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Neuromuscular control: introduction and overview

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This paper introduces some basic concepts of the interdisciplinary field of neuromuscular control, without the intention to be complete. The complexity and multifaceted nature of neuromuscular control systems is briefly addressed. Principles of stability and planning of motion trajectories are discussed. Closed-loop and open-loop control are considered, together with the inherent stability properties of muscles and the geometrical design of animal bodies. Various modelling approaches, as used by several authors in the *Philosophical Transactions of the Royal Society of London*, Series B, May 1999 issue, such as inverse and forward dynamics are outlined. An introductory overview is presented of the other contributions in that issue.

Keywords: birds; evolution; flight; insects; locomotion; muscle

1. INTRODUCTION

(a) *Neuromuscular control: a multifaceted and interdisciplinary field*

A long evolutionary process shaped present animal motion systems. Their organization is often extremely complex and their analysis requires an interdisciplinary approach. In particular, the analysis of neuromuscular control systems faces at least five inherent problem categories that require consideration.

- (i) In neuromuscular control studies, multiple levels of structural organization have to be addressed. This can range from the molecular level (e.g. ion channel dynamics in membranes of neurons, muscle and sensory cells, and actin–myosin interaction), the cellular level (e.g. propagation of action potentials), the organ level (e.g. force and work output by muscles), the organismic level (whole-body dynamics), and the interaction with the environment.
- (ii) The systems at hand have a very large dimension. The control circuits are generally arranged in a parallel and a distributed fashion and exhibit nonlinear properties. Standard linear control theory is therefore only applicable in very special cases. Multidimensional parameter spaces are difficult to explore for the human mind. Fast computers are therefore required to tackle the extensive computational problems.
- (iii) The complex dynamics and the architecture of the components of neuromuscular control systems are generally poorly known. Quantitative measurements of their anatomical and physiological properties are technically difficult and time consuming. The

precision of biological measurements is often much lower than in artificial systems.

- (iv) Analysis of the interaction of the body with the environment is often required to understand the design of musculoskeletal systems and their neuronal controllers. For instance, flight and swimming involve complex interactions between body and fluid.
- (v) During development and growth, neuromuscular control systems continuously adapt themselves to the changing size and functional demands. Unfortunately, an understanding of the evolution of neuromuscular control systems is hampered by an incomplete knowledge of the architecture and dynamics of ancestral forms.

From the above (still incomplete) list of difficulties, it is clear that we can at best hope for a partial understanding of the complex systems under study. In practice, the investigator generally selects subsystems and attempts to reduce the number of variables. Quantitative models are required to tackle the nonlinear behaviour and to test qualitative hypotheses that arise from experimental observations, even if the models are strongly simplified. Simple models tend to focus on principles and often have the advantage of general applicability. Of course, a complete overview of this field is not intended here. In this paper, I shall concentrate on aspects that were discussed during the meeting.

(b) *Trajectory control and stability*

In movement tasks, several alternative trajectories of the body segments are possible. Animals (including people) tend to make smooth and precise movements. According to which (optimization) principles are movement trajectories of body segments planned by the

nervous system? Hogan (1984) proposed that the motor system generates paths that minimize jerkiness (jerk is the time derivative of acceleration). Others have suggested that our movements are planned to maximize efficiency (e.g. Nelson 1983). In several tasks, power output or the velocity of body segments plus added masses are likely to be maximized. Examples are found in sport (e.g. shot putting; Alexander 1991a) and predator–prey interactions (e.g. tentacle extension in squid; Van Leeuwen & Kier 1997). An intriguing alternative was proposed recently by Harris & Wolpert (1998), who suggested that movements are planned according to the principle of maximum precision. Neuronal control signals are corrupted with noise, the variance of which tends to increase with the size of the control signal. Harris & Wolpert (1998) suggested that the shape of the movement trajectory is selected to minimize the variance in the final desired position. Their theory predicted successfully the trajectories in saccadic eye movements and goal-directed arm movements, which are indeed movements that require high precision. However, precision may not always be the main factor in trajectory planning. Movement optimization principles are likely to vary with the imposed functional demand(s).

