# Prey Capture in the Lizard *Agama stellio*

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*ABSTRACT* Prey capture in *Agama stellio* was recorded by high-speed video in combination with the electrical activity of both jaw and hyolingual muscles. Quantification of kinematics and muscle activity patterns facilitated their correlation during kinematic phases. Changes in angular velocity of the gape let the strike be subdivided into four kinematic phases: slow open (SOI and SOII), fast open (FO), fast close (FC), and slow close-power stroke (SC/PS). The SOI phase is marked by initial activity in the tongue protractor, the hyoid protractor, and the ring muscle. These muscles project the tongue beyond the anterior margin of the jaw. During the SOII phase, a low level of activity in the jaw closers correlates with a decline of the jaw-opening velocity. Next, bilateral activity in the jaw openers defines the start of the FO phase. This activity ends at maximal gape. Simultaneously, the hyoid retractor and the hyoglossus become active, causing tongue retraction during the FO phase. At maximal gape, the jaw closers contract simultaneously, initiating the FC phase. After a short pause, they contract again and the prey is crushed during the SC/PS phase. Our results support the hypothesis of tongue projection in agamids by Smith ([1988] J. Morphol. *196*:157–171), and show some striking similarities with muscle activity patterns during the strike in chameleons (Wainwright and Bennett [1992a] J. Exp. Biol. *168*:1–21). Differences are in the activation pattern of the hyoglossus. The agamid tongue projection mechanism appears to be an ideal mechanical precursor for the ballistic tongue projection mechanism of chameleonids; the key derived feature in the chameleon tongue projection mechanism most likely lies in the changed motor pattern controlling the hyoglossus muscle. © 1995 Wiley-Liss, Inc.

Lizards capture prey by means of lingual or jaw prehension (Smith, '84, '88). Some authors argue that jaw-mediated prey capture might be the primitive condition in squamates (Bels and Goosse, '90; referring to the plesiomorphic condition of jaw prehension in Amphibia, Thexton et al., '77; Lauder and Shaffer, '88; Findeis and Bemis, '90; Nishikawa and Cannatella, '91; Anderson, '93), but lingual prey capture is considered by most authors to be more primitive than jaw capture (Schwenk, '88; Schwenk and Bell, '88; Schwenk and Throckmorton, '89).

Most functional morphological studies concerning prey capture in lizards have emphasized a few groups belonging to the Iguania (Agamidae: Schwenk and Throckmorton, '89; Kraklau, '91; Iguanidae: Schwenk and Throckmorton, '89; Bels, '90; Bels and Goosse, '90; Delheusy and Bels, '92; and Chamaeleonidae: Gnanamuthu, '30; Zoond, '33; Bels and Baltus, '87; Bell, '89, '90; Wain-

wright et al., '91; Wainwright and Bennett, '92a,b). The only scleroglossans for which data concerning prey capture exist are *Trachydosaurus rugosus* (Gans et al., '85) and *Lacerta viridis* (Bels and Goosse, '90).

In spite of these many recent studies on species using lingual prey prehension, the activation pattern of the hyolingual muscles has only been examined in *Chamaeleo jacksonii* (Wainwright and Bennett, '92a). Chameleons have long been noted for their highly specialized ballistic tongue projection mechanism, in which the tongue is extended up to twice their body length, projected by contraction of the circular accelerator muscle surrounding the entoglossal process (Wainwright and Bennett, '92a). As the Chamaeleonidae may be the sister group of the Agamidae

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(Camp, '23; Estes et al., '88), or even belonging to the same family (Chamaeleonidae including Leiolepidinae, Agaminae, and Chamaeleoninae: Frost and Etheridge, '89), it has been hypothesized that this unique system of tongue projection derives from a more basic agamid-like precursor (Schwenk and Bell, '88; Smith, '88). A possible activation pattern of the hyolingual muscles during prey capture in Agamidae has been predicted based on morphological and biomechanical data (Smith, '88). The tongue projection mechanism in Agamidae has been assumed to be an ideal mechanical precursor for the highly-derived ballistic tongue projection in Chamaeleonidae. However, this hypothesis has not been tested experimentally, although kinematical data on prey capture in *Agama agama* (Kraklau, '91), and data on the form and function of the hyolingual apparatus in Agamidae (Smith, '88), exist.

The aim of this report is to provide a quantitative analysis of prey capture in *Agama stellio* by combining movement analysis with simultaneous electromyography of the jaw and hyolingual musculature. This permits evaluation of the predicted motor pattern (Smith, '88), comparison of our results for *Agama stellio* to those of *Chamaeleo jacksonii* (Wainwright and Bennett, '92a), and evaluation of the evolutionary transformation processes from an agamid to a chameleonid tongue projection mechanism (Schwenk and Bell, '88; Smith, '88).

## MATERIALS AND METHODS
### Specimens

Five adult specimens (20 ± 3 cm; 42 ± 3 g) of the species *Agama stellio* were used in the experiments. The specimens used in this study were collected in Israel and provided by Dr. E. Kochva. The animals were kept in a glass vivarium on a 12-hr light/dark cycle, and were offered water and food consisting of crickets, grasshoppers, and mealworms *ad libitum*. The environmental temperature varied from 26°C at daytime to 20°C at night; an incandescent bulb provided the animals with a basking place at a higher temperature (30°C). An additional four animals were dissected and stained to characterize all jaw and hyolingual muscles (Bock and Shear, '72). Drawings were made of all stages of the dissection, using a Wild M5 dissecting microscope, provided with a camera lucida.

### Electromyographic and video recordings

The animals used in the electromyographic (EMG) experiments were anesthetized by an intramuscular injection of Ketalar (200 mg/kg bodyweight) before electrode implantation. Bipolar 25-cm-long electrodes were prepared from teflon-insulated 0.065-mm Ni-Cr wire. The insulation was scraped away at the tip, exposing 1 mm of electrode wire. The electrodes were implanted percutaneously into each muscle belly, using hypodermic needles with 2 mm of the electrode bent back as it emerged from the needle barrel. Electrodes were placed in the major jaw closers: the musculus pterygoideus (MPt), the musculus adductor mandibulae externus (MAME), the musculus adductor mandibulae posterior (MAMP), and, in one of the experiments, also in the musculus pseudotemporalis (MPsT). Electrodes were also placed in a jaw opener (the musculus depressor mandibulae, MDM) and into several hyolingual muscles: the musculus genioglossus (MGG), the musculus hyoglossus (MHG), the ring muscle (MRing), the musculus sternohyoideus (MSH), and the musculus mandibulohyoideus (MMH). In one experiment the dorsal cervical muscle (musculus spinalis capitis, MSCa) was implanted. Electrode placement was confirmed by dissection of two animals. Results for the MPsT and the MSCa are based on seven strike sequences in one animal. The results for the other muscles were based upon 21 strike sequences in four animals.

Electrical signals were amplified 2,000 times with Tektronix (Beaverton, OR) 26A2 differential preamplifiers (range 100 Hz–10 KHz) and Honeywell (Denver, CO) Accudata 117 DC amplifiers, and recorded on a Honeywell 96 FM 14-channel tape recorder (medium bandpass) at a speed of 19.05 cm/s.

Prey capture was recorded using a NAC-1000 high speed video system set at 500 frames per second using video lights (TRI-LITE, Cool Light Co. Inc., Hollywood, CA). The animals were filmed in a plexiglass cage (30 × 10 × 10 cm), while feeding on crickets and grasshoppers. The living prey item was held in a clip at the front of the cage and was always placed less than 10 cm from the snout of the lizard. The output of a Tektronix wave pattern generator (square wave) was recorded on the FM tape recorder and sent to a moving electromagnet kept in the visual field. This allowed synchronization of the electromyographic and kinematic records.

## Video data and electromyographical analysis

Only truly lateral prey capture sequences were analyzed (N = 25). Seven clearly visible external markers (color spots) were digitized using the NAC X–Y Coordinator (Fig. 1). Horizontal (X) and vertical (Y) coordinates were recorded for each digitized point at intervals of 2 frames. Aspects calculated were changes in gape profile (distance 2–4; angle 2–3–4), displacement of the upper and the lower jaw (Y-coordinate of points 2 and 4, respectively), prey distance (distance 5–6), cranial elevation (angle 2–3), lower jaw depression (angle 3–4), tongue protrusion (X-coordinate of point 5–X-coordinate of point 4), and body displacement (X-coordinate of point 7). Kinematic profiles were plotted (Fig. 3).

Prey capture was analyzed statistically. Twenty-one variables were determined for every strike sequence: the durations of the slow opening phase (SOI and -II), of the fast opening phase (FO), of the fast closing phase (FC), of the slow close/power stroke phase (SC/PS), and of the total cycle (TC); the maximal values of the gape distance, the tongue protrusion distance, the lower jaw depression, and cranial elevation; the times to the maximal values of the gape distance, the tongue protrusion distance, the lower jaw depression, and cranial elevation; the gape angle at the end of the SOI phase; the time to maximal horizontal body displacement; the horizontal and vertical body displacements; and the duration of tongue protraction and retraction (beginning when the tongue becomes visible between the half-opened jaws and ending when the tongue is no longer visible between the jaws). Frame 1 was arbitrarily chosen at the beginning of the slow opening of the mouth. Time 0 was defined as prey contact.

