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QUANTITATIVE ANALYSIS OF JAW AND HYOLINGUAL MUSCLE ACTIVITY DURING FEEDING IN THE LIZARD *AGAMA STELLIO*

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Summary

The activity of jaw and hyolingual muscles during the entire feeding sequence is examined in the lizard *Agama stellio*, with special focus on the intraoral transport and swallowing stages. Correlation of electromyography (EMG) data with kinematics shows that the kinematic phases (slow opening, SO; fast opening, FO; fast closing, FC; slow closing/power stroke, SC/PS) are characterised by distinct activities in the jaw and hyolingual muscles. The SO phase is clearly the result of tongue protraction (upon protraction, the tongue is pulled against the prey and consequently the lower jaw is pushed down), whereas the FO phase is caused by activity in the jaw opener and dorsal cervical muscles. Both the FC and SC/PS phases are characterised by pronounced activity in the jaw adductor muscles. Tongue retraction is produced by activity in the hyoid and tongue retractor muscles. A quantitative analysis of time-related EMG data shows that, in accordance with the kinematic analyses, three different stages can be recognised as components of the feeding cycle: prey capture, intraoral transport and swallowing. However, analysis of intensity-related data allowed a fourth stage, crushing, to be detected. Whereas there are indications that prey capture, intraoral transport and swallowing are controlled by different motor patterns, the differences between crushing and transport are likely to be caused by feedback mechanisms. Our results show the importance of including intensity-related data in quantitative analyses of EMG recordings in order to discriminate between feeding stages. Additionally, it is shown that both the jaw and the hyolingual muscles play crucial roles during feeding. During all stages, movements of the hyolingual apparatus are an essential part of the feeding cycle. Thus, when examining lizard feeding mechanisms, the activity patterns of the hyolingual muscles should not be neglected.

Key words: electromyography, EMG, feeding, behaviour, lizard, *Agama stellio*, jaw muscle, hyolingual muscle, kinematics.

Introduction

On the basis of observations on regularly chewing tetrapods (e.g. ruminating ungulates), it has been suggested that mammalian feeding cycles might be driven by simple motor pattern generators or neural oscillators (Thexton, 1974, 1976; Dellow, 1976). A comparable mechanism might also be applicable to the transport cycles of lower tetrapods since reptilian and mammalian transport cycles show many similarities (see Bramble and Wake, 1985). The mammalian masticatory cycle may therefore have evolved from the primitive reptilian chewing cycle with relatively little overall change in neuromotor programming (Bramble and Wake, 1985). However, as argued by Smith (1984), biting in lizards is irregular and takes place as independent chewing cycles, preceding or interrupting food transport, and so may not be driven by neural oscillators. Relatively few studies have examined reptilian jaw and hyolingual muscle activity patterns or their control mechanisms during feeding (Throckmorton, 1978; Gorniak *et al.* 1982; Smith, 1982, 1984, 1986; Gans *et al.* 1985; Gans and De Vree, 1986; Wainwright and Bennett, 1992*a*,*b*; Herrel *et al.* 1995). Hypotheses regarding the evolution of feeding cycles and the presence of neural oscillators in reptiles therefore remain speculative and need to be confirmed by further study.

It has likewise been suggested that a basic pattern of tongue function is present within vertebrates as a result of the retention of a primitive neural control pattern (Hiiemae *et al.* 1979; Bramble, 1980). However, the function of the tongue and hyolingual apparatus (especially the action patterns of the hyolingual muscles) remains poorly studied in lower tetrapods in general and in reptiles more specifically (Smith, 1984, 1986; Wainwright and Bennett, 1992*a*,*b*; Herrel *et al.* 1995).

Whether prey capture, intraoral transport and swallowing are driven by the same or a similar motor pattern in vertebrates remains unclear. Although it has been proposed that the intraoral transport cycle has an ancestral status with respect to prey capture for lower tetrapods in general, this may not be true for swallowing (Bramble and Wake, 1985). Tongue-dependent swallowing might even be a derived feature of

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amniotes (Bramble and Wake, 1985). Reptilian swallowing, in contrast to intraoral transport, is clearly divergent from the mammalian swallowing cycle. Whereas in mammals swallowing is integrated into the basic transport cycle, in lizards it seems to be a distinct stage (Smith, 1984). Relatively few studies have investigated prey capture, intraoral transport and swallowing in one animal (e.g. Delheusy and Bels, 1992; Urbani and Bels, 1995; Herrel *et al.* 1996), and no electromyographic studies investigating the activity of both jaw and hyolingual muscles during all feeding stages have been performed. Such an approach would allow the relationships between the feeding stages and the importance of the jaw and hyolingual systems to each of these stages to be examined.

The aims of the present study were, therefore, to provide a quantitative electromyographic analysis of the activity of the jaw and hyolingual muscles during the entire feeding sequence with a special focus on intraoral transport and swallowing in a lizard, *Agama stellio*. On the basis of these data, the role of the jaw and hyolingual muscles during different feeding stages, the relationships between them, and the evolution of the feeding cycle in lower tetrapods will be discussed.

Materials and methods

Specimens

Five adult *Agama stellio* L. (total length 20±3 cm; mass 42±3 g, means + S.D.) were used in experiments. The specimens were collected in Israel and provided by Dr E. Kochva. The animals were kept in a glass vivarium on a 12 h:12 h light:dark cycle and were provided with water and food, consisting of crickets, grasshoppers and mealworms, *ad libitum*. The environmental temperature varied from 26 °C during the day 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 (Bock and Shear, 1972) to characterize all jaw and hyolingual muscles. Drawings were made of all stages of the dissection using a Wild M3Z dissecting microscope with a *camera lucida*.

Electromyographic recordings and analysis

The animals used in the electromyographic (EMG) experiments were anaesthetized using an intramuscular injection of Ketalar (200 mg kg^{-1} body mass) before electrode implantation. Bipolar electrodes (25 cm long) were prepared from Teflon-insulated 0.065 mm Ni–Cr wire. The insulation was removed 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.

During the experiments, electrodes (a maximum of ten electrodes for one recording session) were placed in a number of muscle groups (for identification of muscles, see Fig. 1 and Table 1) of the major jaw closers: the musculus adductor mandibulae externus (superficial anterior and posterior, medial and profundus parts; MAMESA, MAMESP, MAMEM and MAMEP), the musculus pseudotemporalis (superficial and profundus parts; MPsTS and MPsTP), the musculus adductor mandibulae posterior (MAMP) and the musculus pterygoideus (lateral and medial parts; MPtlat and MPtmed). Electrodes were also placed in the jaw openers: the musculus depressor mandibulae (main and accessory heads; MDM and MDMA) and the musculus spinalis capitis (MSCa) and into several hyolingual muscles, the tongue protractors: the musculus genioglossus (lateral and medial parts; MGGL and MGGM); the musculus hyoglossus (MHG), the ring muscle (MRing); hyoid retractors: the musculus sternohyoideus (MSH), the musculus omohyoideus (MOH) and in the hyoid protractors: musculus mandibulohyoideus (parts 1 and 2; MMH1 and MMH2). Electrode placement was confirmed by dorsoventral and lateral X-rays after electrode implantation, and in two animals by dissection following experiments.

Electrical signals were amplified 2000 times with Tektronix 26A2 differential preamplifiers (range 100 Hz to 10 kHz) and Honeywell Accudata 117 d.c. amplifiers and recorded on a Honeywell 96 FM 14-channel tape recorder (medium bandpass) at a speed of 19.05 cm s^{-1}.

The recorded EMG signals were digitized at 10 kHz using a Keithley DAS series 500 12-bit A/D convertor. After digitization, the signals were integrated following the procedure of Beach *et al.* (1982) and the number of spikes (S) as well as the average amplitude (A) and mean number of spikes multiplied by the average amplitude ($S \times A$) per interval (bin) were calculated.

Twelve recording sessions were performed, each consisting of several feeding sequences. The results from two of these recording sessions (from two different animals) were analyzed quantitatively. These two recording sessions were chosen because they represented the maximal number of different jaw or hyolingual muscles implanted. The results from the other recording sessions were used in a qualitative analysis only. In the first recording session, results were obtained from four complete feeding sequences. This session included a total of four prey capture, 61 transport, 30 crushing and 79 swallowing cycles. Although ten electrodes were implanted during each recording session, only seven of these (and the pulse from the X-ray camera) could be amplified simultaneously. Thus, during the first two of these sequences (two prey capture, 43 transport, 15 crushing and 55 swallowing cycles), activity patterns from the MDM, MSCa, MAMESA, MPsTS, MAMP, MPtlat and MPtmed were recorded. During the following two sequences, activity patterns from the MDM, MAMESA, MAMEM, MPsTS, MAMP, MPtlat and MPtmed were recorded. The second recording session consisted of three sequences during which activity patterns of the MDM, MAMEM, MSH, MMH1, MGGM, MHG and MRing were recorded. This resulted in a total of three prey capture, 94 transport, 26 crushing and 67 swallowing cycles.

