Evidence for an elastic projection mechanism in the chameleon tongue

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To capture prey, chameleons ballistically project their tongues as far as 1.5 body lengths with accelerations of up to 500 m s⁻². At the core of a chameleon’s tongue is a cylindrical tongue skeleton surrounded by the accelerator muscle. Previously, the cylindrical accelerator muscle was assumed to power tongue projection directly during the actual fast projection of the tongue. However, high-speed recordings of Chamaeleo melleri and C. pardalis reveal that peak powers of 3000 W kg⁻¹ are necessary to generate the observed accelerations, which exceed the accelerator muscle’s capacity by at least five- to 10-fold. Extrinsic structures might power projection via the tongue skeleton. High-speed fluoroscopy suggests that they contribute less than 10% of the required peak instantaneous power. Thus, the projection power must be generated predominantly within the tongue, and an energy-storage-and-release mechanism must be at work. The key structure in the projection mechanism is probably a cylindrical connective-tissue layer, which surrounds the entoglossal process and was previously suggested to act as lubricating tissue. This tissue layer comprises at least 10 sheaths that envelop the entoglossal process. The outer portion connects anteriorly to the accelerator muscle and the inner portion to the retractor structures. The sheaths contain helical arrays of collagen fibres. Prior to projection, the sheaths are longitudinally loaded by the combined radial contraction and hydrostatic thickening of the accelerator muscle, at an estimated mean power of 144 W kg⁻¹ in C. melleri. Tongue projection is triggered as the accelerator muscle and the loaded portions of the sheaths start to slide over the tip of the entoglossal process. The springs relax radially while pushing off the rounded tip of the entoglossal process, making the elastic energy stored in the helical fibres available for a simultaneous forward acceleration of the tongue pad, accelerator muscle and retractor structures. The energy release continues as the multilayered spring slides over the tip of the smooth and lubricated entoglossal process. This sliding-spring theory predicts that the sheaths deliver most of the instantaneous power required for tongue projection. The release power of the sliding tubular springs exceeds the work rate of the accelerator muscle by at least a factor of 10 because the elastic-energy release occurs much faster than the loading process. Thus, we have identified a unique catapult mechanism that is very different from standard engineering designs. Our morphological and kinematic observations, as well as the available literature data, are consistent with the proposed mechanism of tongue projection, although experimental tests of the sheath strain and the lubrication of the entoglossal process are currently beyond our technical scope.

Keywords: chameleon; tongue; projection mechanism; catapult; elastic energy; power output

1. INTRODUCTION

Prey capture in the chameleon occurs over four different phases. First, prey distance is estimated (Harkness 1977; Ott & Schaeffel 1995) and the tongue slowly protrudes between the jaws (phase I; see also figure 1a–c). Second, the tongue accelerates forward (phase II; Bell 1990; Wainwright et al. 1991; Wainwright & Bennett 1992a; Herrel et al. 2000), at up to 490 m s⁻² (Chamaeleo ousataeli; Wainwright et al. 1991). Third, after a period of near constant velocity (phase III), the tongue pad decelerates (phase IV; see also figure 1a,c) and the prey is caught by active prehension (Herrel et al. 2000) and adhesion to the tongue pad. Finally, the retractor muscle withdraws the tongue back into the mouth (Rice 1973; Wainwright & Bennett 1992a,b).

The first hypotheses about tongue projection (reviewed by Gnanamuthu 1930; Zoond 1933) invoked tongue erection by inflowing blood or inflating of the tongue from the lungs. Duvernoy (1836) first proposed a specialized muscular system that projects the tongue, and many studies assumed the accelerator muscle to be the direct effector of tongue projection (e.g. Zoond 1933; Gnanamuthu 1937; Altevogt & Altevogt 1954; Gans 1967; Bell 1990; Wainwright et al. 1991; Wainwright & Bennett 1992a,b; Van Leeuwen 1997). Zoond (1933) established the currently held view that the accelerator muscle exerts a normal stress on the tapering tip of the entoglossus. The forward-directed reaction force on the tongue pad projects the tongue off the entoglossal process. The cylindrical muscle slides over the tip of the entoglossal process and contracts, reducing its inner diameter. A negative pressure gradient along the active accelerator muscle might contribute to the forward motion (Van Leeuwen 1997). This mechanism requires that the accelerator muscle can generate enough power to accelerate the tongue.

