood erection was supported by the muscle stimulation experiments during which stimulation of these muscles caused rib displacements similar to those observed during hooding. The electrical activity pattern of

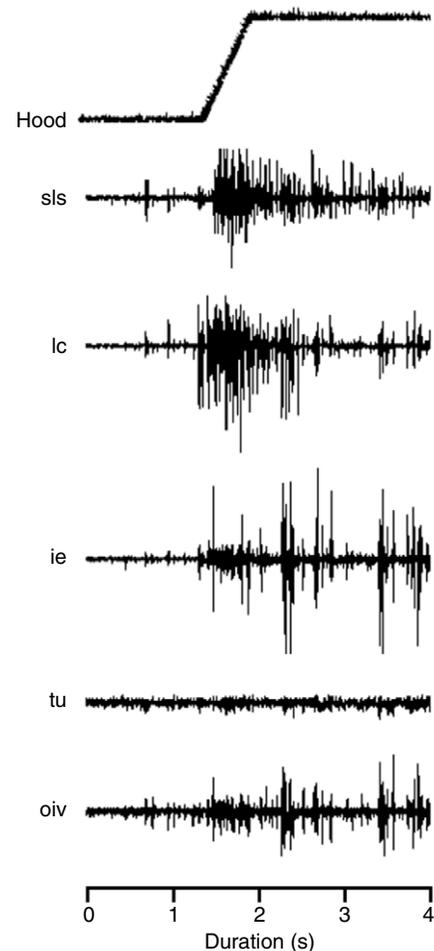


Fig. 8. Data traces from one of the experimental trials showing the expansion of the hood (upper trace, recorded from the SPREG chip) synchronized with electrical activity of some of the costal muscles. Muscle abbreviations: *ie* – intercostalis externus; *lc* – levator costae; *oiv* – obliquus internus pars ventralis; *sls* – supracostalis lateralis superior; *tu* – tuberculocostalis.

these muscles (Fig. 9) also supported this hypothesis in that both muscles were active shortly before the onset of rib displacement and remained active throughout the maintenance of the erect hood. While other muscles may also contribute to the erection of the hood, the lever arms, activity patterns and regional morphological specializations of these two muscles (see below) suggest that they are the primary effectors of hood erection.

The fourth hypothesized function, the bases for hood relaxation, was more difficult to test; in part this was due to the greater levels of temporal and spatial variation present in hood relaxation (when compared with hood erection) and in part because we did not quantify the relative contribution of elastic recoil. Nevertheless, the two costal muscles with lever arms most in line with the displacements of the ribs during hood relaxation – *il* and *oid* – both had an onset of electrical activity shortly before hood relaxation and some electrical activity during relaxation (Fig. 9). Electrical stimulation of these muscles produced rib displacements similar to those observed during hood relaxation.

Collectively, our results suggest the following model for hooding in cobras (Fig. 11). Hood erection begins with the contraction of the cranial-most *sls* and *lc*. The most cranial of these muscles have