Movement trajectories can be perturbed by unexpected events. Stability could be defined as the ability of a system to return to its original state after a disturbance such as a velocity perturbation due to an unpredictable external force. It could also be considered as the ability to return to a desired movement trajectory after some perturbation. Stability aspects of nonlinear systems can be studied, for instance, with the Lyapunov stability criterion in which the properties of an energy potential are considered (see, for example, Arrowsmith & Place (1992) for an introduction). So far, this criterion has not been widely exploited.

What are the possibilities of the body contributing to stability? A few examples are given. Sensory systems in the body, such as the visual and equilibrium system, monitor disturbances and send feedback signals to the neuronal controller, which in turn adapts its output to the muscular system to correct undesired displacements. This type of feedback control adds to stability, but the flow of information and mechanical response consumes considerable time (compared to other options). Less time is consumed in (spinal) muscle reflexes. Stretched muscles feed sensory information monosynaptically back from muscle spindles and Golgi tendon organs to the motor neurons in the spinal cord and brainstem. Increased muscle activation counteracts the stretch (the mechanisms of gain and sensitivity control of this reflex are beyond the present aims). This pathway is relatively fast, but time delays still occur (> 10 ms). These reflexes are, however, fast enough to avoid falling down during, for instance, stumbling.

A further, much faster, stabilizing mechanism arises from the mechanical properties of the muscles themselves. Muscle fibres exert greater forces if their strain rate increases. These properties are known as the Hill-type force–velocity relationship. This mechanical property counteracts the stretching effect on a muscle immediately, and was called a ‘preflex’ by Loeb (1995). In addition, stabilizing effects could result from characteristic force–

length properties of muscle. The role of the giant molecule titin that runs between the myosin filament and the Z-disc is of interest here because it affects the passive force–length characteristics. Joint rotations generally result in changes of the associated muscle moment arms with a possible contribution to stability. The moment arm of the human quadriceps muscles (a group of knee extensors), increases with bending of the knee (Spoor & Van Leeuwen 1992) and could therefore contribute to knee stabilization.

Stabilizing effects also result from the macroscopic whole body design. Racing cars are designed with a low centre of mass and a considerable width between the wheels. Obviously, this design enhances performance and reduces the control problems for the driver. Similar examples from nature are the sprawling postures of insects and spiders (see §3a and especially the contribution of Kubow & Full in this issue). The inherent properties of the biomechanical system that contribute to stability have great advantages because they simplify the tasks of the neuronal controller and improve the response speed to disturbances. Biological neuronal controllers can only be understood if the design of the ‘plant’ to be controlled (e.g. the musculoskeletal apparatus) is incorporated in the analysis.

2. MODELLING

To investigate the function of neuromuscular control systems, quantitative models of the dynamic behaviour of its components are required. It seems, therefore, appropriate to give a summary of some modelling approaches that have been used in this issue.

The dynamic models that have been developed in control studies can generally be divided into inverse dynamics models and forward dynamics models. In the inverse dynamics approach, forces and net moments about joints are calculated from measured positions, velocities and accelerations of body segments, and inertial parameters of body segments. Positions can be obtained from video or film analysis. Velocities and accelerations can subsequently be derived by differentiation. The accelerations so obtained are often inaccurate because of errors in the measured positions. Special differentiation algorithms have been proposed to reduce these errors as much as possible (see Walker (1998) for a recent comparison). Instead, miniature accelerometers could be used, but mounting these transducers on the skin is also likely to result in considerable errors. The obtained net joint moments are insufficient to calculate individual muscle forces (even if individual instantaneous moment arms of all muscles were available), because the problem is indeterminate: a whole family of different force distributions satisfies the same moment. In spite of its limitations, the inverse dynamics method can be very useful in neuromuscular control studies, especially if it is combined with force and electromyographic measurements. In this issue, the inverse approach has been successfully used by Otten to study the control of balancing by a human subject on a narrow ridge.