By contrast, Van Leeuwen et al. (2000) proposed that the accelerator muscle could power tongue projection indirectly by storing elastic energy in connective tissues,
2. MORPHOLOGICAL OBSERVATIONS

Two specimens of *C. pardalis*, one specimen of *C. jacksonii* and two specimens of *C. chamaeleon* were used for morphological dissections of the hyolingual complex. The fibre types in the connective tissue that envelops the entoglossal process were determined by applying Van Gieson staining (for collagen) and Weigert’s resorcin–fuchsin staining (for elastin).

We focus on structures that may be involved directly in tongue projection, i.e. the entoglossal process, a part of the tongue skeleton, and the soft tissues mounted on the entoglossal process. Extrinsic tongue muscles, such as the genioglossus muscle, can transmit power to the projected tongue mass only via the entoglossal process. Four important structural elements were identified in the studied tongues.

(i) The core of the tongue is the entoglossal process (figures 2b, 3 and 4a), a cylindrical parallel-sided cartilage surrounded by a thick and smooth layer of thick longitudinal collagen fibres, the perichondrium. The entoglossal process tapers only in its distal 1–1.5%, if at all (Herrel et al. 2001a; cf. figure 3a). Wainwright & Bennett (1992b) mention a slight taper of the anterior 9% of the entoglossal process in *C. jacksonii*. Its tip is rounded and thickened dorsally by connective tissue (figure 3; indicated as ‘articulating cartilagenous tip’ by Herrel et al. (2001a)), which connects to the inner surface of the covering connective tissue (figures 2c and 3). The often visible longitudinal taper of the entoglossal process (figure 2b; e.g. Gans 1967) results from sections that deviate (both in position and orientation) from the mid-sagittal plane.

(ii) The paired hyoglossi or retractor muscles (see figures 2b and 4a) envelop the posterior portion of the entoglossal process and connect anteriorly to the lateral surface of the accelerator muscle (Rice 1973; Bell 1989; Herrel et al. 2001b). The retractor muscles attach internally to a cylindrical epimysial fascia (figure 4). The muscular part and the internal fascia are here referred to as the retractor complex. In the resting position, the inactive retractor muscles are pleated, and the pitch angle of the collagen fibres in the internal epimysium is ca. 85° (figure 4b(i)).

(iii) The cylindrical accelerator muscle envelops a thick layer of connective tissue (see item iv). The muscle fibres are arranged in transverse planes and form clockwise and anticlockwise spiral-shaped arcs that extend from the peripheral boundary to the internal boundary (Gnanamuthu 1937; Bell 1989; Van Leeuwen 1997; figure 4a(ii)). Muscle tissue is almost incompressible (Wainwright & Bennett 1992b; Van Leeuwen 1997). Hence, when the muscle contracts along the entoglossal process, it becomes thinner and elongates at the same time. The inner and outer surfaces of the muscle are covered by epimysial layers of connective tissue with helically arranged collagen fibres.