The recorded EMG signals were analyzed by analogue-to-digital transformation at 10 KHz using a Keithley DAS series (Keithley Instruments Inc., Cleveland, OH) 500 12-bit A–D convertor. After digitization, the signals were integrated following the procedure of Beach et al. ('82) (100 data = 10 ms per bin), and the number of spikes as well as the average amplitude per interval were calculated. The exact duration of muscular activity and the onset of each muscle relative to the MDM were then measured. Several muscles had more than one activity burst during the course of a strike sequence. Different bursts were defined on the basis of abrupt amplitude differences. EMG variables were then related to the kinematic data.

## RESULTS
### Morphology

The skull of *Agama stellio* is adequately described by El Toubi ('47) and Jollie ('60). *Agama stellio* has no or very little intracranial mobility. The hyoid apparatus has a distinct tapered entoglossal process, one pair of ceratohyals, and two pairs of ceratobranchials. In contrast to *Agama agama,* only the first ceratobranchial is ossified; the remainder are cartilaginous. The entoglossal process is surrounded by the ring muscle.

The jaw and hyolingual muscles in agamids have been described by several authors (Gandolfi, '08; Gnanamuthu, '37; Haas, '73; Gomes, '74; Smith, '88). Only a brief description of the muscles examined is presented here (Fig. 2A,B).

The complex external adductor musculature is composed of a superficial part that can be subdivided into an anterior and a poste-
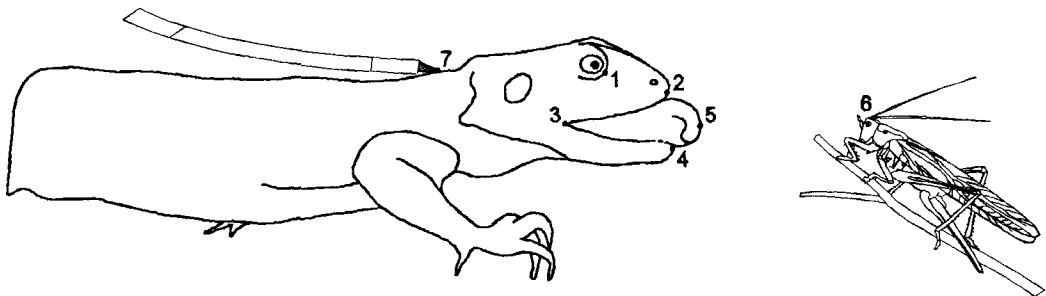


Fig. 1. External markers used to digitize high-speed video images. 1, anterior eye margin; 2, anterior margin of the upper jaw; 3, anguli oris; 4, anterior margin of the lower jaw; 5, most anteriorly situated point of the tongue; 6, point of prey contact; 7, dorsal body point.
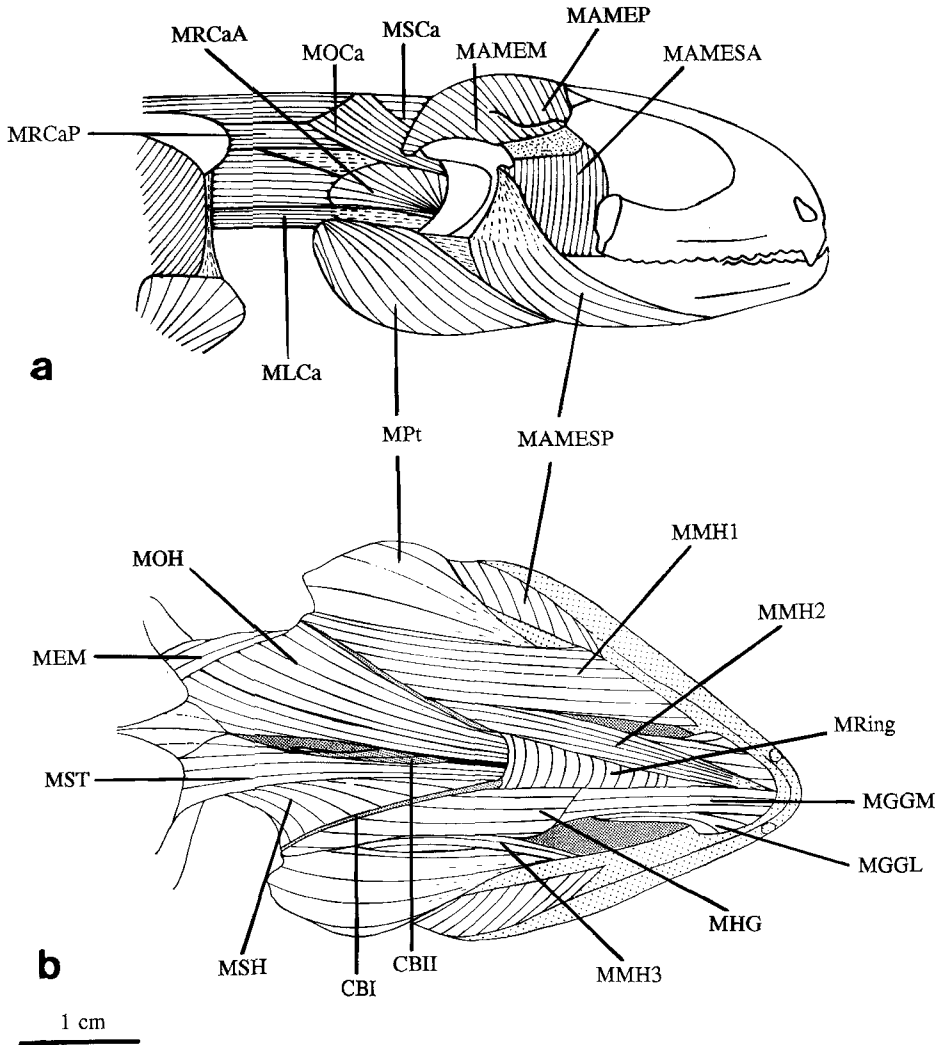
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Fig. 2. *Agama stellio.* Jaw and hyolingual musculature. a: Lateral view after removal of the skin, the quadrato jugal ligament, parts of the jugal, squamosal and postorbital bones, the M. depressor mandibulae, the M. levator anguli oris, and some superficial neck muscles (Mm. levator scapuli superficialis and profundus, the M. longissimus cervicis, and parts of the M. spinalis capitis). b: Ventral view of the hyolingual muscles. The upper half is drawn after removal of the skin, the Mm. intermandibularis anterior (superficialis and profundus) and posterior, and the M. constrictor colli. The bottom half shows a deeper dissection. CBI and CBII, first and second ceratobranchial; MAMEM, MAMEP, Mm. adductor mandibulae externus medialis and profundus; MAMESA, MAMESP, Mm. adductor mandibulae externus superficialis anterior and posterior; MEM, M. episternocleidomastoideus; MGGL, MGGM, Mm. genioglossus medialis and lateralis; MHG, M. hyoglossus; MLCa, M. longissimus capitis; MMH1, MMH2, MMH3, Mm. mandibulohyoideus 1, 2, and 3; MOCa, M. obliquus capitis; MOH, M. omohyoideus; MPt, M. pterygoideus; MRCaA, MRCaP, Mm. rectus capitis anterior and posterior; MRing, ring muscle; MSCa, M. spinalis capitis; MSH, M. sternohyoideus; MST, M. sternothyroideus.

rior portion (MAMESA, MAMESP), a medial part (MAMEM), and a deep part (MAMEP). The anterior superficial part originates at the inner aspect of the temporal arch and inserts on the dorsolateral side of the lower jaw, whereas the posterior superficial part originates on the dorsal aspect of the quadrate by means of an aponeurosis and inserts on the posterolateral side of the dentary. The medial and deep parts both insert on the basal aponeurosis that extends upwards from the coronoid process; the medial part originates

on the parietal and the medial side of the squamosal, the deep part on the paraoccipital process of the exoccipital. The posterior adductor (MAMP) originates on the quadrate and runs directly to its insertion on the medial side of the lower jaw, posterior to the coronoid process. The pseudotemporal muscle (MPsT), which lies anteriorly in the temporal fossa, can be subdivided into a superficial and a deep part; this muscle is relatively small compared to the external adductors. The pterygoid muscle can be divided into a deep medial part and a superficial lateral part. The deep part (MPtmed) of the pterygoid muscle runs from the ventral side of the pterygoid to the medioventral side of the articular. The superficial part (MPtlat) runs posterolaterally and curves around the ventral side of the mandible to insert on the lateral side of the articular. The musculus depressor mandibulae (MDM) has two parts. The main part originates on the posterior edge of the parietal; it overlaps the accessory part (MDMA) near its insertion on the retroarticular process. The accessory head originates on the dorsal face of the squamosal, near the articulation with the quadrate. The dorsal cervical muscle (MSCa) shows a superficial and a deep part. The superficial part of the dorsal cervical muscle originates on the neural spines of the cervical vertebrae and runs anteriorly to insert on the posterior edge of the parietal. The deeper part of the dorsal cervical muscle has a similar origin and inserts on the dorsal side of the occipital bone.