Time-based analysis of electromyograms

The muscle activity patterns recorded during a feeding sequence were first subdivided into separate cycles. Within one cycle, muscle activity patterns were subdivided into several

activity bursts (usually three) on the basis of abrupt amplitude differences, if present. This does not necessarily mean that there was always more than one burst present within each cycle. For each muscle, the onset and the duration of all bursts within one cycle (and for all cycles analyzed) were recorded. Onset variables are expressed relative to the offset (onset plus duration) of the main activity burst in the MDM (=time 0) as this corresponds well to the time of maximal gape.

Intensity-based analysis of electromyograms

As the number of spikes multiplied by the mean amplitude ($S \times A$) is a measure of the intensity of muscle recruitment (Basmajian and De Luca, 1985; Loeb and Gans, 1986), further analyses of intensity-related variables were based primarily on this variable. The means (mean), maxima (max) and sums (sum) of the recruitment levels (RL, where $RL=S \times A$) were calculated per bin (RL_{bin}), per bite cycle (RL_{bite}) and per burst (RL_{burst}) as muscles often showed more than one activity burst during the course of a gape and/or tongue cycle. Within each recording session, the maximal RL_{bite} values (max, sum, mean) recorded for each muscle were determined. The RL_{bite} data for all bite cycles within each recording session were then normalised for each muscle according to their respective maxima. Recruitment levels for each muscle are therefore expressed as a percentage of their maximal RL_{bite} values. A similar procedure was used on the RL_{burst} data, where all values were normalised to the maximal RL_{burst} value for each muscle.

Video and cineradiographic recordings

Video or cineradiographic recordings were obtained simultaneously with the EMG recordings. Cineradiography was carried out using a Siemens Tridoros-Optimatic 880 X-ray apparatus equipped with a Sirecon-2 image intensifier. Feeding bouts were recorded in side view using an Arriflex 16 mm ST camera equipped with a 70 mm lens at a film speed of 50 frames s^{-1}. Before cineradiography, small lead markers were inserted subcutaneously to mark the positions of the upper and lower jaws, the base and the top of the quadrate, the tongue, the frontal and parietal bones and dorsally into the neck using a hypodermic needle (see Herrel *et al.* 1996).

During implantation of the radio-opaque markers, animals were anaesthetized as described above. Placement of the markers was checked using dorsoventral and lateral X-ray photography. During cineradiographic recordings, prey items were injected with barium sulphate to help visualise their position.

Additional recordings of the feeding process were made at a higher filming speed (500 frames s^{-1}) using a NAC-1000 high-speed video system. Video torches (2.4 kW; Tri-Lite, Cool Light Co. Inc., Hollywood, USA) provided the necessary illumination. During both the cineradiographic and the high-speed video recording sessions, the animals were filmed in an acrylic cage (30 cm×10 cm×10 cm), while feeding on grasshoppers (body length 2–2.5 cm). The prey item was always placed less than 10 cm from the snout of the lizard. The output of a Tektronix wave-pattern generator was recorded together with the EMG recordings on the FM tape recorder and sent to a light-emitting diode placed in the field of view of the camera. This allowed synchronisation of the electromyographic and kinematic records. For a description of the video and cineradiographic analysis, see Herrel *et al.* (1996).

Statistical analyses

Several analyses were performed on the electromyographic data to explore similarities between successive feeding stages

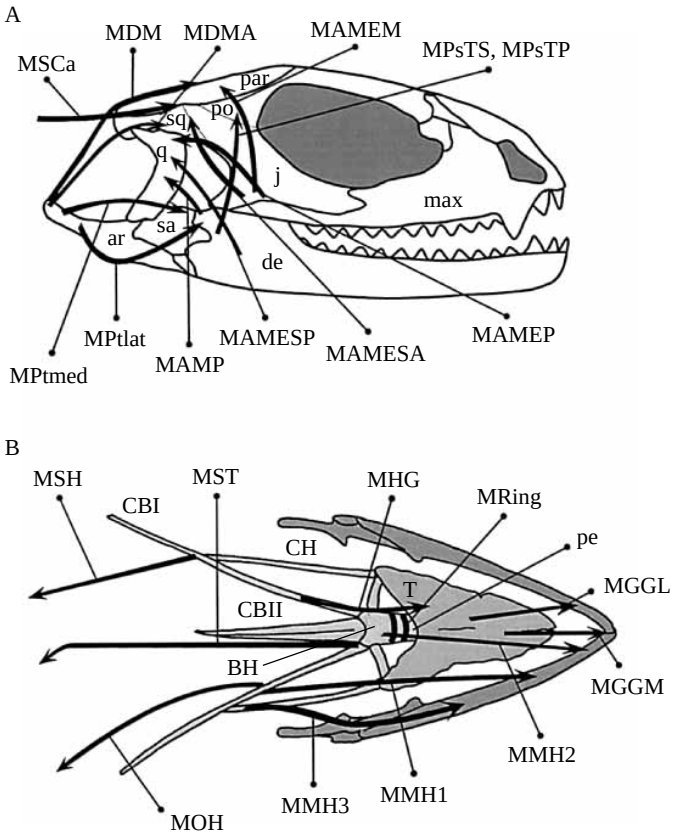

Fig. 1. Schematic representation of jaw and hyolingual muscles of *Agama stellio*. (A) Lateral view of the skull; (B) ventral view of the lower jaw and the hyolingual apparatus. Arrows indicate the major jaw muscles and hyolingual muscles and their predominant lines of action. ar, articulare; BH, basihyoid; CBI, ceratobranchiale 1; CBII, ceratobranchiale 2; CH, ceratohyale; de, dentale; j, jugale; MAMEM, m. adductor mandibulae externus medialis; MAMEP, musculus adductor mandibulae externus profundus; MAMESA, m. adductor mandibulae externus superficialis anterior; MAMESP, m. adductor mandibulae externus superficialis posterior; MAMP, m. adductor mandibulae posterior; max, maxilla; MDM, m. depressor mandibulae; MDMA, m. depressor mandibulae accessorius; MGGL, m. genioglossus lateralis; MGGM, m. genioglossus medialis; MHG, m. hyoglossus; MMH1, m. mandibulohyoideus 1; MMH2, m. mandibulohyoideus 2; MMH3, m. mandibulohyoideus 3; MOH, m. omohyoideus; MPsTS, m. pseudotemporalis superficialis; MPsTP, m. pseudotemporalis profundus; MPtlat, m. pterygoideus lateralis; MPtmed, m. pterygoideus medialis; MRing, ring muscle; MSCa, m. spinalis capitis; MSH, m. sternohyoideus; MST, m. sternothyroideus; par, parietale; pe, processus entoglossus; po, postorbitale; q, quadratum; sa, surangulare; sq, squamosum; T, tongue.

(prey capture, intraoral transport, swallowing). For these analyses, Statistica version 5.0 (Statsoft Inc.) was used.

First, a factor analysis (VARIMAX rotation) was performed on the data set consisting of the time-related variables (onset and duration variables for all muscles) of all bite cycles within one recording session. An analysis of variance (ANOVA) was then performed on the first three factors coupled to a Duncan multiple-range significance test (at the 0.05 level) to explore the relationships between the different stages (cycle types). Next, the same analysis was performed on the intensity-related data set including the RL_{bite} values (max, sum and mean) of all cycles from the first recording session (mainly jaw muscles). The same analysis was then performed on a similar data set from the second recording session (mainly hyolingual muscles).

Results

Morphology

The skull morphology of *Agama stellio* was described previously by El Toubi (1947) and Jollie (1960). *A. stellio* has very little or no intracranial mobility (A. Herrel, personal observations based on cineradiographic recordings during feeding). The hyoid apparatus has a distinct tapered entoglossal process, one pair of ceratohyals and two pairs of ceratobranchials (Fig. 1).