(iv) The thick layer of connective tissue between the entoglossal process and the accelerator muscle (figures 2b and 4a) connects the flexible and ‘articulating’ tip of the entoglossal process with the inner fascia of the accelerator muscle (Gnanamuthu 1930;
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Figure 2. (a) Lateral view of Chamaeleo melleri during the acceleration phase of prey capture. The tongue pad (tp), the accelerator muscle (acc) and the retractor complex (hg) are simultaneously accelerated. (b) A close to sagittal section of the tongue of Chamaeleo jacksonii. The intralingual sheaths (ils) are mounted on the entoglossal process (ep), enclosed by the tubular structure formed by the accelerator muscle (acc) and the retractor complex (hg). The round entoglossal tip appears tapered owing to sectioning oblique to the mid-sagittal plane. (c) Same as (b), but now the entoglossal process is removed and the (sectioned) central sheaths (c-ils) are folded back to illustrate the nested structure of the intralingual collagen sheaths. The peripheral sheaths (p-ils) are still in situ, connected with the accelerator muscle. Scale bars, 10 mm.

Figure 3. Details of the tip of the entoglossal process (ep) showing the dorsal thickening. (a) Lateral view of the entoglossal process of Chamaeleo jacksonii. Muscle tissue and intralingual sheaths were removed. (b) Close to mid-sagittal section of C. jacksonii. The entoglossal tip is thickened by connective tissue, i.e. the ‘articulating cartilagenous tip’ (Herrel et al. 2001a), which connects the perichondrium of the entoglossal process with the innermost intralingual collagen sheath. Abbreviations as in figure 2. Scale bars, 2 mm.

Zoond 1933; Gans 1967; Bell 1989; Herrel et al. 2001a). However, a single tubular tendon connecting the fascia of the accelerator muscle and the tip of the entoglossal process cannot account for the observed tongue elongation during projection. Removing the entoglossal process from the sagitally sectioned tongue (figure 2b,c) revealed that the intralingual ‘tendon’ comprises a nested series of individual sheaths. The innermost sheath was attached to the posterior end of the fascia of the retractor muscle, near the articulation of the entoglossal process and the ceratobranchials. Each subsequent sheath connected slightly anterior to the preceding sheath. After removing this inner set of approximately nine nested sheaths (it is very hard to judge the exact number of thin sheaths from dissections or histological sections), a major portion of the ‘tendon’ was still present. The outer or peripheral tendon sheaths formed a thick layer, connected to the fascia of the accelerator muscle. At least six peripheral sheaths are mutually interconnected by collagenous trabeculae. The fibrous proteins in the nested intralingual sheaths contain collagen (Van Gieson staining), but no elastin (Weigert’s resorcin-fuchsin staining). Collagen-fibre angles were measured on flattened and stained (picro-red) longitudinal sections (figure 4b). The inner cylindrical fascia of the accelerator muscle and the interconnected peripheral sheaths form a complex elastic unit. During tongue projection and elongation, the peripheral sheaths remain structurally associated with the tongue pad. The collagen fibres in the peripheral sheaths form clockwise and anticlockwise helices. The central sheaths are longer than the peripheral sheaths, and the caudally open ends of the central tubular sheaths are attached to the tubular and highly extendable retractor complex (figures 2c and 4a) at approximately evenly distributed intervals. The more central the location of the sheath, the greater its length and the further posterior its attachment point. The retractor complex is the only structural connection between the internal sheaths.

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and acceleration of the posterior end of the muscle, both in an earth-bound frame of reference and relative to the entoglossal process. Insertion of markers at the anterior margin of the retractor muscle would affect the projection of the tongue and was therefore avoided.

Four evenly distributed markers were glued onto the retractor complex (figure 5a; the most caudal ‘retractor marker’ is numbered 4). Initially, the connection between the inactive retractor complex (Wainwright & Bennett 1992a) and the accelerator muscle is slack and pleated. Internally, the retractor complex is connected to the central subset of intralingual sheaths. Consequently, if these intralingual sheaths are to contribute to the acceleration of the tongue, then the retractor complex must accelerate simultaneously with the accelerator muscle. The central sheaths pull forward at their attachment sites along the retractor if they are under tension. Alternatively, if the sheaths do not contribute to the forward acceleration, then the various portions of the retractor muscle will start to accelerate sequentially from anterior to posterior, each portion accelerating only after the initial slack between the accelerator muscle and the retractor mass has vanished and their connection comes under tension. The progressive forward acceleration of the retractor complex would significantly decelerate the tongue tip during ballistic flight (figure 1; phase III). Our results show that this is not the case (§ 4c).