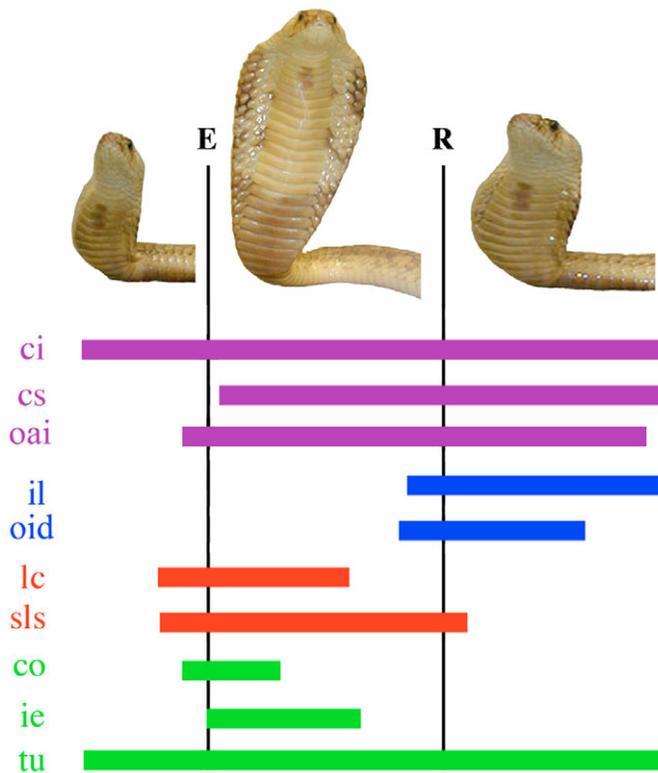


Fig. 9. Summary of the electromyography (EMG) results showing the electrical activity patterns superimposed on a generalized depiction of hood erection (E), hood maintenance and hood relaxation (R). Color coding as in Fig. 1. Muscle abbreviations: ci – costocutaneous inferior; co – costovertebrocostalis; cs – costocutaneous superior; ie – intercostalis externus; il – iliocostalis; lc – levator costae; oai – obliquus abdominus internus; oid – obliquus internus pars dorsalis; sls – supracostalis lateralis superior; tu – tuberculocostalis.

specialized origins (both more dorsal and more robust) and specialized insertions (covering the entire cranial and lateral surfaces of the first ribs). The contraction of these two muscles simultaneously elevates and protracts the ribs; the forces acting on the ribs are strong enough that the articular facet is displaced dorsally at the costovertebral joint (see Hoffstetter, 1939). The displacement of the rib stretches the elastic ligament that courses over the caudoventral surface of the costovertebral joint (Fig. 11). Once displacement of the anterior ribs begins, the intercostal muscles (including co, ie and tu) contract to assist in the displacement of the more posterior ribs, and the costocutaneous (cs and ci) and oai muscles contract to keep the skin relatively taut across the hood.

In many hooding episodes the cobra stops at the early stage of hooding and only presents a 'partial' hood. To fully spread the hood, the sls and lc that insert on the more posterior ribs of the hood are contracted. The force generated, coupled with the ongoing contraction of the other muscles, is adequate to fully protract and elevate all of the ribs of the hood. The combined displacements of the ribs rotate the distal ends of the ribs laterally (producing the flared expansion of the hood) as well as dorsally (which dorsoventrally compresses the region of the hood). The movements of the ribs, coupled with the contractions of the cs, spread the dorsal and lateral scalation leading to prominent visual displays in many cobra species (e.g. Wall, 1921). The hood can be maintained in the erect posture through sustained contraction of the sls and lc; the

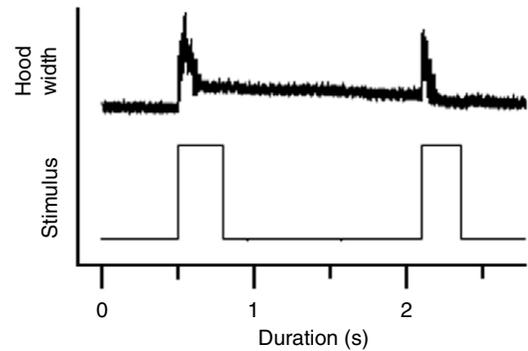


Fig. 10. Results of one of the muscle stimulation trials on supracostalis lateralis superior (sls) stimulation of the muscle (bottom trace) resulted in expansion of the hood (upper trace, recorded from the SPREG chip).

specific shape and relative rigidity of the hood is enhanced through regular (but not continual) activation of the tu and cs. Maintenance of the hood in the erect position, despite the displacement of the rib relative to the diapophysis, appears to be active, not passive, as evidenced by the continued contraction of the sls and lc during hood maintenance.

Four elements contribute to the relaxation of the hood: (1) cessation of contractile activity in the sls and lc; (2) elastic recoil in the ligament spanning the caudoventral surface of the costovertebral joint; (3) onset of contraction in the il and oid; and (4) contractile activity within the tu and costocutaneous (ci and cs), which presumably function to synchronize and coordinate the displacements of the ribs with scalation (Fig. 11). The il and oid are smaller and have shorter lever arms than their antagonists (the sls and lc). This may be one reason why relaxation of the hood is generally a much slower process than is hood erection, although clearly the two actions are associated with different behavioral pressures. Hood relaxation, like hood erection, often occurs in several stages. Presumably the elastic recoil is most important during the initial relaxation stage (because retraction of the rib would reduce the stored elastic energy); however, at the present time the relative contributions to hood relaxation of the torques generated by the il and oid and the elastic recoil of the costovertebral ligament, are unknown.