The fleshy tongue of *Agama stellio* is composed of intrinsic and extrinsic muscles. The intrinsic musculature has been described in detail (Smith, '88). Its most striking feature is the circular ring muscle, characteristic for the Agamidae, and believed to be homologous with the verticalis muscle of the Iguanidae and the accelerator muscle of the Chamaeleonidae. Only in the Agamidae and Chamaeleonidae does it form a complete ring around the entoglossal process.

The extrinsic lingual musculature originates on the mandible or the hyoid, and consists of distinct genioglossus and hyoglossus muscles. The genioglossus (MGG) originates on the anteromedial part of the mandible and runs posteriorly to insert on the tongue. Near its insertion it separates into medial, lateral, and internal parts. The hyoglossus (MHG) originates on the first ceratobranchial and runs anteriorly into the tongue.

Several hyoid muscles lie ventral to the tongue. The mandibulohyoideus (MMH) consists of three portions that originate on the medial side of the mandible and insert on the ceratohyal and the first ceratobranchial. The sternohyoideus and sternothyroideus both originate on or near the episternum and run anteriorly to insert on the basihyal and first ceratobranchial. The omohyoideus originates on the anterior edge of the interclavicula and suprascapula, and its fibers run anterioventrally to insert on the first ceratobranchial.

### Kinematics

The terminology used to describe prey capture is that used by previous workers (Bramble and Wake, '85). A capture cycle is divided into five distinct phases based on the velocity changes in gape angle. Slow opening of the mouth (SOI and SOII) initiates the strike and is followed by the fast opening of the mouth (FO). After maximal gape the mouth is closed rapidly (FC) until the jaws touch the prey at the beginning of the slow close phase (SC), during which the closing speed decreases. The slow close phase may be accompanied by a power stroke (PS) or prey-crushing phase. A capture cycle is generally accompanied by a lunge phase. The lunge consists of an anterior body movement towards the prey involving a rotation of the front of the body around the shoulder joint. Figure 3 presents an example of a strike cycle depicting the changes in gape, prey distance, tongue protrusion, and upper and lower jaw position, and changes in horizontal and vertical body distance. Table 1 notes the prey capture kinematics of 21 strike cycles.

After the first prey item is introduced into the experimental cage, the lizard does not respond and only attacks after several minutes. At the start of each experimental series, the lizards did not react to immobile prey items; however, thereafter even dead prey items were attacked. Response consists of a rotation of the head toward the prey followed by a lunge of the lizard's body.

The gape profile first changes at the beginning of the SOI phase, and the mouth opens until a gape angle of $18 \pm 3°$ is achieved. The jaw opening velocity drops to 0 thereafter, and the gape angle is thus kept more or less constant (SOII phase). Both the SOI and SOII phase each comprise about 35% of the total cycle, their mean duration being 128 ms and 137 ms. SOI usually starts with the beginning of the lunge of the lizard towards
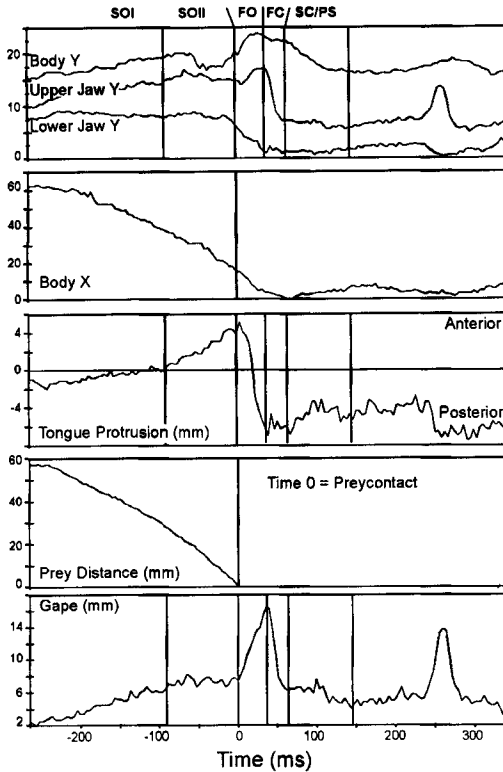
Fig. 3. *Agama stellio.* Kinematic profiles of changes in the vertical (body Y) body displacement, and of the vertical displacements of the upper jaw (upper jaw Y) and lower jaw (lower jaw Y), horizontal (body X) body displacement, tongue protrusion, prey distance, and gape as they occur during the strike. FC, fast close; FO, fast open; SC/PS, slow close and power stroke; SOI, slow open phase one; SOII, slow open phase two.

TABLE 1. *Quantitative prey capture kinematics in Agama stellio (N = 21)*

| Variable | Mean | ± (S.D.) |
|---|---|---|
| Slow Open I (ms) | 128 | 67 |
| Slow Open II (ms) | 137 | 81 |
| Fast Open (ms) | 38 | 8 |
| Fast Close (ms) | 32 | 8 |
| Slow Close/Power Stroke (ms) | 38.5 | 13 |
| Total Cycle (ms) | 374 | 149 |
| Duration of Tongue Protrusion (ms) | 117 | 31 |
| Duration of Tongue Retraction (ms) | 29 | 11 |
| Time to Onset of Tongue Projection (ms)** | 184.5 | 87 |
| Time to Maximal Gape (ms)* | 45 | 12.5 |
| Time to Maximal Lower Jaw Depression (ms)* | 44 | 16 |
| Time to Maximal Cranial Elevation (ms)* | 42 | 26 |
| Time to Maximal Tongue Protusion (ms)* | 2.5 | 11 |
| Time to Maximal Anterior Body Displacement (ms)* | 60 | 21 |
| Maximal Gape (°) | 42 | 7.5 |
| Maximal Lower Jaw Depression (°) | 46 | 14 |
| Maximal Cranial Elevation (°) | 22 | 9 |
| Gape Angle at the end of the SOI-phase (°) | 18 | 3 |
| Maximal Tongue Protrusion distance (mm) | 4.6 | 0.9 |
| Maximal Anterior Body Displacement (mm) | 29 | 19 |
| Maximal Dorso-Ventral Body Displacement (mm) | 6.5 | 4 |
| % SOI | 35 | 6.5 |
| % SOII | 35 | 7 |
| % FO | 10 | 3 |
| % PC | 9 | 3 |
| % SC/PS | 10 | 4 |

*Time to maximal gape, maximal lower jaw depression, maximal cranial elevation, maximal tongue protrusion and maximal anterior body displacement are measured from preycontact.
**Time to onset of tongue projection is measured from the beginning of the SO-phase.
% values are relative to Total Cycle length.

the prey. The lunging lizard initially lifts its body but depresses the head just before FO.

The pattern of tongue protrusion differs during the SOI and SOII phases of the gape cycle. At the end of the SOI phase, the tongue will be protruded so that it reaches the anterior jaw margin and will have its dorsal side curved to the front. During SOII the tongue extends beyond the anterior margin of the lower jaw. The maximal tongue protrusion distance (4.6 mm) is achieved at or prior to prey contact, which normally occurs on both thorax and head of the prey item. The tongue protrusion distance decreases very rapidly after prey contact. At prey contact the body continues to move forward but tongue movement stops or reverses direction. The body may continue to move up to 60 ms after contacting the prey. The tongue with its ad-

hering prey is thereafter retracted past the jaw margins. This lingual retraction takes only 30 ms, in contrast to the tongue protrusion which lasts approximately four times longer (117 ± 31 ms).

The tongue is retracted during FO and FC phases. The FO phase lasts 38 ± 8 ms and ends at the maximal gape angle (approximately 30–57°, mean 42°), which is reached 44 ± 16 ms after prey contact. Unlike the SO phase during which the gape mainly changes by depression of the lower jaw, the change of gape during the FO phase results from a simultaneous depression of the mandible (lower jaw depression angle 45°) and an elevation of the cranium (cranial elevation angle 21°). Maximal depression of the lower jaw

and maximal cranial elevation usually coincide with maximal gape.

After maximal gape, the mouth closes (FC phase) very rapidly (32 ± 8 ms) due to depression of the cranium and elevation of the mandible. During the subsequent SC/PS phase, the lizard lifts up its head and closes its mouth further, thus crushing the prey item.