Markers were also fixed onto the anterior tip of the lower jaw (marker 2 in figure 5a), onto the skull and onto the cerato-branchial cartilage, but these were not used for the analysis presented here.

4. RESULTS AND DISCUSSION

(a) Video analysis falsifies the accelerator muscle as the main direct effector of tongue projection

Figure 1 shows the displacement, velocity and acceleration of the tongue tip during a typical feeding event of Chamaeleo melleri. The calculated specific tongue power peaks at ca. 1800 W kg⁻¹. From high-speed video observations of C. pardalis and C. melleri, we calculated average maximum accelerations of the tongue pad of 340 m s⁻² (s.d. = 33 ms⁻²) and 374 m s⁻² (s.d. = 25 ms⁻²), respectively, of the tongue pad. The mechanical power output per unit mass of the tongue pad was calculated as the product of instantaneous velocity and acceleration. The average maximum mass-specific power output at the tongue pad was 1170 W kg⁻¹ (s.d. = 176 W kg⁻¹) for C. pardalis and 1584 W kg⁻¹ (s.d. = 176 W kg⁻¹) for C. melleri. The accelerator muscle accounts for ca. 50% of the mass of the tongue pad (in fact slightly more in C. melleri). Assuming a direct muscular power mechanism, the accelerator muscle must produce a maximum mass-specific power output of ca. 2340 W kg⁻¹ (C. pardalis) or 3168 W kg⁻¹ (C. melleri). These values are more than five times higher than the maximum mass-specific power outputs reported for most fast muscles. For example, the isolated sartorius muscle
of *Rana pipiens* generates 371 W kg\(^{-1}\) at 25 °C (Lutz & Rome 1994), one of the highest recordings for vertebrate muscles. Recently, a power output of ca. 800 W kg\(^{-1}\) has been reported for the pectoralis muscle of the blue-breasted quail (Askew & Marsh 2001).

In conclusion, the present analysis falsifies the hypothesis that the accelerator muscle is the main direct power source of tongue projection. Two possible candidates remain: (i) an external source that conveys its power to the tongue pad via the entoglossal process; and (ii) the nested collagen sheaths that envelop the entoglossal process. In the latter case, the accelerator muscle might still be the prime energy source for projection if it stores elastic energy in the sheaths prior to projection and the sheaths release this energy at a faster rate during projection.

**(b) The accelerator muscle is active and elongates prior to projection**

The motion of several radio-opaque markers was tracked during tongue projection for a limited range of motion, confined within the boundaries of the X-ray field (figure 5a). The time traces of the tongue tip (marker 1), the jaw (marker 2), the entoglossal process (marker 3) and the retractor complex (marker 4), illustrate our findings (figure 5b). Prey was positioned ca. 25–30 cm from the chameleon, but the projection distance could not be measured exactly because the prey was necessarily outside the field of view.

During the phase of slow tongue protraction \((t = -0.2\ s\ \text{until}\ t = 0\ s)\), the tongue skeleton protruded and the accelerator muscle started to deform 200 ms prior to projection (figure 5c). In this phase, the distance between the tip of the tongue and the marker glued to the posterior end of the accelerator muscle increased by 25% for the most extreme elongation recorded (figure 5c). The accelerator muscle, which is mainly responsible for elongation, covers only ca. 75% of the measured distance, hence it must have elongated by ca. 33%. The peak velocity of the tongue was 5 m s\(^{-1}\). We now know that the accelerator muscle elongates during the slow phase of tongue protraction, a finding confirmed by the *in situ* observations of Zood (1933). Wainwright & Bennett (1992a) demonstrated the onset of electrical activity in the accelerator muscle ca. 200 ms prior to tongue projection as well as a muscular elongation of up to 47% during artificial activation *in vitro*. From these observations, we conclude that the accelerator muscle is active during its elongation and is thus likely to generate mechanical work prior to tongue projection. The crucial role of the accelerator muscle in tongue projection is confirmed by observations that artificial stimulation of this muscle led to tongue projection (Zood 1933), and that tongue projection was impossible after denervation of this muscle (Meyers & Nishikawa 2000).