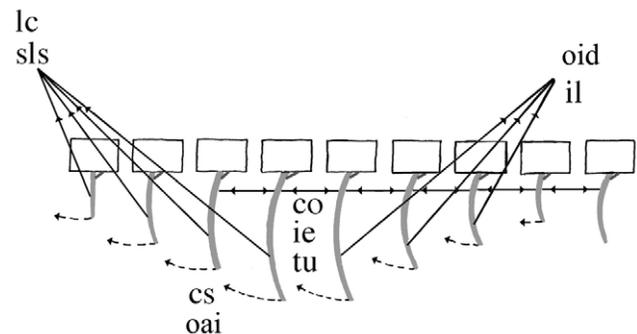


Fig. 11. Generalized model for the functional morphology of hooding. The lines of action for the hood erectors (lc and sls), hood retractors (oid and il), intercostal muscles (co, ie, tu) and costocutaneous muscles (cs and oai) are shown, as is the position of the elastic ligament spanning the costovertebral joint (dark grey). Muscle abbreviations: co – costovertebrocostalis; cs – costocutaneous superior; ie – intercostalis externus; il – iliocostalis; lc – levator costae; oai – obliquus abdominus internus; oid – obliquus internus pars dorsalis; sls – supracostalis lateralis superior; tu – tuberculocostalis.

Intraspecific variation in the hood

Although the hood is widely recognized as one of the characteristic features of cobras, the presence, shape and size of the hood are highly variable within the Najini radiation. There are true cobras (e.g. *Naja pallida*) as well as related species (e.g. *Paranaja*) in which the hood is very narrow or absent. Among the hooded cobras some (e.g. *N. kaouthia*) have broad but relatively short hoods while others (e.g. *N. nivea*) have elongated narrow hoods. The differences in the shape of the hood presumably reflect underlying variation in the degree of elongation and curvature in the ribs that form the hood (Fig. 4). The ability of a cobra to erect a hood, like the caudal termination of the hood itself, appears to be due more to neuro-muscular control rather than specific morphological specializations beyond elongation of the ribs.

Other costal displacement

In addition to the true cobras (*Naja*), and some closely related elapids (e.g. *Ophiophagus*), hoods are also known from a variety of other snakes (e.g. *Hydrodynastes*). Myers postulated that hooding may be a synapomorphy for Xenodontine snakes (Myers, 1986). Other species (e.g. *Acanthophis*) lack regional specialization of the ribs but displace the ribs – often nearly all the ribs in the body – in a similar fashion resulting in a pronounced broad but flattened defensive display (see Carpenter and Fergusson, 1977; Greene, 1988). Elevation of the ribs is also a key component of some specialized ophidian locomotions, particularly gliding (e.g. Socha, 2002) and burrowing (e.g. Young and Morain, 2003). All of these costal displacements are dependent on one of the key features of snakes, the absence of any sternal skeleton (e.g. Romer, 1976); and may all ultimately be a cooption of the regional costal displacements used by snakes for ventilation (e.g. Rosenberg, 1973).

Efficacy of hooding displays

Although some fanciful alternatives for the function of the hood have been suggested – such as serving as an expansive receptive area for the sense organs – most researchers regard the hooding as an aposematic display that increases the apparent size of the cobra, advertising its venomous danger. In this respect hooding is viewed as similar to a variety of other ophidian visual displays that involve inflation or expansion of head and/or neck (e.g. Young et al., 1999; Young et al., 2000). The visual significance of the hood is further demonstrated by the presence in some species of eye spots or similar patterns on the dorsal surface of the hood (e.g. Wall, 1921). Agitated cobras will often turn their back to display the dorsal surface of the hood to their assailant, a pose that renders the snake highly vulnerable. Interestingly enough, despite all of the accounts and photographs of hooded cobras, there does not appear to have been a single study that examined just how effective the hood is as a defensive display.

LIST OF ABBREVIATIONS

ci	costocutaneous inferior
co	costovertebrocostalis
cs	costocutaneous superior
CT	computed tomography
EMG	electromyography
ie	intercostalis externus

il	iliocostalis
iq	intercostalis quadrangularis
lc	levator costae
oai	obliquus abdominus internus
oid	obliquus internus pars dorsalis
oiv	obliquus internus pars ventralis
sli	supracostalis lateralis inferior
sls	supracostalis lateralis superior
ta	transversus abdominus
tu	tuberculo-costalis

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