

PHYSIOLOGY

Power at the Tip of the Tongue

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Chameleons launch their tongues at unsuspecting insects at speeds of 26 body lengths per second. They can catch insect prey located up to 1.5 body lengths away within a tenth of a second. This impressive performance drove biologists to formulate far-fetched explanations, such as that the chameleon's tongue is "erected" through an increase in blood pressure or inflated by the lungs like a party favor. More recent theories invoke the action of the tongue's large accelerator muscle [see (1) for a review]. In a recent issue of the *Proceedings of the Royal Society of London*, de Groot and van Leeuwen (2) report that the chameleon's tongue is projected with more power than can be supplied by any known muscle. These investigators reveal that the chameleon's tongue is, in fact, powered by an ingenious catapult system.

The secret to prey evading capture or to predators capturing prey is rapid acceleration. But there are limitations to how fast muscles can contract. To achieve speeds beyond these limitations, for example, the legs of a jumping kangaroo rat act like levers, which turn slow but forceful muscle contractions into much faster movements. Long levers, however, require enormous forces, which the muscles are required to deliver quickly for the animal to escape. Limited by its muscle power, a jumping kangaroo rat reaches an acceleration of a mere 19g (humans tend to faint at accelerations above 10g) (2). To reach even higher speeds and accelerations, animals have developed catapults to increase their power output. A catapult enables muscles to slowly load an elastic energy store. The catapult then releases this energy very quickly, providing much higher speeds than could be delivered by the muscle directly. Froghoppers (also known as spittlebugs) hold the current record, accelerating at 408g when they catapult themselves into the air (3).

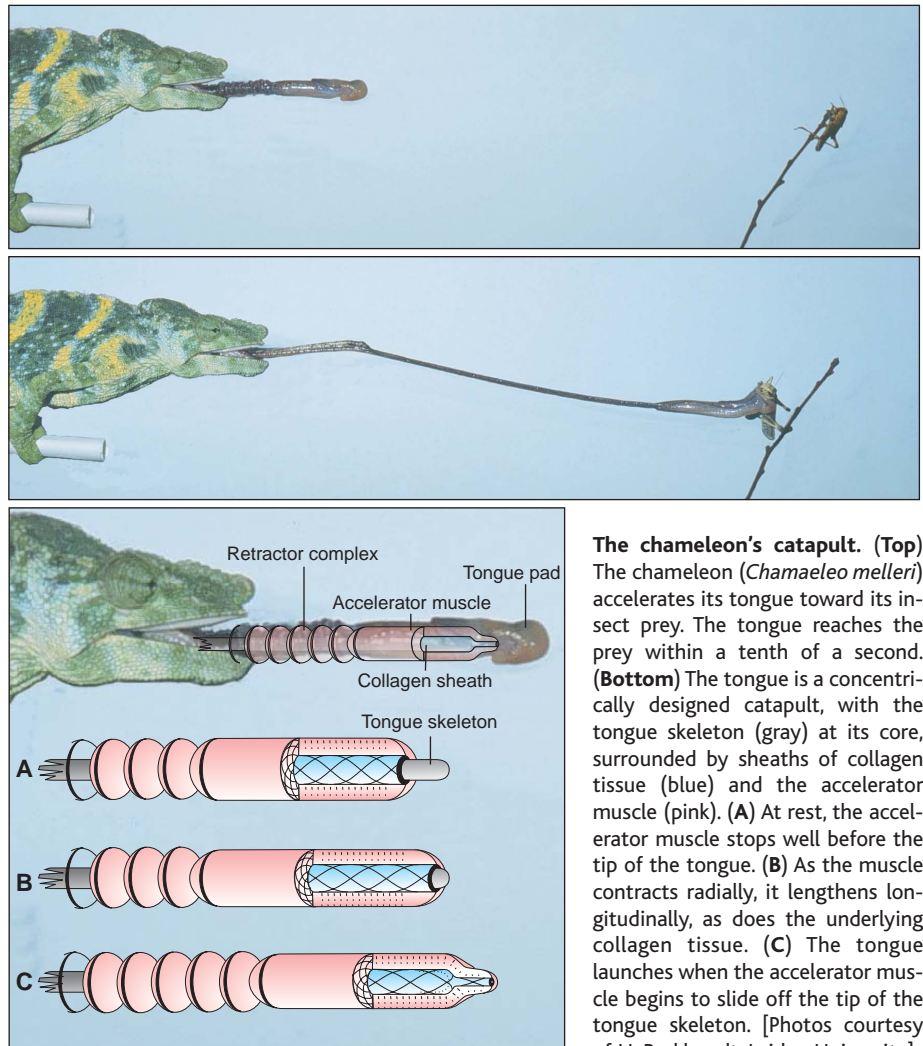
The chameleon's tongue accelerates at 500 m s^{-2} (51g) to speeds of up to 6 m s^{-1} (see the figure) (1). If projection of the chameleon's tongue were powered directly by the accelerator muscle, then this muscle