Coulnd the accelerator muscle produce all the required work (calculated from a peak kinetic energy of 72 mJ for our studied specimen of *C. melleri*, with a tongue mass of 4 g (mainly accelerator muscle and tongue pad) and a maximum velocity of 6 m s\(^{-1}\) for the recorded peak performance) in the active period before projection \((ca. 200\ ms)\)? The mass of the accelerator muscle is ca. 2 g. This would require a mean specific power output of ca. 180 W kg\(^{-1}\) prior to projection, which is well within the physiological range for fast twitch muscle fibres.

The only structures that could change their energetic state as a result of work produced by the accelerator muscle are the adjacent epimysial coverings of the muscle and the intralingual sheaths.

**(c) Contribution of the intralingual sheaths**

The intralingual sheaths fall into two groups based on their structure. The short peripheral sheaths are interconnected and fixed to the epimysium of the accelerator muscle. These sheaths may act as a parallel elastic unit of the accelerator muscle. However, the present experiments cannot determine the contributions of individual sheaths, because introducing radio-opaque markers sufficiently large to be detected by the X-ray equipment would have interfered with the proper functioning of the tongue system.

The longer and more central sheaths do not have interconnections and insert on the fascia of the retractor complex. The markers on the retractor complex therefore indicate the positions of the posterior ends of the longer intralingual sheaths.

During tongue projection, the markers on the retractor complex and the accelerator muscle (figure 5d) move almost simultaneously. The different portions of the retractor complex that are inactive during projection (Wainwright & Bennett 1992a), and have a slack connection to the accelerator muscle, were nevertheless accelerated simultaneously with the accelerator muscle. Within the tongue apparatus, only the intralingual sheaths are in a position to generate the accelerating forces on the entire retractor complex because each sheath connects with its posterior end to this complex. These connections correspond to the lengths of the different sheaths, distributed over the entire length of the folded retractor complex and lend strong support to the aforementioned force-transmitting role in the projection process. The simultaneous forward acceleration of both tongue pad and retractor complex results in a ballistic flight with a more or less constant forward velocity. As mentioned in § 3, sequential forward acceleration of the retractor complex would decelerate the tongue tip during ballistic flight. Instead, we observed a constant-velocity plateau in feeding events over longer distances (e.g. figure 1).

If the sheaths pull the retractor complex forward, what accelerates the sheaths? The required forces are probably the reaction forces of the entoglossal process, which arise from the normal stress exerted by the sheaths under tension as they slide over the tip of the entoglossal process. Finally, full extension of the retractor complex is possible when the portions of the anterior sheath with helical fibres have slipped off the entoglossal complex, enabling the inner sheaths to slide along each other in a telescopic manner.

**(d) Power transmission via the entoglossal process**

In the projection phase, the entoglossal process moves forward, although very little compared with the displacements of the tongue tip and retractor complex (figure 5b). The contribution of the tongue skeleton and the soft tissues mounted onto the tongue skeleton was estimated from the time derivatives of their position data by the following calculations (figure 6). Let the stiff entoglossal process move forward with velocity \(v_{\text{ent}}\). Assume that the soft tissue of the tongue can be represented by a single mass \(m_{\text{tongue}}\) that has velocity \(v_{\text{tongue}}\) and acceleration \(a_{\text{tongue}}\). Let the tongue mass be connected to the entoglossal process.