A schematic representation of the jaw and hyolingual muscles in *Agama stellio* is given in Fig. 1; the origins and insertions of the muscles are given in Table 1. For a more detailed description of the jaw and hyolingual muscles in *A. stellio*, see Herrel *et al.* (1995). For descriptions of the jaw and hyolingual musculature in agamids in general, see Gandolfi (1908), Gnanamuthu (1937), Haas (1973), Gomes (1974) and Smith (1988).

General description of prey capture

A feeding bout in *Agama stellio* consists of prey capture, intraoral transport (including both transport and crushing cycles; see Herrel *et al.* 1996) and swallowing. Prey capture always involves a lunge of the body and the use of the tongue to make contact with the prey. After prey contact, the jaws are opened further and the prey is taken into the mouth using the

Table 1. *Origin and insertion points of the jaw and hyolingual musculature in* Agama stellio

Muscle	Origin	Insertion
*m. depressor mandibulae (MDM)	Posterolateral edge of the parietal	Retroarticular process of the articular
m. depressor mandibulae accessorius (MDMA)	Dorsal face of the squamosal	Retroarticular process of the articular
*m. spinalis capitis (MSCa)	Neural spines of the cervical vertebrae	Posterior edge of the parietal
m. adductor mandibulae externus superficialis anterior (MAMESA)	Inner aspect of the temporal arch	Dorsolateral side of the lower jaw
*m. adductor mandibulae externus superficialis posterior (MAMESP)	Dorsal aspect of the quadrate	Posterolateral side of the dentary
*m. adductor mandibulae externus medialis (MAMEM)	Parietal and medial side of the squamosal	Basal aponeurosis
m. adductor mandibulae externus profundus (MAMEP)	Paraoccipital process of the exoccipital	Basal aponeurosis
*m. pseudotemporalis superficialis (MPsTS)	Anteroventral side of the parietal	Medial side of the lower jaw
m. pseudotemporalis profundus (MPsTP)	Dorsal side of the epipterygoid	Medial side of the lower jaw
*m. adductor mandibulae posterior (MAMP)	Quadrate	Medial side of the lower jaw, posterior to the coronoid process
*m. pterygoideus lateralis (MPtlat)	Ventral side of the pterygoid and ectopterygoid	Lateral side of the articular
*m. pterygoideus medialis (MPtmed)	Lateroventral side of the pterygoid	Medioventral side of the articular
†m. sternothyroideus (MST)	Episternum	Basihyoid
*m. sternohyoideus (MSH)	Episternum plus interclavicula	First ceratobranchial
m. omohyoideus (MOH)	Anterior edge of interclavicula and suprascapula	First ceratobranchial
*m. mandibulohyoideus I (MMH1)	Medial side of the dentary	First ceratobranchial
m. mandibulohyoideus II (MMH2)	Anteromedial side of the dentary (near the mandibular symphysis)	Basihyoid plus proximal part of the first ceratobranchial
†m. mandibulohyoideus III (MMH3)	Posteromedial side of dentary	Ceratohyal
*m. hyoglossus (MHG)	First ceratobranchial	Tongue
*m. genioglossus medialis (MGGM)	Anteromedial side of the dentary	Medial side of the tongue
m. genioglossus lateralis (MGGL)	Anteromedial side of the dentary (posterior to that of the MGGM)	Lateral side of the tongue
*m. verticalis (MRing)	Surrounds the entoglossal process	

* denotes the muscles from which EMG recordings were used in the quantitative analysis.
† denotes the muscles from which no EMG recordings were made.

Table 2. *Average onset and duration times and intensity-related variables of jaw and hyolingual muscle activity during transport*

Muscle	Burst	Burst presence (%)	Onset (ms)		Duration (ms)		Average intensity (%)		
			Mean	S.D.	Mean	S.D.		Mean	S.D.
MDM	Pre	13	–100	12	110	43	*S*	54	17
	Main	100	–71	63	71	26	*A*	37	17
	Post	100	6	76	156	73	*S*×*A*	32	21
MSCa	Pre	14	–42	47	17	5	*S*	48	21
	Main	100	–67	54	69	32	*A*	37	23
	Post	95	15	83	165	112	*S*×*A*	25	24
MAMESA	Pre	68	–64	55	38	49	*S*	36	23
	Main	93	30	84	121	78	*A*	23	23
	Post	73	249	121	114	123	*S*×*A*	20	25
MAMEM	Pre	100	–56	59	53	53	*S*	53	20
	Main	100	48	87	129	50	*A*	35	28
	Post	89	326	162	93	95	*S*×*A*	32	31
MPsTS	Pre	85	–52	60	31	19	*S*	56	22
	Main	98	23	73	136	59	*A*	34	26
	Post	53	261	125	34	27	*S*×*A*	29	28
MAMP	Pre	83	–82	37	42	35	*S*	44	19
	Main	100	9	72	145	68	*A*	28	20
	Post	90	220	106	174	150	*S*×*A*	20	20
MPtmed	Pre	98	–93	31	81	57	*S*	54	17
	Main	100	5	71	157	58	*A*	39	23
	Post	83	201	105	152	126	*S*×*A*	30	25
MPtlat	Pre	88	–87	24	62	49	*S*	56	18
	Main	100	5	71	163	61	*A*	32	15
	Post	90	201	108	209	156	*S*×*A*	23	17
MSH	Pre	59	–303	32	181	94	*S*	52	19
	Main	100	–138	196	226	165	*A*	27	16
	Post	35	15	96	78	32	*S*×*A*	21	16
MMH1	Pre						*S*	53	22
	Main	98	–296	78	242	127	*A*	41	23
	Post	87	11	132	110	63	*S*×*A*	30	23
MGGM	Pre						*S*	66	17
	Main	98	–307	29	339	123	*A*	49	21
	Post	72	45	123	50	31	*S*×*A*	38	22
MRing	Pre						*S*	59	18
	Main	100	–303	47	343	133	*A*	31	18
	Post	69	27	104	104	57	*S*×*A*	25	19
MHG	Pre						*S*	67	16
	Main	100	–306	41	397	161	*A*	36	20
	Post	29	46	212	114	70	*S*×*A*	27	18

Onset variables were measured from the time of maximal gape (offset of the main activity burst in the MDM) to the onset of the muscle burst. Different bursts in the same muscle within one cycle are referred to as pre, main and post bursts. The main burst is the first activity burst in which muscles are fully active; this burst is often preceded by an activity burst of low intensity (pre) and followed by a burst of either high or low intensity (post).

Burst presence indicates the number of times that burst was present in the analyzed sequences (% occurrence).

The average intensity values are averaged over the total cycle and expressed relative to the maximal value recorded for each muscle in all analyzed sequences (N=61 for the MDM, MAMESA, MPsTS, MAMP, MPtmed and MPtlat; N=43 for the MSCa; N=18 for the MAMEM; N=94 for the MSH, MMH1, MGGM, MRing and MHG).

S, number of spikes; *A*, average amplitude; *S*×*A*, number of spikes multiplied by average amplitude.

See Fig. 1 for definitions of muscle abbreviations.

Table 3. *Average onset and duration times and intensity-related variables of jaw and hyolingual muscle activity during crushing*

Muscle	Burst	Burst presence (%)	Onset (ms)		Duration (ms)		Average intensity (%)		
			Mean	S.D.	Mean	S.D.		Mean	S.D.
MDM	Pre	21	–96	8	32	19	*S*	53	12
	Main	100	–66	53	66	19	*A*	36	12
	Post	100	8	60	186	72	*S*×*A*	33	16
MSCa	Pre	33	–85	25	13	5	*S*	47	14
	Main	100	–73	34	58	15	*A*	39	17
	Post	89	0	46	279	149	*S*×*A*	27	19
MAMESA	Pre	75	–92	24	43	33	*S*	42	16
	Main	100	28	72	108	64	*A*	33	21
	Post	75	262	178	91	76	*S*×*A*	26	24
MAMEM	Pre	93	–65	51	32	13	*S*	64	11
	Main	100	33	68	141	47	*A*	48	23
	Post	100	320	184	104	93	*S*×*A*	43	22
MPsTS	Pre	96	–54	55	38	20	*S*	63	16
	Main	100	12	59	145	57	*A*	41	23
	Post	100	286	260	84	78	*S*×*A*	35	25
MAMP	Pre	96	–68	43	36	26	*S*	49	16
	Main	100	10	59	148	51	*A*	33	19
	Post	92	217	123	319	287	*S*×*A*	22	19
MPtmed	Pre	96	–73	52	60	30	*S*	63	19
	Main	100	3	57	163	56	*A*	50	25
	Post	96	198	99	199	158	*S*×*A*	43	28
MPtlat	Pre	83	–71	45	56	35	*S*	60	18
	Main	100	2	56	166	57	*A*	34	15
	Post	100	198	118	371	341	*S*×*A*	26	16
MSH	Pre	81	–343	19	146	99	*S*	52	13
	Main	100	–90	221	190	87	*A*	45	23
	Post	31	28	192	130	112	*S*×*A*	32	17
MMH1	Pre						*S*	47	17
	Main	100	–313	95	245	110	*A*	36	19
	Post	88	–25	137	149	60	*S*×*A*	23	20
MGGM	Pre						*S*	57	16
	Main	100	–321	105	311	121	*A*	39	21
	Post	96	6	158	99	86	*S*×*A*	29	22
MRing	Pre						*S*	49	15
	Main	100	–328	76	320	120	*A*	21	13
	Post	92	24	188	150	157	*S*×*A*	15	13
MHG	Pre						*S*	61	15
	Main	100	–340	28	414	192	*A*	33	16
	Post	35	62	223	171	71	*S*×*A*	24	15