In forward dynamics, the system dynamics is calculated given some input to the system and the system equations. In biomechanics, this implies that motions of

body segments are calculated from the driving forces of the muscles, controlled by neuronal inputs. Ideally, the model should also include models of the neuronal controller and sensory systems that provide feedback to it. This approach is attractive because it more closely follows the information flow in the body than does the inverse method. In practice, this method results in numerous problems. The number of parameters is generally very large, and many unknown or ill-defined factors are often present. In addition, many numerical problems have to be solved. An example of this approach in this issue is the study of the neuromuscular control of swimming in the lamprey by Ekeberg & Grillner, in which the neuronal controller, the muscular system, the interaction with the water, and the sensory feedback were integrated in one model. In this issue, Rienen discusses forward dynamics models of the human body to predict the effects of artificial stimulation in paraplegic patients.

The interaction between body and environment must be included in many models. The geometry and mechanical properties of the natural substrate in terrestrial locomotion are difficult to describe and to measure. In practice, investigators often choose a well-defined flat surface for their experiments and models. This could hide a significant portion of the functional repertoire and demands posed upon the system. Fluid dynamics calculations are required to obtain the reaction forces on the animal in studies of flight and swimming. Encouraging developments are occurring in this area. Recently, Liu *et al.* (1997, 1998) calculated three-dimensional (3D) flow fields around a swimming tadpole and the wings of the hawkmoth using a numerical approximation of the Navier–Stokes equations with the finite volume method, a popular procedure in computational fluid dynamics (CFD) that allows animals with a fairly complex geometry to be accurately described. An introduction to this method is given by Dick (1996). Integrated models of external fluid dynamics with internal muscle mechanics, sensory dynamics and neuronal control dynamics, form a logical further step. The paper by Ekeberg & Grillner on lamprey swimming describes an interesting step towards this goal.

So far, mainly biomechanical aspects of modelling have been addressed. A vast literature exists on the modelling of neurons and neuronal networks. General purpose computational tools are now widely available for this purpose (see, for instance, Bower & Beeman 1998; Hines 1984; De Schutter 1992). Neurons are generally described as branching cables for which Hodgkin–Huxley type equations (these equations describe the membrane electrical dynamics in terms of various ionic conductances) are solved. The abstracted neuron is divided into a number of interconnected compartments for this purpose. Several thousand compartments have been used to predict the dynamics of the cerebellar Purkinje cell (De Schutter & Bower 1994). It is obvious that such detailed neuronal representations are impossible for neuronal groups involved in whole body control problems. Modelers have to decide on the amount of detail to incorporate. Neuronal systems are often difficult to model accurately because the morphological and physiological databases are always incomplete.

3. OVERVIEW OF TOPICS

This section provides an overview of the various contributions to this issue. In several cases, the limitations and perspectives of the applied approaches will be addressed.

(a) *Walking and balancing*

Insects have a large surface to volume ratio. Compared to their weight, they tend to experience high external forces that could easily disturb their walking patterns. Their small size and low mass lead to high demands for the (mechanical) response times if stability is to be maintained. The effects of size and mass distribution on the demands for stability control can be illustrated nicely by balancing sticks (orientated vertically) of varying length and mass on the finger. A wooden stick 0.5 m long and 10 mm wide can be maintained dynamically stable for a considerable time. Stabilizing a pencil for the same time is impossible, at least for this author. It is expected that insects have to exploit the possibilities of the inherent stabilizing properties of muscles, joint geometry and whole body architecture to their limits (see also § 1b).