would need to generate peak powers of up to 3000 W per kg of muscle. This value is considerably higher than any values reported so far for vertebrate muscle (4) and exceeds the chameleon's muscle capacity by almost an order of magnitude (1). This suggested to de Groot and van Leeuwen that the chameleon's tongue must achieve acceleration in some other way, perhaps by acting as a catapult.

Any catapult requires a stiff frame, an energy store, and a power supply. By carefully dissecting the tongues of several chameleons, the authors were able to show that the skeleton of the tongue—a long, stiff rod of cartilage—provides the frame

of the catapult (see the figure). The elastic energy is stored in nested sheaths of collagen tissue that surround the tongue skeleton. These, in turn, are surrounded by the accelerator muscle. When this muscle is activated it contracts radially and, as muscle is incompressible, it lengthens along the skeleton (see the figure). The elongating muscle stretches the attached helical collagen fibers, loading them with elastic energy. When the tongue catapults, the stretched collagen tissue slides off the tongue skeleton (see the figure). Only at the tip of the skeleton can these sheaths relax radially, and, as each annular section squeezes over the taper, it forces the tongue forward. This "sliding spring" mechanism converts the stored elastic energy into kinetic energy and the tongue is launched forward at a dizzying speed.

The investigators demonstrate that the chameleon's catapult does not require a



The chameleon's catapult. (Top) The chameleon (*Chamaeleo melleri*) accelerates its tongue toward its insect prey. The tongue reaches the prey within a tenth of a second. (Bottom) The tongue is a concentrically designed catapult, with the tongue skeleton (gray) at its core, surrounded by sheaths of collagen tissue (blue) and the accelerator muscle (pink). (A) At rest, the accelerator muscle stops well before the tip of the tongue. (B) As the muscle contracts radially, it lengthens longitudinally, as does the underlying collagen tissue. (C) The tongue launches when the accelerator muscle begins to slide off the tip of the tongue skeleton. [Photos courtesy of H. Berkhoudt, Leiden University]

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latch to fire. The tongue-retractor complex (see the figure) prevents the elongating accelerator muscle from sliding backward while the front end of the muscle moves closer and closer to the tip of the tongue bone. The catapult is released at the moment when the muscle's most distal end slips off the tongue skeleton. This built-in trigger adds no extra moving parts or controls to the catapult. All it requires is a tongue skeleton that tapers off only at the very tip, so that the muscle can build up enough elastic energy before it begins sliding off.

The chameleon's "sliding spring" is remarkably compact, efficient, and easy to control. Conventional catapults store tensile energy in a rope or tendon that is loaded and unloaded along the same path. By using a collagen tube rather than a tendon, the chameleon can load the spring by global longitudinal tension but release its energy by local radial contraction. This asymmetric loading-and-unloading pattern has two advantages. First, the loading structure (the accelerator muscle) and the energy-storage structure (the collagen

tube) can be arranged concentrically. The tongue projector is thus compact, with admirably few moving parts or force transducers that would increase wear and reduce efficiency. Second, the sliding spring releases its elastic energy gradually as consecutive portions of the collagen tube slide off the tongue tip. Sudden acceleration is particularly unfavorable when shooting soft projectiles such as a tongue: Much energy can be lost in internal deformations and vibrations. Salamanders of the genus *Hydromantes*, which also project their tongue ballistically (5), avoid this problem by shooting out the stiff tongue skeleton together with the tongue itself.