Onset variables were measured from the time of maximal gape (offset of the main activity burst in the MDM) to the onset of the muscle burst. Different bursts in the same muscle within one cycle are referred to as pre, main and post bursts. The main burst is the first activity burst in which muscles are fully active; this burst is often preceded by an activity burst of low intensity (pre) and followed by a burst of either high or low intensity (post). Burst presence indicates the number of times that burst was present in the analyzed sequences (% occurrence).

The average intensity values are averaged over the total cycle and expressed relative to the maximal value recorded for each muscle in all analyzed sequences (N=30 for the MDM, MAMESA, MPsTS, MAMP, MPtmed and MPtlat; N=15 for the MSCa; N=15 for the MAMEM; N=26 for the MSH, MMH1, MGGM, MRing and MHG).

S, number of spikes; *A*, average amplitude; *S*×*A*, number of spikes multiplied by average amplitude.

See Fig. 1 for definitions of muscle abbreviations.

Table 4. *Average onset and duration times (ms) and intensity-related variables (%) of jaw and hyolingual muscle activity during swallowing*

Muscle	Burst	Burst presence (%)	Onset (ms)		Duration (ms)		Average intensity (%)		
			Mean	S.D.	Mean	S.D.		Mean	S.D.
MDM	Pre	41	–122	223	84	83	*S*	40	19
	Main	93	–98	279	98	75	*A*	15	12
	Post	50	63	311	60	61	*S*×*A*	10	12
MSCa	Pre	22	–255	54	21	25	*S*	21	16
	Main	35	–112	239	73	78	*A*	12	13
	Post	67	55	249	37	53	*S*×*A*	4	5
MAMESA	Pre	43	–141	209	118	122	*S*	14	12
	Main	54	201	365	69	52	*A*	5	7
	Post	19	265	296	100	79	*S*×*A*	2	5
MAMEM	Pre	63	–111	227	77	46	*S*	40	19
	Main	100	255	386	129	43	*A*	15	12
	Post	29	324	251	160	76	*S*×*A*	10	12
MPsTS	Pre	27	–155	166	29	34	*S*	35	18
	Main	87	75	310	47	30	*A*	8	6
	Post	17	323	392	18	14	*S*×*A*	4	4
MAMP	Pre	60	–216	143	110	107	*S*	35	10
	Main	99	18	300	273	183	*A*	9	5
	Post	64	284	304	171	129	*S*×*A*	4	4
MPtmed	Pre	66	–125	196	93	114	*S*	27	17
	Main	93	66	318	68	61	*A*	8	12
	Post	33	223	265	145	179	*S*×*A*	5	10
MPtlat	Pre	74	–270	41	219	264	*S*	47	15
	Main	100	53	281	169	64	*A*	16	9
	Post	56	261	290	196	218	*S*×*A*	10	8
MSH	Pre	45	–236	186	88	95	*S*	32	18
	Main	100	–207	211	199	138	*A*	13	14
	Post	52	127	242	98	62	*S*×*A*	10	15
MMH1	Pre	10	–369	46	67	38	*S*	35	22
	Main	96	–301	179	212	136	*A*	23	20
	Post	57	–7	229	76	51	*S*×*A*	13	18
MGGM	Pre	4	–382	17	113	61	*S*	56	21
	Main	94	–344	149	390	108	*A*	35	19
	Post	25	103	207	46	31	*S*×*A*	25	18
MRing	Pre	6	–396	26	100	85	*S*	39	19
	Main	97	–362	146	413	149	*A*	15	12
	Post	46	109	211	139	107	*S*×*A*	10	11
MHG	Pre	10	–409	16	109	72	*S*	46	18
	Main	100	–372	132	443	154	*A*	17	14
	Post	54	136	242	121	90	*S*×*A*	12	13

Onset variables were measured from the time of maximal gape (offset of the main activity burst in the MDM) to the onset of the muscle burst. Different bursts in the same muscle within one cycle are referred to as pre, main and post bursts. The main burst is the first activity burst in which muscles are fully active; often this burst is preceded by an activity burst of low intensity (pre) and followed by a burst of either high or low intensity (post).

Burst presence indicates the number of times that burst was present in the analyzed sequences (% occurrence).

The average intensity values are averaged over the total cycle and expressed relative to the maximal value recorded for each muscle in all analyzed sequences (N=79 for the MDM, MAMESA, MPsTS, MAMP, MPtmed and MPtlat; N=55 for the MSCa; N=22 for the MAMEM; N=67 for the MSH, MMH1, MGGM, MRing and MHG).

S, number of spikes; *A*, average amplitude; *S*×*A*, number of spikes multiplied by average amplitude.

See Fig. 1 for definitions of muscle abbreviations.

tongue (Herrel *et al.* 1995). Once the prey has been seized, a number of cyclic movements of the jaws and tongue are used to crush the prey and to transport it to the back of the oral cavity. Once the prey item has been adequately reduced and positioned lengthwise within the mouth, swallowing occurs. During swallowing, the tongue is first used to pull and then to push the prey down into the oesophagus (Herrel *et al.* 1996).

Electromyography

Quantitative analysis

On the basis of the movements of jaws and tongue, three distinct stages (prey capture, intraoral transport and swallowing) can be recognised in *Agama stellio* (Herrel *et al.* 1996). In order to investigate whether each of these stages is characterised by a distinct motor activation pattern, a quantitative analysis of the EMG data was performed. For prey capture, the EMG data reported by Herrel *et al.* (1995) from the same set of experiments were used.

Time-based data from the first recording session are given in Tables 2–4. Muscle activity patterns during three cycle types [prey capture (see Herrel *et al.* 1995), swallowing and intraoral transport] differ significantly (all effects: Rao's R=27.2, P<0.01, d.f.=9, 318; univariate F-tests: factor 1, F=34.3, P<0.01; factor 2, F=40.1, P<0.01; factor 3, F=3.9, P=0.01, d.f.=3, 133). Using univariate analysis, the first factor (eigenvalue 15.0; 35.7 % of variation explained) separates prey capture significantly from both other stages. The onset variables for the pre and main burst of all muscles except for the MPtlat show high loadings on the first factor and can thus be used to discriminate between prey capture and the other stages (see Table 5). For the second factor (eigenvalue 7.0; 16.6 % of variation explained), prey capture and swallowing are separated from intraoral transport. Only the onset of the post burst of the MAMESA as well as the duration of the post burst of the MPtlat and MDM show high loadings on this factor (Table 5). For the third factor (eigenvalue 3.5; 8.2 % of variation explained), the different stages are no longer separated.