via a tubular spring (representing the collection of tubular sheaths) that slides along the entoglossal process with a relative speed $v_{\text{slide}} = v_{\text{tongue}} - v_{\text{ent}}$. The total power, $P_{\text{tot}}$, delivered to the tongue is $P_{\text{ent}} = m_{\text{tongue}} a_{\text{tongue}} v_{\text{tongue}}$. According to our sliding-spring theory, the spring contributes $P_{\text{ent}} = m_{\text{tongue}} a_{\text{tongue}} v_{\text{slide}}$ to this total power, and the hyo-branchial apparatus conveys via the entoglossal process an amount of $P_{\text{tongue}} = m_{\text{tongue}} a_{\text{tongue}} v_{\text{tongue}}$. The power contributions can be normalized relative to peak tongue power as: $P_{\text{ent}} = a_{\text{tongue}} v_{\text{slide}} / (a_{\text{tongue}} v_{\text{tongue}})_{\text{max}}$ and $P_{\text{tongue}} = a_{\text{tongue}} v_{\text{tongue}} / (a_{\text{tongue}} v_{\text{tongue}})_{\text{max}}$ (figure 6; see table 1 in electronic appendix A). It appears that the peak power transmitted by the entoglossal process is ca. 10% of the total peak power. The efficacy of the power transmission by the entoglossal process depends on sufficient stiffness of the tongue pad. Peak power transmissions by the entoglossal process fall ca. 8 ms before the peak power of the total system, when most of the accelerator muscle and sheaths are still under considerable tension and thereby contributing to the stiffness of the tongue pad. The soft tissues mounted on the entoglossal process generate more than 90% of the peak power of the total system. More than 90% of the total power peak is generated by the soft tissues in the tongue. The contribution of the soft tissues is further explained in § 4d. The inset shows the central entoglossal process, the intralingual sheaths (dark grey, with a loaded region, a release zone and a relaxed portion) and the tongue pad (white), with the velocities and accelerations that were used to compute the respective powers as explained in § 4d. Calculations are based on digitized marker positions that were low-pass filtered with a cut-off frequency of 65 Hz (recursive third-order Butterworth).

Figure 6. Relative power contributions of the entoglossal process (open diamonds) and the soft tissues mounted on it (open circles) to the total instantaneous power to the tongue pad (filled circles). Power values were normalized relative to the peak total power. Peak power transmission by the entoglossal process occurs before the power peak of the total system. More than 90% of the total power peak is generated by the soft tissues in the tongue. The contribution of the soft tissues is further explained in § 4d. The inset shows the central entoglossal process, the intralingual sheaths (dark grey, with a loaded region, a release zone and a relaxed portion) and the tongue pad (white), with the velocities and accelerations that were used to compute the respective powers as explained in § 4d. Calculations are based on digitized marker positions that were low-pass filtered with a cut-off frequency of 65 Hz (recursive third-order Butterworth).

5. GENERAL DISCUSSION

We expect the proposed mechanism to be generally applicable to chameleons although the analysis was based on only a few species. We will therefore speak about ‘the chameleon’ in this discussion. Of course, details will vary among species. Considering (i) the physiological limitations of power production by muscular tissue, (ii) the low power contribution of the lingual skeleton to the tongue projection and (iii) the structural arguments for the acceleration of the retractor complex, an elastic release mechanism must be at work during the projection of the chameleon tongue. Three characteristics of the elastic mechanism are the muscular work prior to tongue projection, the elastic storage capacity of the generated work and a quick-release mechanism.

