EVOLUTIONARY MECHANICS OF PROTRUSIBLE TENTACLES AND TONGUES

by

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ABSTRACT

This paper provides a comparison at multiple levels of structural organization of the biomechanics of protrusible muscular systems with different origins and phylogenetic history. The high-performance prey capture tentacles in squid, the tongues of frogs and salamanders, and the tongue of the chameleon are used as examples.

The tentacles of squid are muscular organs that lack bony elements. They are rapidly elongated during prey capture (typical extension time 25 ms, peak acceleration of approximately 250 m.s\(^{-2}\)) by extensor muscles that have remarkably short sarcomeres (myosin filaments are only 0.5 to 1.0 µm, compared with 1.6 µm in vertebrates). Short sarcomeres generate only relatively small forces, but relatively high absolute strain rates for a given interfilamentary sliding velocity (at low external loads). A forward dynamics model (VAN LEEUWEN & KIER, 1997) predicts the movements of the tentacles with reasonable accuracy and predicts also that the short sarcomeres provide optimal extension velocity.

Several frogs (Hemisotidae and Microhylidae) have a similar extension mechanism in their tongue (denoted as hydrostatic elongators by NISHIKAWA, 1999b) to that found in the tentacles of squid. The extension performance is, however, limited relative to that observed in squid. This can be explained by two factors. First, the extensor fibres run in one direction only, while in the squid the fibres are arranged in circumferential arcs as well as in two other fibre groups that run at right angles to each other. The unidirectional fibre orientation results in a smaller extension for a given shortening of the extensor fibres than observed in the tentacle. Second, the myosin filaments in the extensor muscle of the frog tongue are similar to those found in other vertebrate skeletal muscle. It is likely that the filament lengths are not optimised for a high peak extension velocity although data are lacking thus far. These limitations have been circumvented by several groups of frog (Bufonidae, Ranidae and others) that 'throw' their tongue out of the mouth by a rapid jaw movement (inertial elongators).

The ballistic tongues of many plethodontid salamanders extend in less than 10 ms. The most extreme performance is found in Hydromantes supramontis, which elongates the tongue up to 80% of body length. The paired cylindrical protractor muscles envelope two elongate epibranchials, the posterior 'legs' of the tongue skeleton. The complete tongue skeleton is projected with the tongue pad. The normal stress of the protractor muscle on
the tapered epibranchials is postulated to be the main projection force (DEBAN et al., 1997). We suggest that a build up of a 'pre-stress' in the protractor and an associated storage of elastic energy in connective tissues prior to projection may be essential for rapid projection. Detailed kinematic studies of plethodontid tongue projection are needed.

The ballistic chameleon tongue has a remarkable performance, with a reported peak acceleration of the tongue during prey capture of about 500 m.s^{-2}. A cylindrical accelerator muscle envelopes the elongated entoglossal bone and is projected out of the mouth with the tongue pad. The extreme performance is likely due to a combination of several factors. First, the arrangement of muscle fibres in spiral arcs allows for close packing and uniform work output of the accelerator muscle fibres (VAN LEEUWEN, 1997). Second, pre-stress in hyobranchial muscles and elastic energy storage in connective tissues prior to projection may also be an essential element.

In future work, more attention should be paid to the possibility of elastic energy storage mechanisms in high-performance protrusible tentacles and tongues.

**KEY WORDS:** chameleon, frog, salamanders, squid, toad, dynamics, kinematics, tentacles, tongues.

**INTRODUCTION**

This paper reviews mechanical aspects of protrusible muscular organs that are used to capture prey: tentacles of squid and the tongues of amphibians and reptiles. These organs typically consist of tightly packed, three-dimensional arrays of muscle fibres and they are often capable of a very rapid change in shape, lasting for instance only 10-100 ms and leading to longitudinal muscle fibre strains of up to 0.8. The biomechanics of these muscular systems is complex. Activation of the muscle fibres may cause large deformations, which are generally difficult to predict because of the fibre-fluid nature of the tissues and the non-linear properties of these components. The high number of degrees of freedom of movement of these systems leads potentially to complex and distributed control.

Several important questions arise in the study of protrusible muscular systems. Examples are:

1. The performance of a protrusible muscular system depends heavily on the control and integrated design of several tissues at many structural levels (molecule, organelle, cell, tissue, organ). How are the different architectural levels integrated to yield a functional system?

2. How can the extension dynamics be understood in the light of muscle contraction dynamics (strain rate, power output etc.), intramuscular pressure development, and elastic energy storage and release mechanisms.