In this issue, Kubow & Full explore whether the sprawled configuration of the insect's legs can support the mechanical stabilization of walking. They propose a simple model with a geometry that has been derived from the cockroach; it focuses on the horizontal projection of the body, neglecting vertical force patterns. The model predicts that a perturbation of the velocity and orientation of the animal results in changed moment arms of ground reaction forces of the supporting legs with respect to the centre of mass. The changed lever arms in turn tend to restore the animal to its unperturbed locomotion trajectory. Interestingly, this forward dynamics model does not include any neural feedback; nevertheless, it is remarkably stable. The message derived from this model is clear: geometry matters in the design of neuromuscular control systems. The authors assumed that the ground reaction forces and the positioning of the legs with respect to the body are not affected by the mechanical perturbation. These assumptions have so far not been tested by (technically difficult) experiments. Changes in these parameters will undoubtedly occur, if only because of intrinsic mechanical properties of the leg muscles (discussion about 'prelex' in § 1b). New insights are expected to result from an extension of the model to three dimensions and a quantification of the musculoskeletal dynamics of the legs.

Large terrestrial animals have to cope with different mechanical demands. Body mass scales with l^3 (l is any length measure), whereas surfaces scale with l^2 . Maximum force generated by muscles is proportional to surface area. Identical postures would lead to the highest stresses in the largest animals if differently sized animals were geometrically similar. In practice, large animals tend to avoid sprawled postures and stand on relatively straight and close to vertically aligned limbs. This cursorial posture reduces joint moments and the mechanical stresses in muscles, tendons and bones. In addition, the dynamic range (i.e. speed and acceleration of locomotion) of animals is size limited. On the assumption that the maximum strength of tissues is invariant with size, it is even possible to predict the maximum speed of

locomotion of extinct animals such as dinosaurs (Alexander 1991b). A cursorial posture is much easier to control for a large animal than it would be for a very small animal, and therefore forms a realistic option from the viewpoint of neuronal control. The much higher inertia of the system gives more room for neuronal feedback control. Delays in feedback loops can generally be kept well within the characteristic time constants of the mechanical system.

Nevertheless, to reduce the problems of stability and control, robot designers have often preferred to use sprawled postures, even if the size of their robots was large. In this issue, Papantoniou *et al.* describe the mechanical and control problems that arise if one aims to design a robot which should move similarly to the extinct dinosaur *Iguanodon*. A prototype capable of autonomous movement is currently operational. Its efficiency is estimated to surpass that of the extinct dinosaur, but with a much lower maximum speed of locomotion, owing to a limited energy supply. Initiatives such as that of Papantoniou *et al.* will help to revolutionize the exhibits in natural history museums. Current robots are very much simpler than animals. We are only starting to discover the many ingenious solutions of animal design and control. Biological reverse engineering is, and will be, a rich source of inspiration for intelligent robot designers.

Mechanical aspects of walking have been successfully studied with inverted pendulum models of the body. Is an inverted pendulum model also a suitable model to study balancing during standing? In this issue, Otten studied the control of balancing by a healthy human subject during standing with one leg on a narrow ridge. Calculations of net joint moments in a multi-segment model of the human body reveal that the hip joint plays a crucial role in this balancing problem. Otten also shows that an inverted pendulum model for balancing during standing fails to explain the control mechanism for this task. An inverted pendulum is balanced by rapid corrections of its basal support. Obviously this is not an option in the balancing task on the ridge. The dynamics of a multi-segment arrangement allows a much richer repertoire of control solutions than an inverted pendulum. This is nicely illustrated by choosing a balancing problem that cannot be solved by inverted pendulum behaviour. Otten's biomechanical approach sheds light on the solutions generated by the neuronal controller. The applied inverse dynamics approach, however, cannot be used to address the question of how the internal design of the neuronal controller is adapted to fulfill its functional demands.

The next challenging question is: what therapeutic interventions can be made available if the neuronal controller is irreversibly impaired? Artificial stimulation is the logical step to make, but the control of complex multi-joint systems is exceedingly difficult. In this issue, Riener provides an overview of model-assisted designs of neuroprostheses for paraplegic patients. So far, the functional gain resulting from artificial stimulation in paraplegics is low, despite decades of development. Detailed knowledge of the musculoskeletal dynamics (in patients generally significantly affected by long-term deactivation) is required for a successful design. Inverse dynamics and forward dynamics multi-segment models of

the body are invaluable tools (i) to judge the effects of artificial stimulation, and (ii) to predict the behaviour of the real system in response to a range of stimulus patterns, enabling an exploration of the parameter space which would not be possible under the limited experimental conditions.