Using the intensity-related data (Tables 2–4) from both the first (all effects: Rao's R=18.6, P<0.01, d.f. 9, 409; univariate F-tests: factor 1, F=9.6, P<0.01; factor 2, F=19.6, P<0.01; factor 3, F=16.2, P<0.01, d.f.=3, 170) and the second (all effects: Rao's R=18.8, P<0.01, d.f.=12, 495; univariate F-tests: factor 1, F=10.7, P<0.01; factor 2, F=48.3, P<0.01; factor 3, F=2.3, P=0.05, d.f.=4, 189) recording sessions, four stages (including crushing) are significantly different from one another. For data from the first recording session, prey capture and swallowing are separated by the first factor (eigenvalue 11.7; 64.7 % of variation explained), whereas crushing is separated from all other stages by the second factor (eigenvalue 2.4; 13.4 % of variation explained) and transport cycles are separated from all other stages by the third factor (eigenvalue

Table 5. *Results from the factor analysis: rotated factor matrix based on a timing-related (onset and duration variables) data set containing all bites from the first recording session*

Variable	Factor 1	Factor 2	Factor 3
Onset pre burst MAMESA	0.94	0.07	0.01
Onset main burst MDM	0.93	–0.12	0.24
Onset main burst MAMP	0.93	–0.12	0.25
Onset pre burst MPtmed	0.92	–0.08	–0.06
Onset main burst MPsT	0.90	–0.12	0.25
Onset main burst MPtmed	0.90	–0.17	0.28
Duration pre burst MDM	0.89	0.08	0.25
Onset pre burst MPsT	0.88	0.17	–0.17
Duration pre burst MAMP	0.87	0.07	0.02
Onset main burst MAMESA	0.87	–0.04	0.27
Onset post burst MDM	0.80	0.17	0.07
Duration post burst MDM	–0.07	0.78	–0.26
Duration post burst MPtlat	–0.12	0.73	0.02
Onset post burst MAMESA	0.05	0.72	0.27

Only variables with factor loadings higher than 0.7 on factor 1 (top) and factor 2 (bottom) are given.

Variation explained: factor 1, 35.7 %, eigenvalue 15; factor 2, 16.6 %, eigenvalue 7; factor 3, 8.2 %, eigenvalue 3.5.

See Fig. 1 for definitions of muscle abbreviations.

Table 6. *Results from factor analysis: rotated factor matrix based on an intensity-related (sum, maximum and mean* S×A *values) data set containing all bites from the first recording session*

Variable	Factor 1	Factor 2	Factor 3
Mean *S*×*A* MPtmed	0.89	0.30	0.17
Sum *S*×*A* MPtmed	0.89	0.21	0.22
Maximum *S*×*A* MPtmed	0.88	0.23	0.29
Mean *S*×*A* MPtlat	0.80	0.20	0.29
Maximum *S*×*A* MPtlat	0.75	0.23	0.48
Sum *S*×*A* MPtlat	0.75	0.18	0.35
Sum *S*×*A* MAMESA	0.08	0.91	0.21
Mean *S*×*A* MAMESA	0.18	0.90	0.17
Mean *S*×*A* MAMP	0.30	0.83	0.17
Sum *S*×*A* MAMP	0.19	0.82	0.22
Maximum *S*×*A* MAMESA	0.14	0.82	0.33
Mean *S*×*A* MPsT	0.54	0.75	0.14
Sum *S*×*A* MPsT	0.55	0.75	0.14
Maximum *S*×*A* MAMP	0.46	0.70	0.35
Mean *S*×*A* MDM	0.27	0.23	0.85
Sum *S*×*A* MDM	0.40	0.27	0.80
Maximum *S*×*A* MDM	0.42	0.39	0.76

Only variables with factor loadings higher than 0.7 on factor 1 (top), factor 2 (middle) and factor 3 (bottom) are given.

Variation explained: factor 1, 64.7 %, eigenvalue 11.7; factor 2, 13.4 %, eigenvalue 2.4; factor 3, 6.2 %, eigenvalue 1.1.

See Materials and methods for explanation of muscle activity variables.

S, number of spikes; *A*, mean amplitude.

See Fig. 1 for definitions of muscle abbreviations.

1.1; 6.2 % of variation explained). Both the MPtlat and the MPtmed *RL* (=*S*×*A*) show high loadings on the first factor (Table 6). Since prey capture and swallowing are separated by the first factor, the difference between these two stages is mainly caused by the activity of the MPt. The recruitment levels of the MAMESA, MPsT and MAMP show high loadings on the second factor, thus indicating their importance in separating crushing from the other stages (Table 6). The jaw opener (MDM) *RL* value shows high loadings on the third factor and can therefore be considered to be useful in separating transport from the other stages.

Using the intensity-related data set from the second recording session, all stages differ significantly from one another. Prey capture is separated from other stages by the first factor (eigenvalue 11.6; 55.4 % of variation explained); all other stages (with the exception of prey capture with respect to crushing) are separated from each other by the second factor (eigenvalue 2.9; 14.2 % of variation explained) and crushing is separated from prey capture by the third factor (eigenvalue 1.4; 6.7 % of variation explained). The *RL* (=*S*×*A*) values of the tongue and hyoid protractors show high loadings (Table 7) on the first factor and are therefore important in separating prey capture from the other stages. The jaw opener and closer *RL* values show high loadings with the second factor and can thus be considered to be variables relevant to all stages. The *RL* value of the hyoid retractor (MSH) is the only variable with high loadings on the third factor and is thus important in the separation of prey capture from crushing.

Table 7. *Results from factor analysis: rotated factor matrix based on an intensity-related (sum, maximum and mean* S×A *values) data set containing all bites from the first recording session*

Variable	Factor 1	Factor 2	Factor 3
Mean *S*×*A* MRing	0.85	0.11	0.34
Mean *S*×*A* MGGM	0.84	0.09	0.05
Sum *S*×*A* MRing	0.82	0.05	0.45
Sum *S*×*A* MGGM	0.82	0.03	0.12
Maximum *S*×*A* MGGM	0.81	0.28	0.01
Maximum *S*×*A* MRing	0.80	0.30	0.26
Mean *S*×*A* MHG	0.77	0.36	0.17
Mean *S*×*A* MMH1	0.75	0.05	0.43
Maximum *S*×*A* MMH1	0.72	0.29	0.18
Sum *S*×*A* MMH1	0.71	–0.01	0.53
Sum *S*×*A* MAMEM	0.06	0.90	0.23
Mean *S*×*A* MAMEM	–0.09	0.89	0.23
Maximum *S*×*A* MAMEM	0.11	0.86	0.20
Maximum *S*×*A* MDM	0.59	0.71	0.08
Sum *S*×*A* MSH	0.36	0.40	0.73

Only variables with factor loadings higher than 0.7 on factor 1 (top), factor 2 (middle) and factor 3 (bottom) are given.

Variation explained: factor 1, 55.4 %, eigenvalue 11.6; factor 2, 14.2 %, eigenvalue 2.9; factor 3, 6.7 %, eigenvalue 1.4.

See Materials and methods for explanation of muscle activity variables.

S, number of spikes; *A*, mean amplitude.

See Fig. 1 for definitions of muscle abbreviations.

Qualitative analysis

The generalised muscle activity patterns of the jaw and hyolingual muscles are described below in relation to the kinematics of the jaws and tongue reported previously (Herrel *et al.* 1996). Transport and crushing cycles are discussed together as intraoral transport as it has been shown above that these two stages differ mainly in the intensity of muscular contraction rather than in the muscular activation pattern (EMG onset and duration). On the basis of the kinematic data, a gape cycle can be subdivided into four distinct phases: the slow opening phase, SO; the fast opening phase, FO; the fast closing phase, FC; and the slow closing/power-stroke phase, SC/PS (Bramble and Wake, 1985). For a description of muscle activity patterns during prey capture, see Herrel *et al.* (1995).

Intraoral transport

During intraoral transport, a jaw cycle begins with the slow opening phase (SO). During this phase, activity of both the muscles of the tongue (MGGM, MGGL) and the hyoid protractors (MMH1, MMH2) is present. The MHG and the MRing are also active (Figs 2, 3; Tables 2, 3). All these muscles show a gradual increase in their activity which ends just before or a short time after maximal gape. At the end of the SO phase, some of the jaw closers show low-intensity activity (e.g. Fig. 3; during the third cycle, a distinct period of low-intensity activity is present in the MAMESA, MPtlat and MPtmed). This is the SOII phase. At the end of this phase, the jaw closers cease their activity and the jaw openers (MDM, MDMA) and the dorsal craniocervical muscles (MSCa) become maximally active, resulting in fast opening of the mouth (the FO phase). Prior to the FO phase, the hyoid retractors (MSH, MOH) become active and cause retraction of the hyoid apparatus. A burst of activity in the MHG also results in retraction of the tongue. At maximal gape, the jaw openers (MDM, MDMA) cease their activity. The jaw closers become active simultaneously at (MPsT, MAMP, MPtlat and MPtmed) or just after (MAMESA, MAMEM) maximal gape and cause fast closure of the mouth (the FC phase). After a short pause, the jaw closers become active again (Fig. 3), thus initiating the slow closing (SC) phase, sometimes accompanied by a power-stroke (PS) phase characterised by pronounced activity of the jaw closers. During this phase, the jaw openers often show low-intensity activity. The jaw openers and closers are always bilaterally simultaneously activated.