The shortest phase in a prey capture cycle is the FC phase (8.9%), followed by the FO phase (10.3%) and the SC phase (10.3%). The SO phase is clearly the longest and most variable phase of the strike cycle. During the first part of the SO phase the lizard may respond to external stimuli by modulating certain aspects of the strike (e.g., orientation of head and tongue in relation to the position of the prey item, timing of the moment of release of the tongue, or even completely breaking off the strike). Once the tongue is protracted beyond the jaw margin, no further modulation is noted by the techniques we used.

### Electromyography

The muscle activity patterns recorded during the strike were integrated and related to the movement analysis (Figs. 4, 5). Figure 8 gives a summary of the onset and duration of the activity in the different jaw and hyolingual muscles in relation to the kinematic phases; Table 2 gives the corresponding numerical data. The activity patterns are first described for all muscles separately. In the following description of muscle activity patterns, maximum activity is always referring to the maximum activity that was recorded within that muscle in a recording session.

### Musculus hyoglossus (MHG, Figs. 5, 7, 8)

The M. hyoglossus is the first muscle that becomes active during the strike. It becomes active about 335 ms before, and lasts up to 15 ms after, maximal gape. Its activity rises rapidly and remains at 50% of maximum level throughout the SOI phase. At the beginning of the SOII phase the intensity increases to 80–100% of maximum. At the beginning of the FO phase, the activity decreases and the MHG becomes fully active thereafter. Sometimes (in 25% of the examined strikes) the activity level drops to 0 shortly after prey contact. In these strikes a second burst starts approximately 10 ms before maximal gape and lasts about 150 ms.

TABLE 2. *Summary of EMG timing variables for jaw and hyolingual muscles of* Agama stellio *(N = 21)*[1]

| MUSCLE burst presence (%) | DURATION (ms) | | ONSET (ms) | |
|---|---|---|---|---|
| | MEAN | ± (S.D.) | MEAN | ± (S.D.) |
| MHG   100 | 350 | 160 | −335 | 170 |
| 25 | 150 | 70 | −10 | 60 |
| MGG   100 | 325 | 100 | −316 | 100 |
| 16 | 75 | 25 | −15 | 25 |
| MRing   100 | 260 | 70 | −252 | 80 |
| 71 | 76 | 60 | 10 | 25 |
| MMH   100 | 250 | 140 | −280 | 140 |
| 93 | 60 | 28 | −15 | 8 |
| MSH   100 | 40 | 10 | −30 | 20 |
| 100 | 110 | 35 | 34 | 18 |
| MDM   92 | 170 | 80 | −255 | 70 |
| 100 | 40 | 10 | −40 | 10 |
| 100 | 80 | 45 | 56 | 10 |
| MAME   100 | 170 | 140 | −190 | 150 |
| 100 | 42 | 16 | −10 | 30 |
| 100 | 62 | 25 | −41 | 25 |
| MAMP   92 | 150 | 77 | −170 | 90 |
| 100 | 40 | 10 | −13 | 30 |
| 100 | 90 | 60 | 46 | 30 |
| MPtmed   100 | 112 | 54 | −118 | 41 |
| 100 | 35 | 5 | 10 | 15 |
| 100 | 56 | 22 | 58 | 17 |
| MPtlat   100 | 68 | 48 | −72 | 50 |
| 100 | 35 | 5 | 10 | 15 |
| 100 | 63 | 25 | 60 | 16 |

[1]Onset variables are measured from maximal gape to the onset of the muscle burst. Different bursts in the same muscle are ordered chronologically from top to bottom. Burst presence indicates the number of times that burst was present (in %) in the analyzed sequences.

### Musculus genioglossus (MGG, Figs. 5, 7, 8)

Shortly after the onset of the MHG, the MGG becomes active. Its activity starts 316 ms before maximal gape and lasts up to maximal gape. Activity level gradually increases to a maximum at the end of the SO phase. Activity then decreases to 30% of maximum at the beginning of the FO phase, but maximum activity is again observed at maximal gape. The activity level drops abruptly to 0 thereafter. As in the MHG, the activity level occasionally (16% of observed cases) drops to 0 just after prey contact. A second burst then follows, which begins 15 ms before maximal gape, with a mean duration of 75 ms.

### Ring muscle (MRing, Figs. 5, 7, 8)

The MRing becomes active 252 ms before maximal gape and remains active until maximal gape is achieved. The MRing often (71% of observed cases) has a second activity burst of lower amplitude, beginning 10 ms after maximal gape (50 ms after prey contact) and lasting an average of 80 ms. The intensity pattern is very similar to that of the MGG,
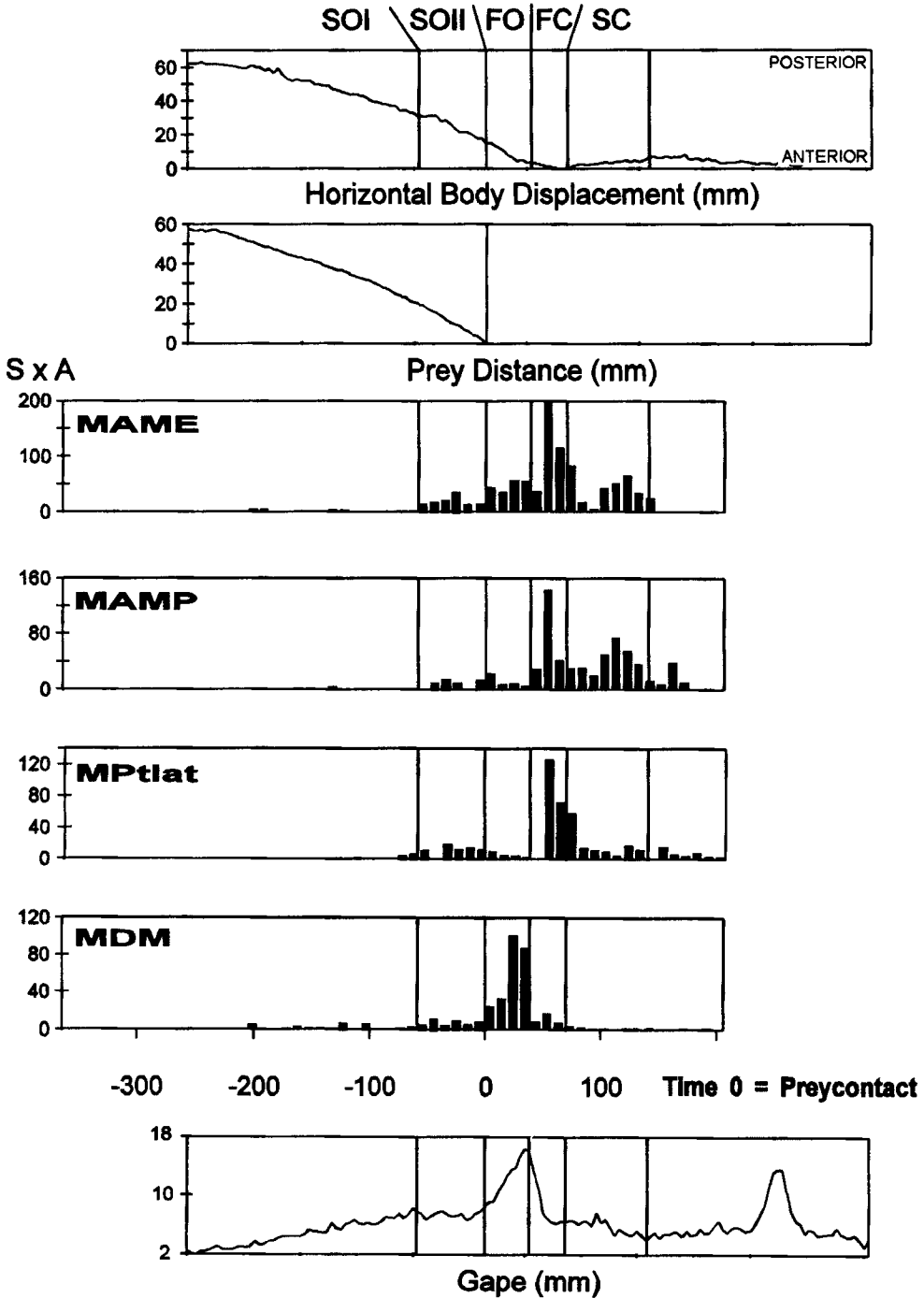
Fig. 4. *Agama stellio.* Integrated EMG (expressed as spike number × amplitude, S × A) of several jaw muscles, correlated with kinematic profiles of horizontal body displacement, prey distance, and gape during the strike. FC, fast close; FO, fast open; MAME, M. adductor man-dibulae externus; MAMP, M. adductor mandibulae posterior; MDM, M. depressor mandibulae; MPtlat, M. pterygoideus lateralis; SC, slow close; SOI, slow open phase one; SOII, slow open phase two.
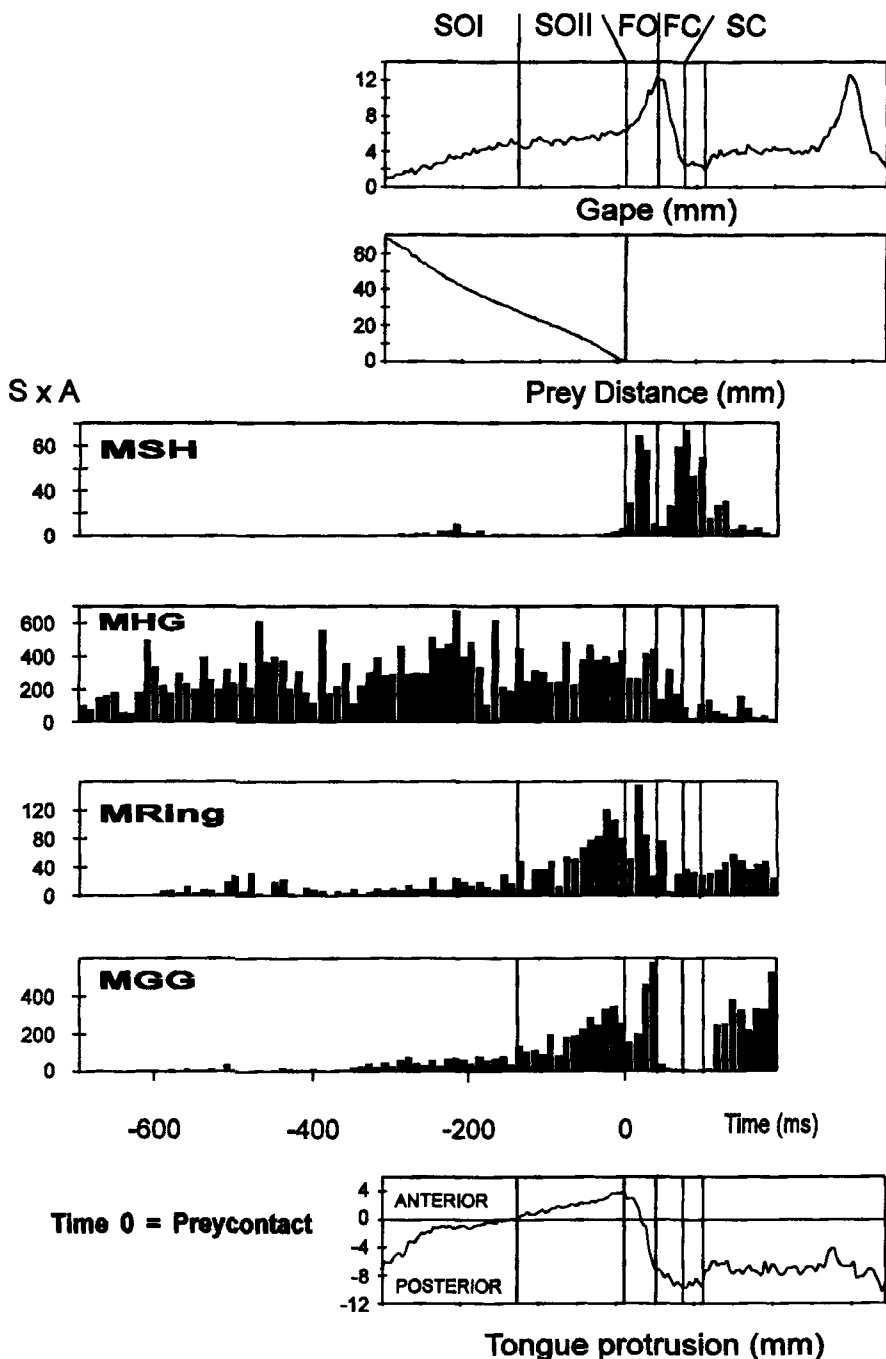
Fig. 5. *Agama stellio*. Integrated EMG (expressed as spike number × amplitude, S × A) of several hyolingual muscles, correlated with kinematic profiles of gape, prey distance, and tongue protrusion during the strike. FC, fast close; FO, fast open; MGG, M. genioglossus; MHG, M. hyoglossus; MRing, ring muscle; MSH, M. sternohyoideus; SC, slow close; SOI, slow open phase one; SOII, slow open phase two.