(b) *Swimming and flying*

An understanding of swimming and flight requires models of the neuronal control systems, musculoskeletal mechanics, the interaction between body and external medium, and sensory dynamics. This is a daunting task which requires that many simplifications be made. Liu *et al.* (1997) modelled the unsteady flow generated by an undulating tadpole in three dimensions. The forward motion of the body and the body deformation during swimming as measured from films of swimming tadpoles was used as input for the model. Due to various inaccuracies, this method leads to a force distribution on the body that is not completely compatible with the real forward body motion. The CFD model for anguilliform swimming by Carling *et al.* (1998) has solved the propulsion problems. The flow field and forward body motion were calculated from prescribed body undulations. This approach is, however, still limited to two dimensions.

The organization of the spinal cord of the lamprey is relatively simple and relatively well-known. The driving activity patterns for swimming have been measured and modelled by various authors. For instance, Williams (1992) has modelled the spinal cord of the lamprey as a chain of simplified coupled oscillators. Lampreys exhibit an intersegmental posterior delay in activation pattern which can be reconstructed with such models under the assumption of an asymmetry in the descending and ascending coupling strengths between the oscillators. Interestingly, the wave travels posteriorly for dominant ascending coupling, an initially counter-intuitive finding. Much more complicated models of spinal cord dynamics have been proposed by Ekeberg and colleagues (see references in Ekeberg & Grillner, this issue). They modelled a network with neurons comprising multiple segments and Hodgkin–Huxley descriptions of physiologically characterized ion conductances.

A model of the dynamics of segmental musculature and body dynamics has been proposed by Bowtell & Williams (1991). This model grossly simplifies the complex architecture of the myomeres and does not yet incorporate reaction forces from the water.

In conclusion, various components are now available with which to build a model of a neuronally controlled swimming lamprey, and connections between sub-models need to be made. In this issue, Ekeberg & Grillner describe such an integrated model, albeit with very simplified components. Simplifications are required for acceptable computational loads. Sub-models are also included of vestibular and intraspinal stretch receptors that feed information back into the neuronal model. The model is capable of a rich behaviour that includes complex yaw, pitch and roll movements. Of course, it is not difficult to criticize a model of this nature on specific points. For example, the fluid interaction was reduced to static drag forces. The model lamprey is therefore swimming in an artificial medium. However, various

sub-models can, in principle, be replaced by improved versions, thereby increasingly contributing to our understanding of a highly complex locomotor system.

Studies of flight control face problems of similar complexity to those found in swimming. Flies manoeuvre by changing the mechanical output of a set of steering muscles in the thorax that control wing motion and the associated aerodynamic reaction forces on the wings. The steering muscles are mainly controlled via visual interneurons and input from mechanosensory equilibrium organs, the halteres. The feedback of both systems results in voluntary and reflexive corrections of flight trajectories. The halteres (very small club-shaped structures) have evolved from a pair of hind wings and beat up and down during flight, in antiphase to the forewings. Dickinson discusses in this issue how a fly in tethered flight (*Drosophila melanogaster*) makes compensatory adjustments in its wing-beat frequency and stroke amplitude to imposed perturbations of its orientation. The changes in wing kinematics in response to rotation of the fly varied with the stimulus direction. The magnitude of the changes in stroke amplitude and frequency appeared to be linearly proportional to the velocity of angular rotation, indicating that the halteres detect Coriolis forces as proposed earlier by Pringle (1948) in this journal. Coriolis forces are inertial forces on an object that result from a rotating frame of reference. The Coriolis acceleration \mathbf{a}_C is calculated as twice the cross-product of the angular rotation of the moving frame and the particle velocity in the moving frame: $2\boldsymbol{\omega} \times \mathbf{v}_m$ (see, for example, Spiegel 1967). The Coriolis force on a particle is simply its mass multiplied by \mathbf{a}_C . The linear response found by Dickinson is, in fact, remarkable because the effect of the Coriolis forces is mediated via sensory cells at the base of the haltere, the nervous system and the steering muscles. All these components are expected to have nonlinear characteristics. This also holds for the interaction between wing and air. Separate measurements of the dynamic properties of all the contributing components are required to provide definite answers to this puzzle.