The muscular activation pattern described here is basically the same for both transport and crushing cycles. The major differences between these two stages are related to the intensity of muscular contractions in both the jaw openers and closers

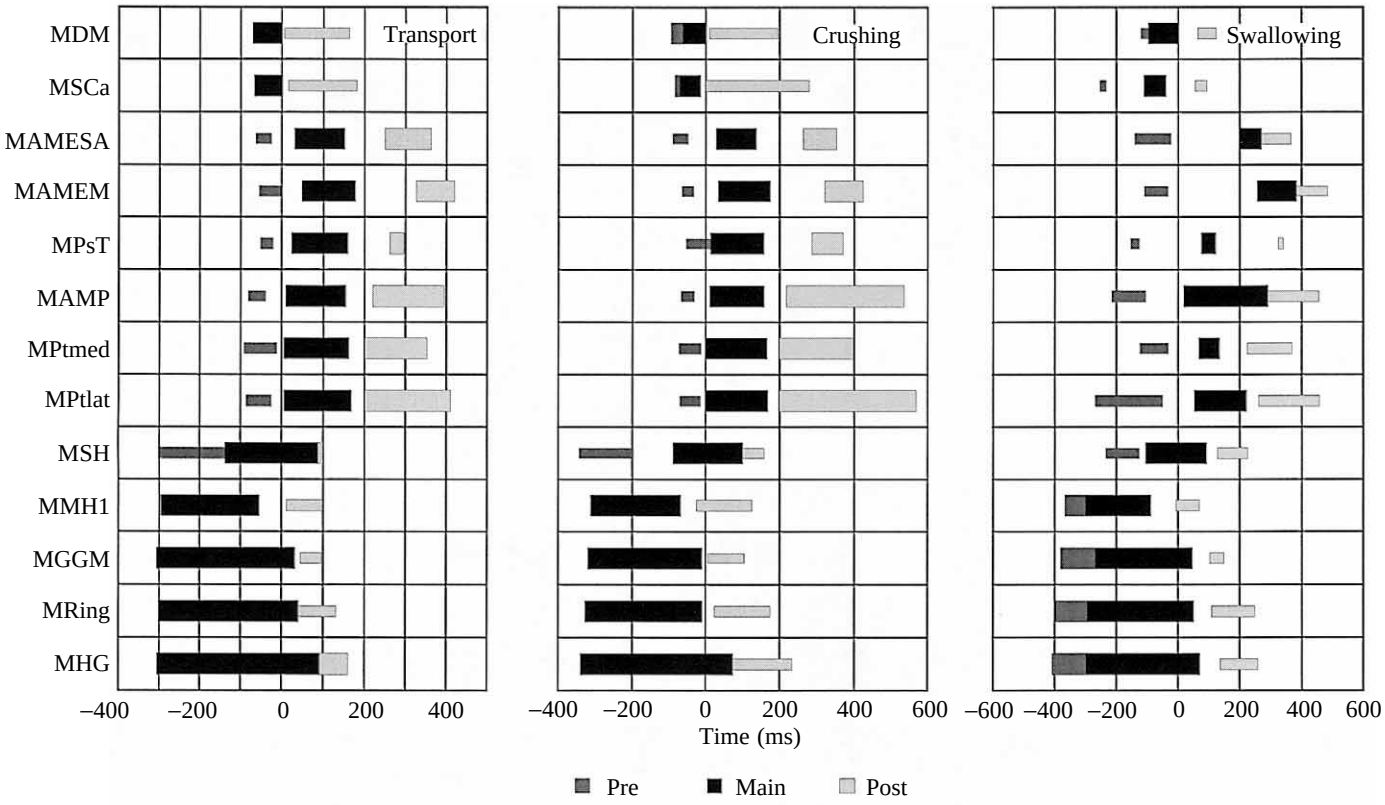

Fig. 2. Summary of electromyographic activity in *Agama stellio*. Bars show mean onset and duration data from all analyzed feeding sequences. Different bursts in the same muscle within one cycle are referred to as pre, main and post bursts. The main burst is the first activity burst in which the muscles are fully active; this burst is often preceded by an activity burst of low intensity (pre) and followed by a burst of either high or low intensity (post). Narrow bars represent low-amplitude activity. Time is expressed relative to the time of maximal gape (=time 0). See Fig. 1 for definitions of muscle abbreviations.

(Fig. 3). Although there were slight differences observed in onset and/or duration times between transport and crushing cycles (e.g. MAMESA in Fig. 3), on average they were not significantly different (see above). Within transport and/or crushing stages, there is also a substantial amount of variation between cycles present in the timing (e.g. onset and duration of the MAMESA, Fig. 3) and intensity (e.g. the MAMP, MPtlat, MPsT and MSCa, Fig. 3) of the muscular activity (Tables 2, 3). This presumably results from changes in the position of the prey within the oral cavity, as well as from changes in the degree of reduction of the prey during the intraoral transport stage.

Swallowing

During swallowing (Figs 2, 4; Table 4), the prey is transported from within the oral cavity to the pharynx. The associated EMGs are quite distinct from those of intraoral transport. Swallowing is characterised by a shorter FO phase, a much lower maximal gape value and the absence of an SC/PS phase (see Herrel *et al.* 1996); activity differences occur mainly in the jaw muscle activity patterns. As during intraoral transport, a cycle is initiated by pronounced activity of the tongue protractors (MGGM, MGGL). The hyoid protractors (MMH1, MMH2) then become active, but at a lower amplitude than during intraoral transport. Activity in the MHG and the MRing persists during swallowing. Nevertheless, differences in relative timing of the onset of activity are present (see Table 4). At the end of the SO phase, the MDM becomes active and the FO phase is initiated. Activity in the MDM is, as during intraoral transport, accompanied by activity in the MSCa. However, during late swallowing, the activity in the MDM and the MSCa may be absent. At maximal gape, the jaw opener muscles (MDM, MSCa) become silent and the jaw closers (MAMEP, MAMP, MPtlat, MPtmed) become active. However, in contrast to intraoral transport, only the deeper parts of the MAME, the MAMP and the MPt remain active during swallowing. The first muscles to cease their activity during swallowing are the MAMESA, MAMEM and MPsT (see Table 4, burst presence). Just before maximal gape, the hyoid retractor (MSH) becomes active and, in combination with the activity of the MHG, causes retraction of the hyolingual apparatus.

During swallowing, a substantial amount of variation was found (see Fig. 5; Table 4) in the intensity, onset and duration of the muscle activity. Differences observed during swallowing are generally less pronounced than during intraoral transport and are presumably related to the position of the prey with respect to the tongue.

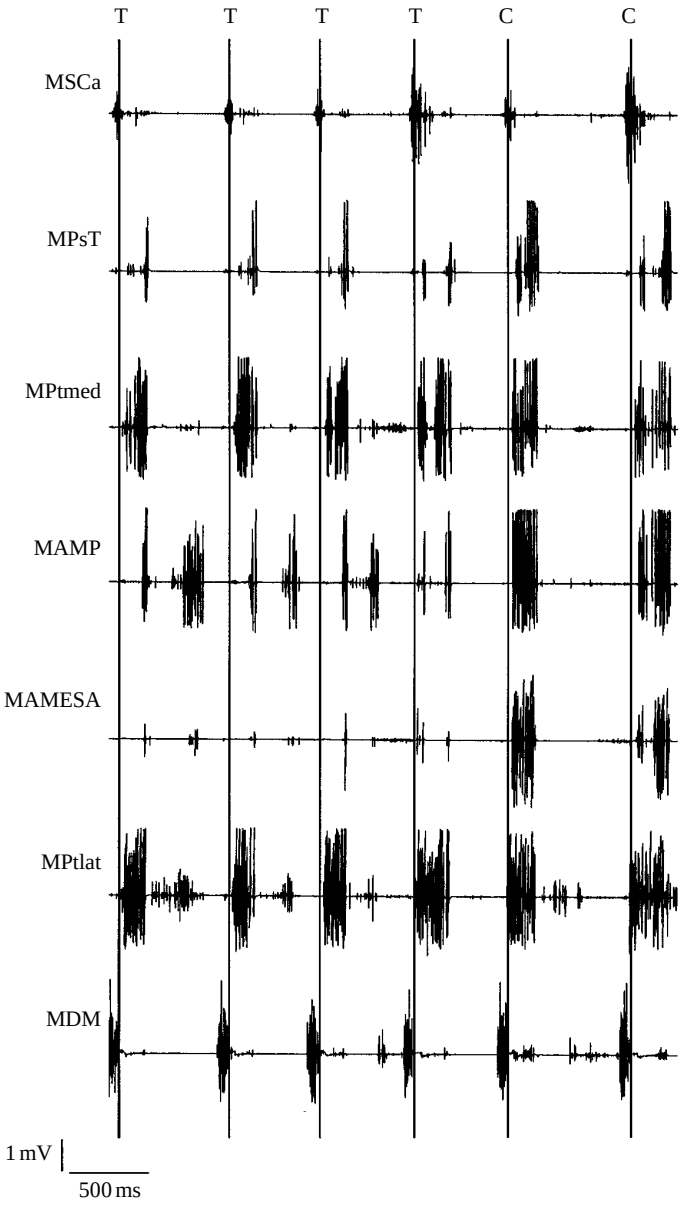

Fig. 3. Representative electromyograms from the first recording session from an individual *Agama stellio*. Vertical lines indicate time of maximal gape. C, crushing; T, transport. See Fig. 1 for definitions of muscle abbreviations.