In a primitive catapult, the force and acceleration are directly proportional to the extension of the spring (Hooke's law) and, therefore, are greatest at the moment of release. Conventional engineering designs, such as the compound bow, modify these characteristics by means of non-Hookean springs and dynamic levers. In a sliding-spring catapult (1), the course of energy release is determined in a radically different

way. Its components are arranged in parallel along an axis that corresponds to the time course of the driving force. Thus, spatial modulation of elastic loading along this axis programs the time course of the launching force. The chameleon can presumably "tune" the launch of its tongue by changing muscle recruitment (on the animal's time scale), or the muscle's shape and size (on an evolutionary time scale), without having to "invent" new lever elements or change the mechanical properties of existing elements. The extraordinary degree of functional integration in the chameleon's tongue, so unlike the modular designs of mechanical engineers, might explain how the chameleon has hidden its secret catapult from biologists for so long.

References

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ATMOSPHERIC SCIENCE

In Search of Paleo-ENSO

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In the past several years there has been a shift in the perceived importance of the tropical Pacific Ocean to global climate on glacial-interglacial and millennial time scales. Modeling studies have indicated that the El Niño–Southern Oscillation phenomenon (ENSO), which is the primary source of year-to-year variations in tropical sea surface temperature (SST) in the modern world, may be highly sensitive to orbital influences (1, 2). In these studies, the dynamical interaction between the atmosphere and ocean in the tropics is influenced by the modulation of the seasonal cycle of solar radiation by the precession of Earth; simulated tropical Pacific SST anomalies, akin either to warm El Niño or cold La Niña events, can be sustained for several hundreds to thousands of years and generate a globally synchronous climate response. Just as ENSO-related SST variations exert a major effect on modern atmospheric circulation and climate, models suggest that changes in tropical Pacific

SST patterns might also have had large consequences for global climate during the last glacial maximum (LGM) about 20,000 years ago (3). There is, however, still a large uncertainty as to the relationships between ENSO characteristics and the background mean climate state. Given that instrumental data are limited to the past century, paleoceanographic records can provide better constraints for assessing future effects of global warming on ENSO and their ramifications for Earth's climate (4).

Because ENSO is an interannual phenomenon with a strong seasonal signal, its long-term history is best reconstructed from annually banded corals (5). However, their reliability as recorders of long-term climate change is still debatable (6). Similarly, lake sediments with annually resolved varves provide valuable insights into variations in ENSO throughout the Holocene, but as yet we have no record that spans the LGM (7, 8). More recently, however, lower resolution sediment records from key locations in the tropical Pacific have also been used to infer long-term variability in ENSO and its possible role on both orbital and millennial time scales. In particular, two lines of evidence, both based on reconstructions of SST and salinity from measurements of Mg/Ca and $\delta^{18}\text{O}$

in foraminifera shells, have been proposed in support of long-term ENSO variability.

The first of these suggests that LGM relaxation of SST gradients within the cold tongue of the eastern equatorial Pacific was likely a result of reduced upwelling caused by weakening of the trade winds in an "El Niño-like" fashion (9). The second, which argues for "super ENSO" conditions during the cold Northern Hemisphere stadial intervals, is based on changes in the distribution of surface salinity and, by inference, precipitation in the western equatorial Pacific (10). These observations are very intriguing, yet they raise questions as to whether they are representative of the entire tropical oceans or only reflect local conditions (11). For example, the western Pacific salinity record is in a site that is currently strongly influenced by the east Asian monsoon system, which is tightly linked to Northern Hemisphere climate (12). There are also questions as to the fidelity of, and compatibility among, different paleo-proxies. For instance, faunal-based studies argue for intensification of the eastern equatorial Pacific cold tongue with the corollary of prevailing La Niña-like conditions during the LGM, in contrast with Mg/Ca-based SST reconstructions (13, 14). These concerns about the reliability of paleo-proxies in capturing the full scope of climate variability clearly need to be addressed (15).

Even in the absence of important uncertainties in paleoceanographic records, interpreting proxy evidence for changes in

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