The paper by Sokoloff & Goslow in this issue considers muscle design in relation to flight control in birds. Wake visualization has shown that birds and bats use two main gait patterns in steady flapping flight (Spedding *et al.* 1984; Spedding 1987; see Rayner & Gordon (1998) for a recent short overview): the vortex ring gait and the continuous vortex gait. The vortex ring gait is characterized by closed elliptic vortex elements. The vortex elements in the continuous vortex gait follow approximately the path of the wing tips. The wings and flight muscles function differently in both gaits. During the upstroke in the vortex ring gait, the wings are folded and do not generate much lift. In the continuous gait, the wings are aerodynamically active during both up- and downstrokes, and flexing during the upstroke is limited.

Different force patterns are generated by the flight muscles for each gait. Force-length patterns produced by the pectoralis, the main flight muscle, have been experimentally recorded in the pigeon using the vortex ring gait during slow flight (Biewener *et al.* 1998). The pigeon pectoralis starts to develop force as it is still being stretched; it then shortens by 32% of its resting length during the downstroke, generating about 10 J kg^{-1} of

energy. Similar recordings are not yet available for the continuous vortex gait.

Sokoloff & Goslow raise the intriguing question of how force is generated and transmitted in the pectoralis muscle of the pigeon. Their data show that the pectoralis muscle of birds contains short muscle fibres that do not extend from the origin to the tendon that inserts into the humerus. The in-series fibres overlap with tapered ends. Individual motor units do not span the distance between origin and insertion. This requires complex problems to be solved by the controller, because unbalanced activation and force generation in serially arranged muscle fibres would affect the efficiency and power output of the system.

(c) *Vocalization in birds*

Vocalization in birds is another intriguing and rapidly developing field in which air flow is controlled through neuromuscular systems. Detailed information is available about the neural circuitry (Wild 1997), but insight into its dynamic functioning is still limited. Two main mechanisms of vocalization have been distinguished. First, sound could be generated without (a significant contribution of) oscillating surfaces. These so called 'whistles' have an almost pure tone character and probably reflect an unstable air jet. Recent studies have not, however, supported this type of mechanism (Goller & Larsen 1997, 1998; Ballintijn & Ten Cate 1998) in pigeons (a 'non-songbird') and songbirds. Alternatively, voiced sounds are produced by a flow-induced vibration of membranes (in non-songbirds; Goller & Larsen 1997) or labia and membranes (in songbirds; Goller & Larsen 1998) in the syrinx (the principal vocal organ around the junction of trachea and primary bronchi). During phonation, air is pushed through the primary bronchi towards the mouth, while bronchial and tracheal membranes are pushed inwards by pressure in the interclavicular air sac. Endoscopic observations have shown that during phonation in songbirds, the syrinx deforms so that the medial and lateral labia (just distal to the medial membranes of the bronchi) are pushed inwards forming a 'vocal slit' which is analogous to the laryngeal vocal slit in mammals (Goller & Larsen 1998). The flow of air sets the labia into oscillation with a fundamental frequency corresponding to that of the recorded sound. The trachea, larynx and mouth act as complex acoustic filters.