increasing during the second part of the SO phase to 80–100% of maximum.

## Musculus mandibulohyoideus (MMH, Figs. 5, 8)

Around the time that the MRing becomes active, the MMH shows its first activity. As with the MGG and the MRing, the MMH remains active until maximal gape. On average its activity lasts 250 ms. The intensity level is moderate (30%) during the SOI phase, then increases to reach its maximum shortly after prey contact. Coinciding with the beginning of activity in the MSH, the MMH shows a second burst of a lower amplitude (±50% of maximal amplitude).

## Musculus sternohyoideus (MSH, Figs. 5, 7, 8)

At 30 ms before maximal gape (about 15 ms after prey contact), the MSH becomes active for about 40 ms. The MSH shows a second activity burst 30 ms after maximal gape which lasts approximately 110 ms. Both bursts are of high amplitude.

## Musculus depressor mandibulae (MDM, Figs. 4, 6–8)

The MDM is active at low amplitude (15% of maximum amplitude) during the SO phase, beginning 250 ms and ending 80 ms before maximal gape. A high-level burst of activity starts 40 ms prior to, and ceases abruptly at, maximal gape. A third low-level (10–30% of maximal amplitude) burst of activity usually occurs 20 ms after maximal gape, and lasts approximately 80 ms during the FC and SC/PS phase.

## Musculus adductor mandibulae externus (MAME, Figs. 4, 6–8)

The MAME is the first jaw closer to become active during the strike. Its initial burst is of low amplitude (±15% of maximal amplitude) during the SO phase, starting approximately 190 ms, and ending 20 ms, before maximal gape. The following activity burst is of high amplitude and starts 10 ms before maximal gape and lasts 40 ms. Activity then stops for about 20 ms, after which the MAME again becomes active for about 60 ms. The intensity of this last burst varies from 30–80% of maximal amplitude. The superficial parts of the MAME (MAMESA and MAMESP) rarely show a first burst of lower amplitude during the SO phase, nor a distinc-

tive third burst during the SC/PS phase (Fig. 6).

## Musculus adductor mandibulae posterior (MAMP, Figs. 4, 6, 8)

The MAMP is the second jaw closer that becomes active (170 ms before maximal gape). The first activity burst in the MAMP is of low amplitude and ceases just prior to maximal gape. As in the MAME, a high-level activity burst starts 10 ms before maximal gape, and lasts 30–40 ms. Activity then stops for about 20 ms, after which the MAMP resumes its activity at low amplitude (40–80% of maximum) for another 90 ms.

## Musculus pterygoideus medialis and lateralis (MPtmed-MPtlat, Figs. 4, 6, 8)

The medial part usually becomes active 50 ms (120 ms before maximal gape) before the lateral (70 ms before maximal gape) part of the MPt. At maximal gape the MPt shows its highest activity level for about 30 ms. As with the other jaw closers, the MPt has a third burst of low amplitude activity which lasts for 60 ms and starts after a pause of about 20 ms.

## Musculus pseudotemporalis (MPsT, Fig. 6)

The MPsT usually has three activity bursts. The first burst is of low amplitude and is often absent during the strike. When present, it starts about 150 ms before maximal gape and lasts on average 140 ms. The main activity in the MPsT starts at maximal gape and lasts 30 ms. A third low-amplitude burst begins 40 ms after maximal gape and lasts about 50 ms.

## Musculus spinalis capitis (MSCa, Fig. 6)

The MSCa becomes active at low amplitude around the same time the MDM becomes active. This first burst lasts through the SOI and SOII phases and stops approximately 100 ms before maximal gape. The burst with the highest activity level in the MSCa begins 60 ms before, and ceases at, maximal gape. A third burst of lower amplitude is present 20 ms after maximal gape (during the SC/PS phase), and lasts 30–80 ms.