(a) Muscular work prior to the tongue projection

The accelerator muscle is active, elongates and is therefore likely to produce work prior to tongue projection, thereby loading the elastic intralingual collagen sheaths during the distributed forward motion of this muscle. The posterior margin of the accelerator muscle remains more or less in place, as is apparent from the radiographs. The accelerator muscle could deliver work on the sheaths by exerting normal stresses (at right angles to the outer sheath surface). These stresses cause longitudinal deformation according to the hydrostatic principle, generate longitudinal stresses in the collagen trabeculae that interconnect the peripheral sheaths and the accelerator muscle, and cause friction stresses (parallel to the outer sheath surface) and shear deformation as illustrated in figure 7. We made rough estimates of the longitudinal strain rate and the work that could be delivered by the radial and longitudinal muscle-force components, taking into account the
observed lengthening of the accelerator muscle of ca. 33%, the recorded peak velocity of 5 m s\(^{-1}\) and an assumed maximum muscle stress of 200 kPa (Woledge et al. 1985). In order to elongate, the muscle acts like a hydrostat, in a similar way to a squid extending its tentacular stalks (Kier & Van Leeuwen 1997), but at a lower average longitudinal strain rate of ca. 0.33/(0.2 s) = 1.65 s\(^{-1}\). A simple mathematical simulation of the mechanism reveals that the work done in radial compression is negligible compared with the work done in muscular elongation: compression is ca. 2% of the longitudinal elongation. Hence, the muscle loads the sheath elastically primarily by shear and by stretching the interconnections of the trabeculae with the peripheral intralingual sheaths. The normal and shear stresses exerted by the active muscle elongate the intralingual sheaths and load the internal helical collagen lattice. This loading pattern is consistent with the relatively high fluid content of the matrix (compared with tendons) and with the observed high local glycoprotein contents (concluded from a PAS positive reaction) of the peripheral sheaths.

(b) Elastic storage capacity of the generated work

Energy generated by muscular stress is stored in the deformed intralingual sheaths and their matrix of collagen fibres. Despite the stiff collagen fibres, the intralingual sheaths allow sufficient deformation because the fibre angle with the longitudinal axis is ca. 55° in the internal epimysium and peripheral sheaths. As the cylinders elongate under external radial compressive and shear loads, the fibre angle must drop and fibre strain must rise. Effective loading of the sheaths requires force transfer via collagen trabeculae and shear and radial compression between neighbouring sheets, thereby elongating the most peripheral sheaths probably slightly more than the more central sheaths (figure 7b). Any possible shear forces between the innermost sheath and the tongue skeleton are reduced by the smooth and (presumed) lubricated entoglossal perichondrium. The portion of the central sheaths that posteriorly exceeds the posterior margin of the accelerator muscle, and therefore cannot be strained by it, contains longitudinally arranged collagen fibres (figure 4b(ii)), which is consistent with its force-transmitting function. In the anterior portion, which is covered by the accelerator muscle, the fibres are arranged in a helical fashion (figure 4b(iii)), which results in high extensibility and is consistent with its energy-storing function.

Without a means of obtaining the mechanical properties of the sheaths in vivo, their capacity to store energy is estimated as follows: based on the wet weight of the sheaths of a specimen of C. melleri (560 mg) and the required energy storage (80% of 72 mJ; 57.6 mJ), the energy stored in the sheaths is ca. 0.1 mJ mm\(^{-1}\). This value is approximately one-third of the value for sheep plantaris tendon under...
maximum physiological stress (Ker 1999) and five times the energy density of a maximally loaded human heel pad (Ker 1999). The tendon has a higher collagen-fibre density than the sheaths, and the heel pad has a lower fibre density (owing to the high fat content), which is in qualitative agreement with the present findings.

