Neuromechanics: an integrative approach for understanding motor control

Kiisa Nishikawa,[1,*] Andrew A. Biewener,[2,†,*] Peter Aerts,[§] Anna N. Ahn,[‡] Hillel J. Chiel,[◇] Monica A. Daley,[†] Thomas L. Daniel,[a] Robert J. Full,[○] Melina E. Hale,[#] Tyson L. Hedrick,[a] A. Kristopher Lappin,[*] T. Richard Nichols,[£] Roger D. Quinn,[**] Richard A. Satterlie,[††] and Brett Szymik[††]

[*]Department of Biological Sciences, California State Polytechnic University, Pomona, CA 91768; [†]Concord Field Station, Museum of Comparative Zoology, Harvard University, Bedford, MA 01730, USA; [§]Department of Biology, University of Antwerp, and Department of Movement and Sport Sciences, University of Ghent, Belgium; [‡]Department of Biology, Harvey Mudd College, Claremont, CA 91711; [◇]Department of Biology, Case Western Reserve University, Cleveland, OH 44106; [a]Department of Biology, University of Washington, Seattle, WA 98195-1800; [○]Department of Integrative Biology, University of California, Berkeley, CA 94720-3140; [#]Department of Organismal Biology and Anatomy, University of Chicago, Chicago, IL 60637; [£]Department of Physiology, Emory University, Atlanta, GA 30322; [**]Department of Mechanical and Aerospace Engineering, Case Western Reserve University, Cleveland, OH 44106; [††]Department of Biology, University of North Carolina, Wilmington, NC 28409, USA

Synopsis Neuromechanics seeks to understand how muscles, sense organs, motor pattern generators, and brain interact to produce coordinated movement, not only in complex terrain but also when confronted with unexpected perturbations. Applications of neuromechanics include ameliorating human health problems (including prosthesis design and restoration of movement following brain or spinal cord injury), as well as the design, actuation and control of mobile robots. In animals, coordinated movement emerges from the interplay among descending output from the central nervous system, sensory input from body and environment, muscle dynamics, and the emergent dynamics of the whole animal. The inevitable coupling between neural information processing and the emergent mechanical behavior of animals is a central theme of neuromechanics. Fundamentally, motor control involves a series of transformations of information, from brain and spinal cord to muscles to body, and back to brain. The control problem revolves around the specific transfer functions that describe each transformation. The transfer functions depend on the rules of organization and operation that determine the dynamic behavior of each subsystem (i.e., central processing, force generation, emergent dynamics, and sensory processing). In this review, we (1) consider the contributions of muscles, (2) sensory processing, and (3) central networks to motor control, (4) provide examples to illustrate the interplay among brain, muscles, sense organs and the environment in the control of movement, and (5) describe advances in both robotics and neuromechanics that have emerged from application of biological principles in robotic design. Taken together, these studies demonstrate that (1) intrinsic properties of muscle contribute to dynamic stability and control of movement, particularly immediately after perturbations; (2) proprioceptive feedback reinforces these intrinsic self-stabilizing properties of muscle; (3) control systems must contend with inevitable time delays that can simplify or complicate control; and (4) like most animals under a variety of circumstances, some robots use a trial and error process to tune central feedforward control to emergent body dynamics.

Introduction

Movement science is a vast topic that spans a wide range of disciplines, not only within biology (e.g., biomechanics, muscle physiology, neuroscience), but also in other fields including engineering, medicine, sports, mathematics, and psychology. A major goal of movement science is to understand how movement is controlled. This area of research seeks to understand how muscles, sense organs, and the central nervous system interact to produce coordinated, dynamically stable movement under steady conditions, as well as when animals negotiate complex terrain and experience unexpected perturbations. Applications include

ameliorating a wide range of human health problems, from prosthesis design to brain and spinal cord injury, as well as design and actuation of mobile robots. Historically, studies of motor control developed mostly within the field of neuroscience (e.g., in the areas of behavioral neuroscience, central pattern generators (CPGs), neurophysiology, proprioception, psychophysics). Over the past 20 years however, the ideas that muscle and body mechanics also contribute to control of movement have become well-established (Chiel and Beer 1997; Full and Koditschek 1999; Loeb et al. 1999).

A significant impediment to understanding control of movement is the formidable complexity of animal bodies (i.e., high-dimensionality, nonlinearity) (Full and Koditschek 1999). From a design perspective, it seems clear that algorithms for controlling a system must take into account the details of how that system works. Although it might seem that the complexity of animal bodies would mean that the algorithms for controlling complex bodies must necessarily be complex, an alternative view is that the mechanics of the moving parts in relation to their interaction with the environment may actually simplify control (Loeb et al. 1999; Koditschek et al. 2004; Ting and Macpherson 2005).