## General

When evaluating different muscle activity patterns in relation to observed kinematic profiles, it appears that activity in the MHG initially results in a protraction of the hyoid.
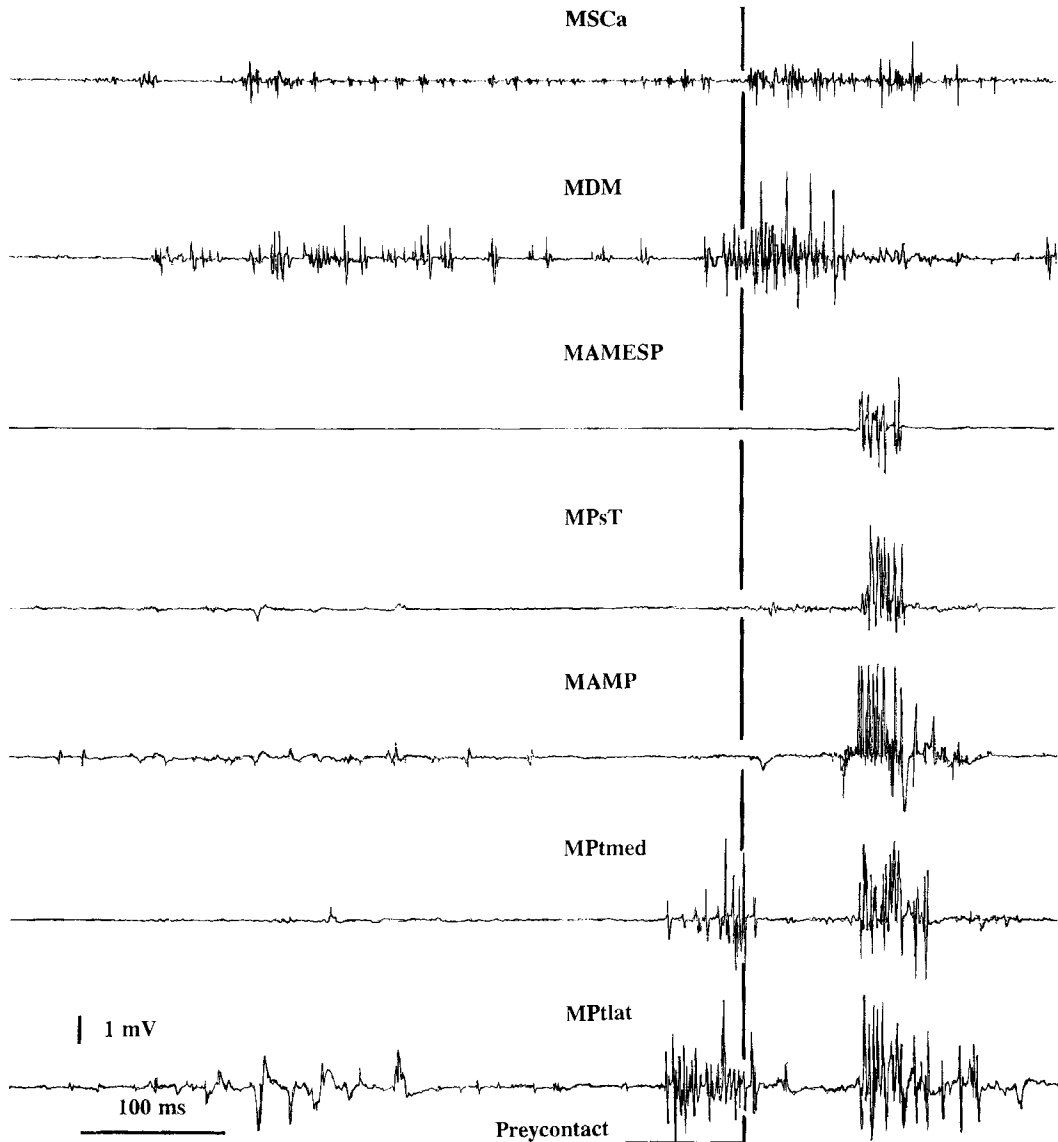
MSCa

MDM

MAMESP

MPsT

MAMP

MPtmed

| 1 mV

100 ms

MPtlat

Preycontact

Fig. 6. *Agama stellio.* Representative original EMG recordings from several jaw muscles, as well as from the musculus spinalis capitis (MSCa) during the strike. MDM, M. depressor mandibulae; MAMESP, M. adductor man-dibulae externus superficialis posterior; MPsT, M. pseu-dotemporalis; MAMP, M. adductor mandibulae poste-rior; MPtmed, M. pterygoideus medialis; MPtlat, M. pterygoideus lateralis.

However, once the hyoid (MMH) and the tongue (MGG) protractors become active, the action of the MHG will deform the tongue, curving its dorsal side anteriorly before prey contact (see Schwenk and Throckmorton, '89). Following the onset of the MHG, the MGG and the MRing become active, protrud-ing the tongue beyond the anterior mandibu-lar margin. At the same time, activity in the MMH (the hyoid protractor) causes hyoid protraction.

The jaw opener (MDM) and the dorsal cer-vical muscles (MSCa) show their highest ac-tivity level during the FO phase. This high activity in the MDM results in a rapid depres-sion of the lower jaw. Simultaneously, high
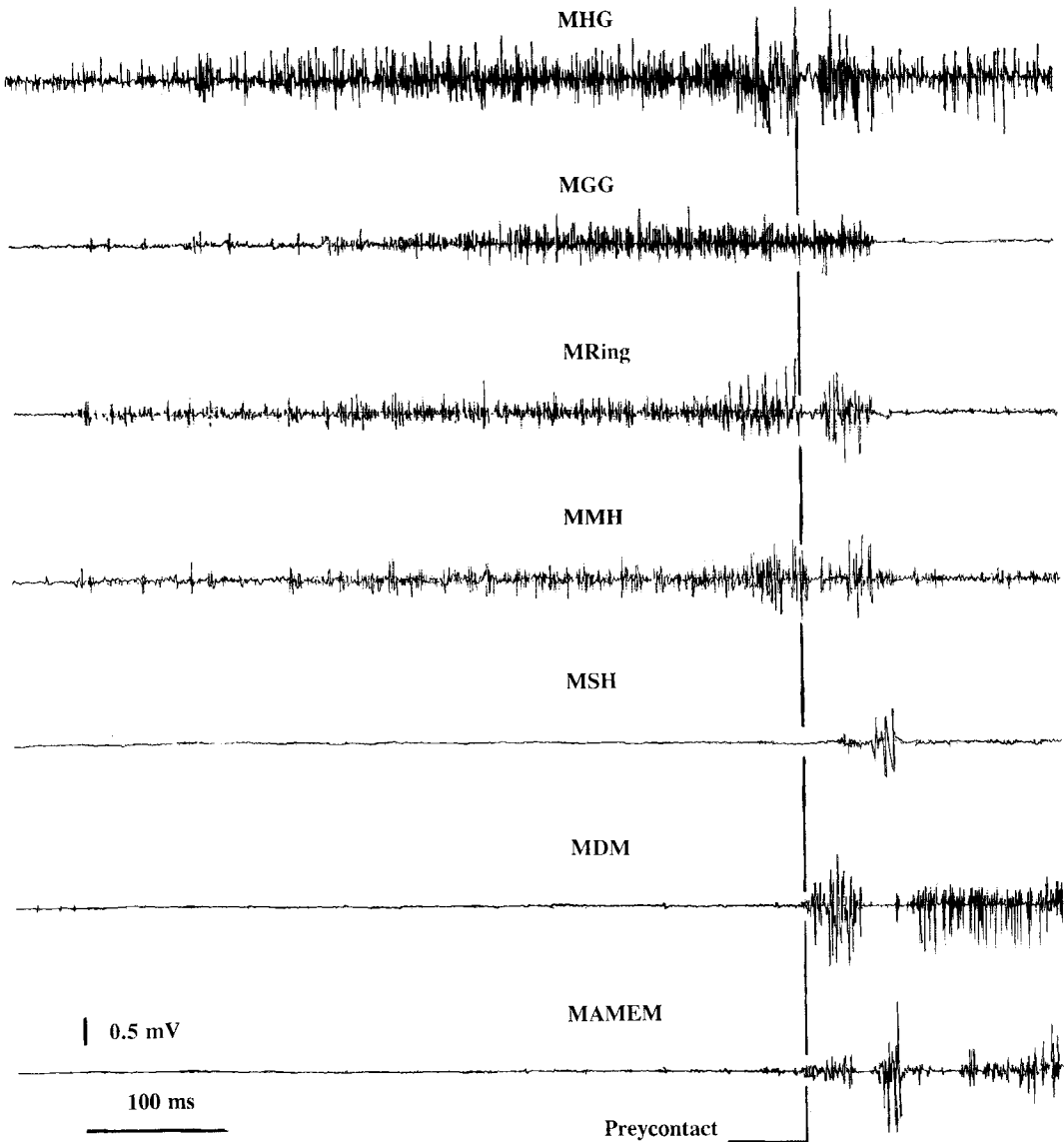
Fig. 7. *Agama stellio*. Representative original EMG recordings from several hyolingual muscles, as well as from the M. depressor mandibulae (MDM) and the M. adductor mandibulae externus (MAME) during the strike.

MHG, M. hyoglossus; MGG, M. genioglossus; MRing, ring muscle; MMH, M. mandibulohyoideus; MSH, M. sternohyoideus.

activity in the MSCa elevates the neurocranium. Sometimes a third low level activity burst is present in the MDM. This burst corresponds to the SC/PS phase, in which the MDM presumably plays an important role in the stabilization of the jaw joint. During the FO phase, the activity of the MSH, and of the MHG, rapidly retracts the hyoid, as well as the tongue with its adhering prey.