(c) The quick-release mechanism

The delayed release mechanism, proposed by Wainwright & Bennett (1992b), is consistent with the recorded forward elongation of the accelerator muscle prior to projection (figures 5c and 7a(ii,iii)) and the thickened tip of the entoglossal process, consisting of deformable connective tissue (see also Herrel et al. 2001a). This tip may initially function as a passive block, preventing any movement or downward orientation of the head resulting from releasing the tongue, and thus allowing the accelerator muscle to generate considerable pressures until the block is finally overcome when the anterior portion of the accelerator muscle and the loaded sheaths slide over and compress the entoglossal tip (figure 7a(iv)). The sudden decrease in internal diameter reduces the strain in the muscle and the sheath fibres (figure 7a(iv),b(iv)), and a quick release of the locally stored elastic energy follows. The distal reduction in muscle-fibre stress lowers the local pressure, generating a longitudinal negative pressure gradient towards the tongue tip, analogous to that found in the stalk of the tentacles in squid (Van Leeuwen & Kier 1997). According to our sliding-spring theory, the tongue accelerates forward, continuing the process of energy release, until the strained portion of the sheaths has slipped completely off the entoglossal tip. The locally distributed normal stress of the sheaths on the entoglossal tip results in a projecting force component. This force is distributed through the stiffened loaded intralingual sheaths along both the accelerator muscle and the retractor muscle, accelerating almost simultaneously the accelerator and retractor parts of the tongue. The release of the tongue starts only after the accelerator muscle has actively elongated by ca. 33% while storing elastic energy. The quick-release mechanism requires the peak acceleration to be above a minimum acceleration threshold, which was indeed observed. It also explains the observations of ourselves and Herrel et al. (2001b) that chameleons back off when prey is at a short distance, to ensure successful capture.

The proposed mechanism of tongue projection provides a coherent mechanistic explanation for the available previously published experimental data. The proposed mechanism encompasses interpretations of previous reports (Zoond 1933; Altevogt & Altevogt 1954; Bell 1990; Wainwright et al. 1991; Wainwright & Bennett 1992a,b; Van Leeuwen 1997). Conversely, we oppose the notion that the main projection power is generated directly by the accelerator muscle. Instead muscle power is slowly stored in the hyoid apparatus (figure 7a(iii)), and a tensile-strain energy is stored in the helical collagen fibres of the sheaths, until the loaded portion of the sheaths starts to slide over the tip of the entoglossal process. This allows the inner radius of the sheaths to decrease (figure 7a(iii,iv)), releasing the tensile energy and generating work until the loaded portion of the accelerator muscle and the underlying sheaths have passed the entoglossal tip. This process ensures a continuing (fairly constant) force to accelerate the tongue with increasing power, unlike the longitudinal release in tendons, which generates initially high, but exponentially decreasing, forces. Applied to the soft tissue of the tongue (instead of stiff skeletal elements), such a reversible longitudinal release mechanism would cause higher internal deformations of the tongue, which, in turn, would dissipate a relatively large portion of the stored energy, whereas the relatively constant force in the chameleon tongue reduces the internal deformation of the soft body. On a molecular level, however, both mechanisms are reversible, based on the elongation and shortening of elastic (collagen) molecules.
The family Plethodontidae (a group of lungless salamanders) independently evolved tongue projections that are similar in performance to those found in chameleons (Lombard & Wake 1977). In *Hydromantes supermontis*, the forked hyobranchial skeleton is projected out of the mouth, whereas the protractor muscles that, at rest, envelop the skeleton remain inside the mouth (Deban et al. 1997). Quite interestingly, a substantial connective-tissue layer is also present between the muscles and the tongue skeleton, which could have a similar role to the connective-tissue sheaths in the chameleon. This analysis underpins the suggestion of Van Leeuwen et al. (2000) that the extreme tongue-projection performance in the genus *Hydromantes* requires an elastic mechanism.

In conclusion, we have strong experimental and morphological evidence that tongue projection in the chameleon involves elastic-energy storage and release, and that the intralingual sheaths play a major role in this mechanism. The unique tongue mechanism deviates from the conventional catapault design in its multilayered tubular springs with helically arranged fibres and associated accelerator muscle, the forward motion during loading, initiation of projection by extension of the anterior springs beyond the entoglossal tip, and the sequential energy release along the springs by sliding and radial thinning. The salient features of the proposed mechanism agree with the available previous experimental observations and with the structural components present in the tongue. The next challenge is to construct a biomechanical model of the system that predicts the tongue projection quantitatively.

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