Many songbirds are capable of remarkable variety in their song. Sudden jumps do occur in the harmonic structure of the song. The question arises to what extent these transitions are a result of complex changes in the output of the neural controller. Recently, Fee *et al.* (1998) have shown with a syrinx preparation of a songbird that song harmonic transitions such as frequency doubling can be obtained with a remarkably simple control signal (a slowly varying pressure load of the syrinx). A similar effect was generated with a simple mechanical model (based on a previous outstanding model by Fletcher (1988)). This suggests that the complexity of the sound repertoire is significantly determined by the nonlinear behaviour of the syrinx and aerodynamic flow. The neural controller can therefore only be understood if detailed knowledge of the mechanical behaviour of the syrinx is available.

In this issue, Suthers *et al.* provide a detailed review of the control of vocalization in birds. They pay particular attention to the role of the respiratory system in vocalization, the complex timing and effects of the intrinsic muscles of the syrinx on the song, the role of sensory feedback (also to compensate mechanical perturbations), and aspects of motor learning.

(d) *Mechanics, control and evolution of frog tongues and other muscular hydrostats*

Vertebrate tongues are muscular hydrostats, i.e. muscular organs that are not supported by bony elements. Other examples are the arms and tentacles in squid and the trunk of the elephant. The mechanics and control of these muscular organs is difficult to understand because of the complexity of the soft body mechanics with an almost infinite number of degrees of freedom. The muscle fibres often follow complex paths, and fibre groups with different orientations may be arranged in interwoven patterns. Models of the neuronal controller and muscular system are necessary for significant progress in this complex field.

So far, few investigators have attempted to model the mechanics of muscular hydrostats. The human tongue has been elegantly modelled with a finite element approach by Wilhelms-Tricarico (1995). This complex 3D model was designed as an instrument for the study of the role of the tongue in speech control. The very high computational load of this model still limits the number of elements that can be used, and therefore the accuracy by which muscle-fibre arrangements can be described. Van Leeuwen & Kier (1997) presented a forward dynamics model of the tentacle strike in squid that included mass inertia and multiple segments, each receiving their own activation signal as input. This model accurately predicted the extension of the tentacle. A linear forward motion of a tentacle resulting in the least drag is the only feasible option in water. Extensor muscle fibres are therefore preferably arranged in transverse planes. Variation of the kinematics and force transmission at the level of the muscle-fibre arrangement is therefore limited. Extensor-fibre contraction results in elongation because of the local conservation of muscle volume. During the strike, the muscular stalk of the tentacle has only to push forward a fairly low mass (the terminal club plus a small added mass of water). The low macroscopic load also results in a low load on the sarcomeres. Van Leeuwen & Kier (1997) calculated that relatively short sarcomeres (as actually found in the extensor fibres) result in the highest extension speeds. Short sarcomeres are less forceful than long sarcomeres, but result in more sites along the muscle fibres where filaments can slide along each other, and thus in higher strain rates at small loads.

How does the performance of frog tongues with much longer sarcomeres in their protractor muscle fibres, compare to that of squid tentacles? In this issue, Nishikawa explores the mechanics, control and evolution of tongue protraction during prey capture in frogs. Based on anatomical and experimental observations, three main mechanical types of protrusible frog tongues are distinguished. In two types, only longitudinally arranged muscle fibres are present. Only one of these last two types shows a performance comparable to squid tentacles.

However, jaw motion delivers most of the required mechanical power for tongue protraction in these 'inertial elongators'. Hence, the limitations of longitudinally arranged muscle fibres and long sarcomeres are circumvented. A remarkably precise control of tongue and jaw muscles results in an almost linear path of the tongue pad, in spite of jaw rotations and changing curvatures of the tongue. Is feedback control an option in protrusible muscular hydrostats during prey capture? The fastest extensions of tongues or tentacles occur in 15–30 ms so that open loop control is the only possibility. Sensory feedback cannot play a role because of speed limitations in neuronal conduction and synaptic transmission, and the electromechanical delay of muscle fibres. In a third tongue type, the hydrostatic elongators, muscle extensor fibres are found in transverse planes. As expected from mechanical analysis, these tongues generally exhibit much lower peak extension speeds than found in the inertial elongators. Interestingly, Nishikawa shows that this last slow tongue type differs markedly in motor unit organization and sensory feedback.

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