The jaw closers, with the exception of the MAMEs, all show a low-amplitude burst during the SO phase that ceases just before maximal gape. The onset of this low-level activity coincides with the beginning of the SOII phase. At about maximal gape, the jaw closers become highly active and produce jaw closure. After an activity pause, the jaw adductors again become active during the so-
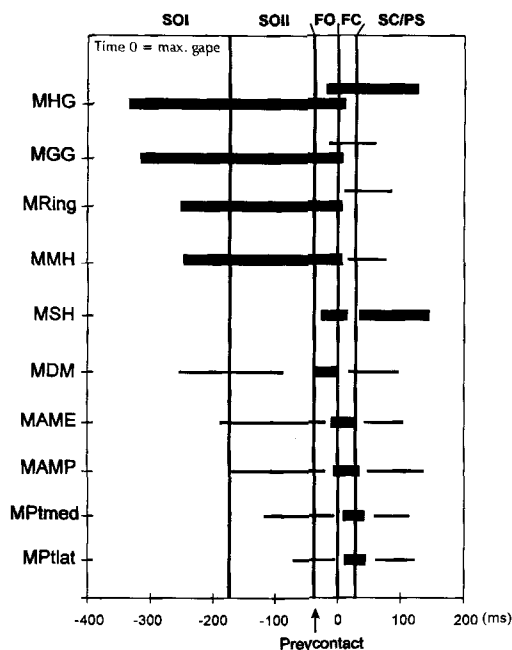
Fig. 8. *Agama stellio*. Summary EMG bar diagram illustrating pattern of onset and offset in jaw and hyolingual muscles during the strike. All bars are based on average values (N = 21 for all muscles). Narrow bars represent low-amplitude activity. MHG, M. hyoglossus; MGG, M. genioglossus; MRing, ring muscle; MMH, M. mandibulohyoideus; MSH, M. sternohyoideus; MDM, M. depressor mandibulae; MAME, M. adductor mandibulae externus; MAMP, M. adductor mandibulae posterior; MPtmed, M. pterygoideus medialis; MPtlat, M. pterygoideus lateralis; SOI, slow open phase one; SOII, slow open phase two; FO, fast open; FC, fast close; SC, slow close; PS, power stroke.

called PS phase in which the prey is crushed. However, the MAMEs shows no or very little activity during the SC/PS phase. Following the strike, the first few bites are clearly reduction bites, showing high jaw adductor activity during the SC/PS phase.

### DISCUSSION
#### Comparative kinematics

The kinematics of prey capture has been studied in a number of species. The behavior of *Iguana iguana* and *Sauromalus obesus* (Schwenk and Throckmorton, '89) is confirmed here. The maximal gape value of *Agama stellio* (42°) corresponds best to the values found for *Iguana iguana* (42°) and *Sauromalus obesus* (38°). The relative tongue protrusion distances range from 0.17–0.54 (Schwenk and Throckmorton, '89). In *Agama stellio* this value is 0.18, again best corre-

sponding to the values for *Iguana* (0.2) and *Sauromalus* (0.17). However, *Agama stellio* has a longer total strike cycle (374 ms) than do *Dipsosaurus dorsalis* (292 ms) and *Phrynocephalus helioscopus* (281 ms) (Schwenk and Throckmorton, '89).

The only other study dealing with prey capture by agamids is that of *Agama agama* (Kraklau, '91), using high-speed video recordings. The results reported here for *Agama stellio* are similar to those for *Agama agama*. The most striking differences are the duration of the total cycle, the beginning of the FO phase, and the timing of the lunge phase. In *Agama stellio* the FO phase always starts at prey contact, whereas the FO phase of *Agama agama* seems to start well before prey contact (Fig. 7) (Kraklau, '91). Unfortunately, Kraklau ('91) does not include a table giving the duration of different kinematic phases. In *Agama agama* the total cycle lasts on average 949 ms (Table 1, GAPECYC), whereas in *Agama stellio* it lasts only about 374 ms. However, in *Agama stellio* the first activity in some of the muscles involved in the strike (hyoglossus, genioglossus) starts approximately 80 ms before any jaw opening movement is present. This huge difference in duration might be related to the different ways in which the strike takes place in the two animals. We defined the beginning of the slow opening phase, and thus the strike, as the moment when the mouth starts to open; the lizard then begins to move towards the prey. Kraklau ('91) defined the beginning of a strike sequence in *Agama agama* as coinciding with the beginning of the preparatory phase, during which the gape gradually increases and the tongue is protruded. At the end of this preparatory phase the tongue is situated 4 mm beyond the gape, although no body movements have occurred yet. A rapid forward body movement only occurs during the following lunge phase (Kraklau, '91). In *Agama stellio*, on the other hand, the protrusion of the tongue coincides with the displacement of the body towards the prey (Fig. 3). This difference in strike behavior might be related to ecological differences in foraging strategies between the two species (a typical sit-and-wait ambush foraging vs. a more active foraging strategy).

Prey capture kinematics have been studied in several iguanid species. The results for *Agama stellio* are similar to those for *Anolis equestris* (Bels, '90), as far as gape profiles and tongue movements are concerned. How-

ever, one major difference lies in the presence or absence of an SOII phase; Bels ('90) argues that the SOII phase may be completely absent in *A. equestris*. In *A. stellio* this stage invariably occurred during prey capture, even when the lizards were offered only very small prey items. Another difference lies in the head movement after prey contact. In *Agama stellio* the anterior movement of the head continues into FC, whereas in *Anolis equestris* the head movement is reversed at maximal gape. This difference was also found when comparing prey capture in *Anolis equestris* with prey capture in *Oplurus cuvieri* (Bels and Delheusy, '92). For *Oplurus cuvieri* (Delheusy and Bels, '92), a strike cycle shows SOI and -II, FO, and FC phases. No slow close and/or power stroke phases are recognized. Relative phase durations are very similar to those found for *Agama stellio*, but the maximal gape value is smaller for *Oplurus* (35°). Although *Anolis carolinensis* does not use its tongue in prey capture (Bels and Goosse, '90), its gape profiles are very similar to those of other iguanids, as well as to those of *Agama stellio*.

Comparison of prey capture kinematics of *Agama stellio* with those of chameleons (*Chamaeleo dilepis*, Bels and Baltus, '87; *Chamaeleo oustaleti*, Wainwright et al., '91; *Chamaeleo jacksonii*, Wainwright and Bennett, '92a) indicates that the latter show no body displacement during prey capture, perhaps because they can project the tongue up to twice their body length. Also, in chameleons the head is depressed during tongue retraction, whereas the head of *Agama stellio* is elevated during this phase. The elevation of the head during tongue retraction in *A. stellio* most likely reflects the fact that in our experiments, prey is provided on the ground so that the head has to be depressed during projection of the tongue. As the chameleons were offered prey positioned at the level of the head (Wainwright et al., '91), no initial depression was required. The depression of the head observed during tongue retraction in chameleons might facilitate the retraction of the tongue, which is pulled downwards by gravity.

Unfortunately, very little data exist on prey capture in scleroglossan lizards. Prey capture has been examined only for *Lacerta viridis* (Bels and Goosse, '90; Goosse and Bels, '92) and *Trachydosaurus rugosus* (Gans et al., '85). For the latter, only a qualitative description of prey capture is present. These papers suggest that the main difference between scleroglossans and iguanians lies in the first phase of the jaw cycle. Scleroglossans show no SO phase. This absence of SO apparently relates to jaw-mediated prey capture (although *Trachydosaurus* uses its tongue to draw a prey item across the ground to its mouth, the tongue is not used to lift the prey item into the mouth), which does not involve SO. However, jaw-mediated prey capture in *Anolis carolinensis* does show an SO phase (Bels and Goosse, '90), making it tempting to assume that the pattern seen in Iguanidae (tongue prehension, gape profile with SO) is a secondary modification of the basic pattern (jaw prehension, gape profile without SO). Within the Iguania, tongue-mediated prey capture could be considered as plesiomorphic. However, to test this view, one needs muscle activity patterns of prey capture in members of the Iguanidae.

All these presently available studies suggest no striking differences in prey capture kinematics between iguanids and agamids. However, iguanians and scleroglossans do differ markedly, thus further supporting the existence of two monophyletic lineages within the squamata (Schwenk, '88; Estes et al., '88), and demonstrating a strong correlation between phylogeny and tongue function.

### Comparative EMG

The only lepidosaurian species for which electromyographical data of the prey capture process are available are *Sphenodon punctatus* (Gorniak et al., '82) and *Chamaeleo jacksonii* (Wainwright and Bennett, '92a).

When catching a prey item, *Sphenodon* uses either lingual or jaw prehension, depending on size of the prey. Big prey (newborn mice) are caught with the jaws, and small prey (crickets, cockroaches) are caught by use of the tongue (Gorniak et al., '82). Unfortunately, no tongue or hyoid muscles were examined in *Sphenodon punctatus*, so that the comparison will be restricted to jaw muscle activity patterns.