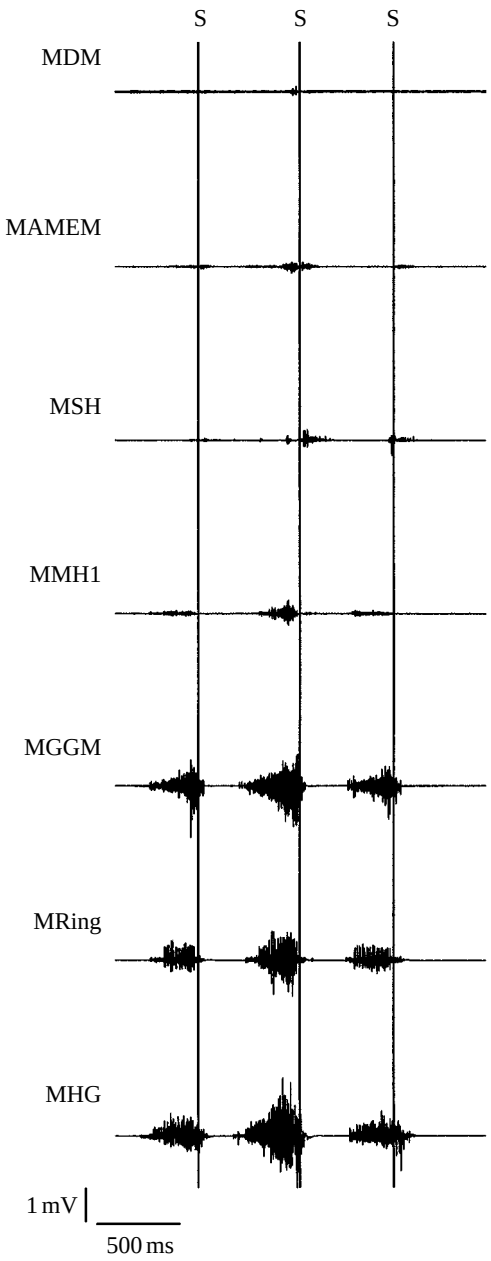

Fig. 4. Representative electromyograms from the second recording session using an individual *Agama stellio*. Vertical lines indicate times of maximal gape. All records are for swallowing cycles (S). See Fig. 1 for definitions of muscle abbreviations.

Discussion

Roles of jaw and hyolingual musculature

Despite the complexity of the squamate jaw musculature, muscle activity patterns are remarkably similar (all muscles becoming active approximately simultaneously and during the same kinematic phases) for all jaw closers (MAMESA, MAMESP, MAMEM, MAMEP, MPsTS, MPsTP, MAMP, MPtlat and MPtmed) during feeding in *A. stellio*. All jaw closers exhibited activity during one or more of three periods: during the second part of the SO phase of prey capture and intraoral transport, during the FC phase of prey capture, intraoral transport and swallowing, and during the SC/PS phase of prey capture and intraoral transport. However, in *A. stellio*, the jaw closers fulfil only one functional role: the closing of the jaws. Similarly, in *Trachydosaurus rugosus* (Gans *et al.* 1985), the jaw closers (MAME, MPsT and MPt) are also active simultaneously and can be considered to be true jaw closers. In *Uromastix aegyptius* (Throckmorton, 1978), however, the activity patterns of the superficial and deep portions of the MPt are different: activity in the superficial part occurs during jaw closing (simultaneously with activity of the MAME), while the deep part is active during jaw opening. Hence, the two parts are assumed to have different functions: jaw elevation for the

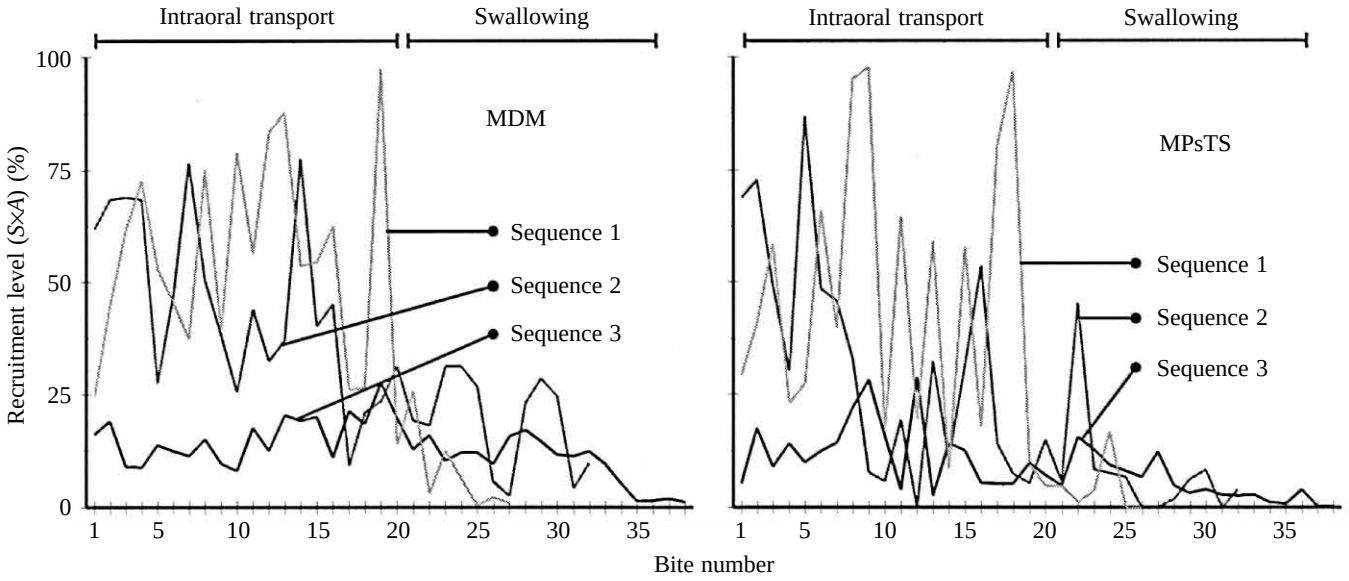

Fig. 5. Recruitment levels ($S \times A$ values, where S is the number of spikes and A is the average spike amplitude) of sequential bite cycles for three feeding sequences from the first recording session. The variability both within and between feeding sequences is clearly illustrated. MDM, m. depressor mandibulae; MPsT, m. pseudotemporalis.

superficial part and jaw protraction for the deep part. This functional subdivision of the activity of the MPt is related to the kinetic nature of the skull in *U. aegyptius* (Throckmorton, 1976, 1978). Another characteristic of jaw muscle activity patterns in *A. stellio* is the simultaneous activation of both sides in all muscles, suggesting a fairly simple motor pattern. While this is also observed in *T. rugosus* (Gans *et al.* 1985), in *Varanus exanthematicus* (Smith, 1982) temporal differentiation and even unilateral muscle activity may be present in the jaw adductors (MAME, MPsT, MPt).

Some differences in activity patterns of the jaw muscles of *A. stellio* were observed. In general, all deep muscles (MAMEP, MAMP) and also the MPt continue their activity into the later parts of the feeding sequence, whereas the more superficial muscles (MAMES, MAMEM, MPsT) tend to cease their activity much earlier. A similar observation was made in *Caiman crocodilus* (Cleuren, 1996). In *Alligator mississippiensis* (Sato *et al.* 1992), it has been shown that the muscles (MAMEP, MAMP, MPsT) which remain active throughout the feeding sequence in *C. crocodilus* are primarily composed of red muscle fibres. Although no quantitative data on the muscle fibre composition are available for *A. stellio*, it is proposed that the different muscle activity patterns in this lizard may be due to similar differences in fibre composition (more red, aerobic muscle fibres in the deeper parts) of the different jaw adductors.