The first muscle to become active during prey capture in *Sphenodon* is the anterior part of the depressor mandibulae, followed by its posterior part. This activity is maintained until maximal gape, when the jaw closers show their first activity. The only jaw closer that shows a low-level activity just prior to maximal gape is the superficial part of the MAME. At maximal gape all jaw closers become more active, reaching their highest activity level when the teeth touch the

prey item. This activity in the jaw closers is maintained until the prey is crushed.

The first difference seen when comparing these results with our results for *Agama stellio* is that in *Sphenodon* no adductor activity is present during the first part of the opening phase (no division in a slow and a fast opening phase is apparent during prey capture). Although no tongue muscle activity patterns in *Sphenodon* were recorded, it is striking that the depressor shows a pronounced activity from the beginning of the opening of the mouth, whereas in *Agama stellio* there is very little activity during this phase in the depressor. A final difference is the absence of a pause in the adductor activity between the closing and the crushing phases. Some differences might be explained by examining prey capture kinematics. When *Sphenodon* catches a prey item with its tongue, the tongue is first protruded without curving of the dorsal surface. Meanwhile, the jaws are opened and tongue clearance is present from the beginning (Fig. 4B in Gorniak et al., '82). It is only when the mouth is already half-opened that the dorsal surface of the tongue becomes curved. However, in *Agama stellio* the tongue bulges immediately upon protrusion, and it is the tongue that depresses the lower jaw. This explains why *Agama stellio* shows very little activity in the jaw opener, at least until the onset of the fast opening of the mouth. Thus *Sphenodon* shows a gape profile without a distinct SO phase, as seen in scleroglossans, rather than an iguanian gape profile. In comparison with the gape profile of *Sphenodon* (with no SO phase), the iguanian gape profile, showing tongue protrusion with an immediate curving of the dorsal surface of the tongue, represents a derived feature. Because *Sphenodon* catches bigger prey items with its jaws (gape profile lacks SO phase), tongue prehension, both here and in the Iguania, could thus be considered to be derived, and the scleroglossan jaw prehension should thus represent the plesiomorphic condition. In this case, the jaw prehension of iguanians, as seen in *Anolis carolinensis* (Bels and Goosse, '90), would represent a secondary modification because the gape profile retains features of tongue-mediated prey capture.

The function of all major tongue and hyoid muscles, as well as of several jaw closers and the jaw opener, was examined during prey capture by *Chamaeleo jacksonii*. Comparison of the prey capture process in *Chamaeleo*
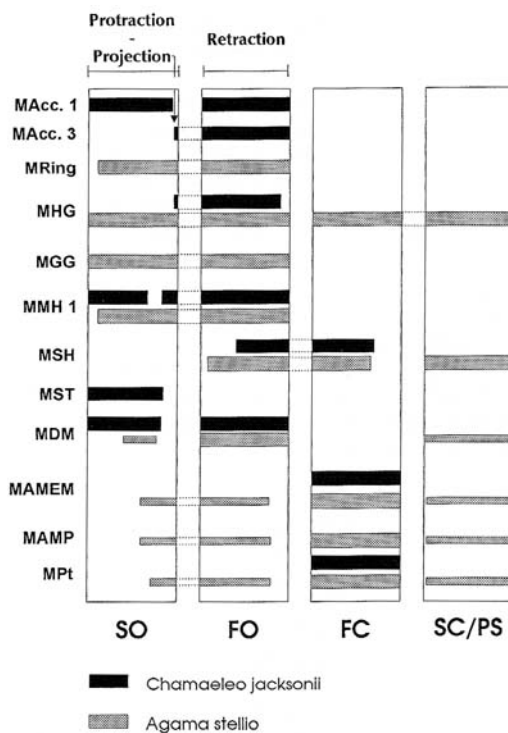


Fig. 9. Comparative EMG bar diagrams of the activity pattern in jaw and hyolingual muscles during the strike in *Chamaeleo jacksonii* (solid bars) and *Agama stellio* (stippled bars). Narrow bars represent low-amplitude activity. Dashed lines indicate that activity is continuous over phase boundaries. The MST is present in agamids, but its activity pattern was not recorded for *Agama stellio*. The MAcc. 1 in the Chamaeleonidae is considered to be the homologue of the MRing in the Agamidae. Data for *Chamaeleo jacksonii* were taken from, and modified after, Wainwright and Bennett ('92a). MAcc. 1, M. accelerator region 1 (posterior); MAcc. 3, M. accelerator region 3 (anterior); MRing, ring muscle; MHG, M. hyoglossus; MGG, M. genioglossus; MMH 1, M. mandibulohyoideus 1; MSH, M. sternohyoideus; MST, M. sternothyroideus; MDM, M. depressor mandibulae; MAMEM, M. adductor mandibulae externus medialis; MAMP, M. adductor mandibulae posterior; MPt, M. pterygoideus; SO, slow open; FO, fast open; FC, fast close; SC, slow close; PS, power stroke.

and in *Agama stellio* requires consideration of the differences in time scale present (up to 1,500 ms for *Chamaeleo;* 400 ms for *Agama stellio*). Figure 9 illustrates and allows comparison of the muscle activity patterns during the strike in *Chamaeleo jacksonii* (Wainwright and Bennett, '92a) and *Agama stellio* on the same relative time scale. The SO phase in *Chamaeleo* is marked by activity in the hyoid protractor, followed by activity in the accelerator muscle. The accelerator becomes

silent 10 ms before the actual projection. A second activity burst occurs 15 ms after the onset of tongue projection, corresponding in part to the activity in the homologous ring muscle of *Agama stellio*. The latter also shows a double burst pattern (Fig. 6), but the timing of the activity period of the two bursts differs. In *Agama stellio* the first burst lasts until maximal gape is achieved and is then followed by a burst of lower amplitude. However, the MHG shows a major difference in motor pattern. In *Chamaeleo*, this muscle becomes active only 10 ms prior to, or at the onset of, tongue projection; it remains active throughout the entire retraction of the tongue, whereas in *Agama stellio* this muscle is the first one to show any activity during the strike.

Nevertheless, the muscle remains active during FO and FC, and the muscle can thus cooperate with the MSH to retract the hyoid and tongue. Two major functional roles might be attributed to the hyoglossus muscle in *Agama stellio*. Its most obvious role is that of retracting the tongue in cooperation with the hyoid retractors, and also of rigidifying a basically flaccid structure, thus facilitating its projection along a fixed trajectory. Throughout this process the tongue is curved dorsally, thus rotating its dorsal side into an anterior position. The hyoglossus muscle in Agamidae is well-suited for this purpose, as it traverses the tongue, from base to anterior tip.

### The tongue projection mechanism in agamids and its phylogenetic significance

Smith ('88) used a morphological study of the tongue, the hyoid, and their musculature to formulate a hypothesis on the tongue projection mechanism in agamids. According to Smith, contraction of the circular ring muscle produces force against the lingual process, causing the tongue to slide anteriorly, as the coefficient of friction between the tongue and the lingual process is low. Hence, tongue protrusion requires simultaneous activity in the ring muscle and the genioglossus. Because such simultaneous activity is indeed observed during tongue projection in *Agama stellio*, our results do not contradict this hypothesis.

The observation of a chameleon-like tongue protrusion mechanism in the agamid *Phrynocephalus helioscopus* led Schwenk and Bell ('88) to hypothesize a three-part transformation series for tongue protrusion. In the first step, protraction of the hyoid, combined with activity in the extrinsic tongue muscles, protrudes the tongue. The next step includes an additional lingual translation, allowing the protrusion of the tongue beyond the mandibular margin; this includes increased activity in the intrinsic lingual muscles. The final step includes forceful action of the intrinsic muscles, translating the tongue off the end of the entoglossal process. Thus, the agamid mechanism is considered as intermediate (step 2 in the transformation series), the chameleon mechanism being the most derived state. Observations of *Agama stellio* suggest that agamids can indeed be considered as transitional forms, in which the intrinsic musculature cooperates during tongue protrusion, although some aspects of the basic mechanism, e.g., protraction of the hyoid, are retained. A mechanical basis for such a transformation series was proposed by Smith ('88), involving: 1) anterior pull by the MGG; 2) in agamids, sliding of the whole tongue on the entoglossal process as a result of activity in the ring muscle; and 3) in chameleonids, generation of higher forces on the lingual process to produce ballistic projection.

Three morphological changes can be added to the model of Smith ('88) to allow for an evolutionary transformation process from an agamid to a chameleonid tongue projection mechanism. First, the genioglossus muscle is lost and no longer restrains the tongue upon projection. Second, the entoglossal process is elongated (cf. Smith, '88), allowing high force-production and maximal acceleration of the tongue. Third, the hyoglossal musculature has to change. The changes that are required include changes in muscle architecture (perforation of the Z regions; Rice, '73) allowing supercontractability, and changes in the underlying motor pattern controlling tongue and hyoid muscles. Most likely, the change in motor pattern controlling the hyoglossus muscle is one of the key derived features in the chameleon tongue projection mechanism.

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