On the basis of tongue morphology and observations of tongue movements during feeding, several roles have been suggested for the hyolingual musculature (see Table 1 in Delheusy *et al.* 1994, for an overview). The hyolingual muscles in *A. stellio* can be subdivided into four basic groups: the tongue protractors (MGGL and MGGM), the hyoid protractors (MMH1 and MMH2), the hyoid retractors (MOH and MSH) and the m. hyoglossus (MHG). The MHG, which is active during both tongue protraction and retraction, can only function as a tongue retractor when working together with the hyoid retractors. During tongue protraction (activity in the MGG), activity in the MHG will cause shortening of the tongue. The combination of tongue protraction and tongue shortening causes the tongue to bulge, thus pushing it against the prey item. A similar function of the MHG during tongue protraction is found in *Anolis equestris* (J. Cleuren and F. De Vree, personal communication). Remarkably, the tongue and hyoid protractors are nearly always simultaneously active during all feeding stages, although the anatomical relationships of the tongue and hyoid indicate no obligatory correlation between tongue and hyoid movements (Smith, 1984).

Not only the extrinsic musculature (i.e. those muscles originating on the mandible or the hyoid and inserting on the tongue) but also the intrinsic tongue muscles (those muscles with their origin and insertion on the tongue) play an important role during feeding in *A. stellio*. Of the intrinsic muscles, activity could be recorded from only one, the MRing. Activity of the MRing resulting in whole-tongue movement occurs both during prey capture (Herrel *et al.* 1995) and during the other feeding stages. Thus, in *A. stellio*, two of the three mechanisms of tongue movement (tongue protraction by the MGG and whole-tongue movements caused by the sliding of the tongue on the entoglossal process and due to the activity of the MRing) proposed for lizards (Smith, 1984, 1988) are observed during feeding.

In summary, it can be stated that in *A. stellio* both jaw and hyolingual muscles are essential during all stages of a feeding sequence. During feeding, the jaw and hyolingual apparatus are integrated to form one functional feeding unit in which both components perform a specific role.

Relationships among feeding stages

Although we have shown that the jaw and hyolingual muscles perform similar tasks during all stages of feeding, quantitative EMG data for these muscles can be used to discriminate between the different feeding stages, depending on the type of data examined. Whereas prey capture, intraoral transport and swallowing can be separated irrespective of the type of data (kinematic, EMG) used, crushing and transport are only separable using intensity-related EMG data. Among lizards, only in *Chamaeleo jacksonii* has a separation of crushing and transport stages been demonstrated using kinematic data (So *et al.* 1992). However, in all other studies in which multivariate analyses were performed on kinematic data, no discrimination between crushing and transport stages was possible (Kraklau, 1991; Delheusy and Bels, 1992; Urbani and Bels, 1995; Herrel *et al.* 1996). So *et al.* (1992) state that: 'chewing and transport behaviours may represent two extremes of a continuum rather than entirely distinct activities'. For all squamates examined, therefore, transport and crushing (chewing of So *et al.* 1992) are apparently closely related. Prey capture and swallowing are also kinematically similar in most species examined (Delheusy and Bels, 1992; Urbani and Bels, 1995). However, in *A. stellio*, prey capture, intraoral transport and swallowing seem to be distinct stages.

Quantitative electromyographic data for the whole feeding sequence are available for *Caiman crocodilus* (Cleuren, 1996).

In this crocodilian reptile, prey capture, transport, crushing, repositioning and swallowing stages are separable in multivariate space and significantly different on the basis of time-related EMG data. Hence, in *Caiman crocodilus* (Cleuren and De Vree, 1992; Cleuren, 1996), crushing can also be considered to be a distinct stage, clearly different from transport. However, the type of prey transport is completely different between the lizard *A. stellio* (lingual transport) and the crocodilian *C. crocodilus* (inertial transport), which may account for this difference. It is therefore likely that crushing cycles in other inertial feeders such as *Varanus exanthematicus* would also be separated from transport cycles (see Smith, 1982). As inertial transport mechanisms are considered to be derived (Bels *et al.* 1994) in lower tetrapods, the ancestral mechanism of prey crushing presumably involved modulation of the transport cycle (mainly in the intensity of muscle contraction) when needed. Evolution from a basic transport cycle into capture and/or swallowing cycles, whereby transitional stages would include modulations of the intensity as well as the onset of muscular activity, seems plausible.

It has been suggested that feeding cycles might be driven by simple motor pattern generators. According to Ewert *et al.* (1994), a motor pattern can be considered as the spatiotemporal pattern of excitation and inhibition in motoneurones necessary to activate and coordinate the muscle contractions. Can we determine, from our new EMG results for *A. stellio*, whether the different functional stages recognised are generated by different motor patterns? The separation of prey capture, swallowing and intraoral transport stages on the basis of both time- and intensity-related data suggests that different motor patterns are indeed used. However, as noted above, this observation might not apply to the distinction between transport and crushing as these cycle types are only separable using differences in intensity of the muscular activation.

Davis and Kovac (1981) and Rossignol *et al.* (1988) noted that sensory (proprioceptive) feedback will play a role in the coordination and maintenance of a motor pattern and, therefore, that the observed muscle activity patterns differ between feeding stages. This was also found in *A. stellio* in the recruitment levels of the jaw and hyolingual muscles during feeding. The recruitment levels of these muscle groups differ not only between feeding sequences and stages, but also within stages (bite-to-bite differences, see Fig. 5). It is possible that, during the SO phase of intraoral transport cycles (see Herrel *et al.* 1996), information regarding the food type, degree of reduction and/or food position is fed back to the control system. One should therefore be cautious in attributing the observed differences between cycles to separate motor patterns.

Evolutionary implications

Similarities in jaw muscle activity patterns between *A. stellio* and other lepidosaurian reptiles from such groups as diverse as the Rhynchocephalia (*Sphenodon punctatus*; Gorniak *et al.* 1982), Scincidae (*Trachydosaurus rugosus*; Gans *et al.* 1985), Agamidae (*Uromastix aegyptius*; Throckmorton, 1978) and Varanidae (*Varanus* sp.; Smith, 1982) suggest a common basic muscular activation pattern (see Bramble and Wake, 1985). Key elements in this basic pattern are the activation of the jaw opener (MDM) and dorsal cervical muscles (MSCa) during the FO phase and bilaterally simultaneous activation of both external (MAMESA, MAMESP, MAMEM, MAMEP, MAMP) and internal (MPsTS, MPsTP, MPtlat, MPtmed) adductors during the FC and SC/PS phases. Within the different lepidosaurian groups, this basic pattern differs in relation to specialisations of the feeding apparatus (e.g. specialisations for inertial feeding in *Varanus exanthematicus*, a kinetic skull in *U. aegyptius*, a unique shearing mechanism in *S. punctatus* and adaptations to durophagy in *T. rugosus*).

As noted above, both the jaw and the hyolingual apparatus play crucial roles during feeding in lizards. Functional similarities in the hyolingual musculature within lizards are common. The muscle activation patterns seen in *A. stellio* do not diverge greatly from the results for other lizards (Smith, 1984, 1986) or the activity patterns suggested for the primitive mode of food transport and reduction (Bels *et al.* 1994). There are even a number of similarities present between lizards and mammals in the movements of the hyolingual apparatus and the coordination of the jaw and hyolingual systems (see Smith, 1984). On the basis of these similarities, a basic vertebrate pattern of tongue function has been proposed (Hiiemae *et al.* 1979; Bramble, 1980). However, as noted by Smith (1984), these similarities may also be due to convergence or to the retention of a primitive pattern. Our data do not allow further speculation on this topic, but do suggest the presence of a basic

lepidosaurian pattern of tongue function as proposed by Bels *et al.* (1994). Again, specialisations of the hyolingual apparatus related to vomerolfaction as in *Varanus* sp. (Smith, 1986), social display as in *Anolis carolinensis* and *A. equestris* (Bels, 1990; Font and Rome, 1990) or ballistic prey capture as in chameleons (Wainwright and Bennett, 1992*a*) might cause deviations from this basic pattern.

Before any firmer conclusions can be drawn regarding the evolutionary transformation of the jaw and hyolingual systems, more data regarding the jaw and hyolingual motor patterns and, especially their control mechanisms in lepidosaurian reptiles, are needed.

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