Motor control fundamentally involves a series of transformations of information among different levels and components of the neuromuscular and skeletal systems. Sensory information (proprioceptive and exteroceptive) is transduced by sensory structures that in turn transfer a subset of their information to the central nervous system which, following yet another transformation, issues a set of motor commands. The motor commands trigger force development in muscles, which drive movement and control the mechanics of the body. The mechanical coupling between musculoskeletal elements and the muscles controlling them is yet another transformation of information in the system. Muscles, via joint torques, drive the body's motion, whose inertia and shape determine its trajectory in space. Importantly, external forces from the environment, as well as intersegmental forces, also influence the trajectory of movement. That trajectory and its time history determine the visual and mechanical information that is available to the system. Finally, the mechanics and physics of sensory structures determine the bandwidth of information that is available to the nervous system for control (Göpfert and Robert 2002). Understanding how control is achieved, therefore, depends on knowledge of the specific transfer functions that describe each transformation. In turn, the transfer functions depend upon the rules of organization and operation that determine the dynamic behavior of each subsystem.

The inevitable coupling between neural information processing and the emergent mechanical behavior of animals is a central theme in neurobiology today. Such "neuromechanical" approaches ask how mechanical systems may offload some tasks of the neural system; how size, shape, structural properties, and even the physics of the medium may determine how the neural system functions to control movement; and how processing of sensory information may limit the range or rates of movement that are feasible.

In this review, we discuss relevant work in neuromechanics, although we refer more extensively to work carried out in the authors' laboratories. In doing so, we consider the contributions of (1) muscles, (2) sensory processing, and (3) central networks to motor control, (4) use examples to illustrate the interplay among the central nervous system, musculoskeletal system, sense organs, and the environment in the control of movement, and (5) describe advances in robotics and neuromechanics that have emerged from application of biological principles in robotic design. We end with a discussion of the emerging principles of neuromechanics and their implications for understanding motor control.

Part I. Contributions of muscle to motor control

Skeletal muscle is often treated as a simple black box through which a neural signal passes to produce a mechanical output. The mechanical behavior of a given muscle is typically assumed to be predictable, given its anatomy, stimulation pattern, and/or basic contractile properties. Musculoskeletal anatomy alone is often used as an indicator of muscle function. For example, it seems straightforward to infer the functions of the *biceps brachii* muscle (i.e., elbow flexion) and the *triceps brachii* muscle (i.e., elbow extension) from the basic anatomy of their origins and insertions.

In addition to anatomy, the activation (or stimulation) pattern experienced by a muscle also influences its force output. Whereas a single stimulus results in a small twitch contraction, multiple stimuli at a low frequency produce higher forces. Very high forces, as during a tetanic contraction, can be elicited using high frequency stimuli. Finally, the basic contractile properties of a

muscle, such as its contraction kinetics, force–length relationship, and force–velocity relationship, are also known to affect its mechanical output (Josephson 1999).

Although muscles are often viewed as motors that produce movement by shortening to perform mechanical work (termed "actuation" in engineering and robotics), they may serve a variety of other functions during movement. They may stabilize motion at joints, store elastic energy in connective tissues (e.g., tendons or apodemes), and absorb work as well as perform it (Biewener 1998; Biewener and Roberts 2000; Dickinson et al. 2000). Whereas swimming and flying require substantial positive work to produce the fluid forces needed for movement, steady locomotion over level ground often involves the use of muscles to produce force economically; muscles facilitate elastic energy recovery to achieve minimal net work output. When movement becomes nonsteady or requires changes in grade, shifts in motor recruitment will reflect the changing need for muscles to perform or absorb work. The function of a muscle during movement may also depend on the biomechanical context (e.g., position or mechanical advantage; Sutton et al. 2004; Uyeno and Kier 2005; Novakovic et al. 2006).

Muscle as a device for translating a control signal into a mechanical output

Although it is well-established that muscles can perform a range of functions in addition to actuation, it is less clear what factors determine the particular role(s) that a given muscle will play during movement. The hindlimb muscles of the death-head cockroach, *Blaberus discoidalis*, illustrate this problem. In the hindlimb of *Blaberus*, muscles 178 and 179 are two of six muscles positioned to generate extensor moments at the coxa-femur joint (Carbonell 1947). These two muscles have very similar anatomy and nearly identical moment arm relationships with joint angle (Full and Ahn 1995). Because a single motor neuron innervates both muscles (Pearson and Iles 1971), they also experience identical activation patterns during running *in vivo* and during nerve stimulation *in situ* (Ahn et al. 2006). In addition, muscles 178 and 179 have similar contraction kinetics, force–velocity relationships, and force–length relationships (Ahn et al. 2006).

Despite these many similarities, mechanical energy production *in situ* differs between muscles 178 and 179 (Fig. 1). Full et al. (1998) used the work loop
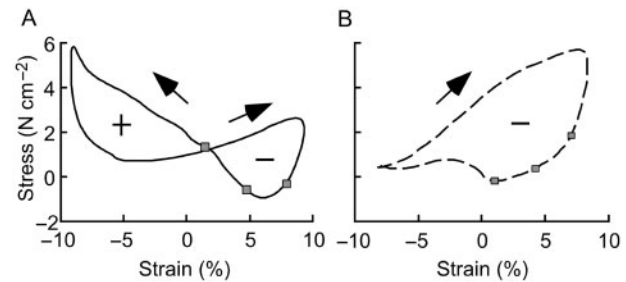

Fig. 1 Representative work loop plots for muscles 178 and 179 of the insect leg under *in vivo* running conditions. Gray squares represent the pulses of stimuli. This stimulation pattern was determined during running at the animal's preferred speed. (**A**) Mechanical work for muscle 178 (solid line). Muscle 178 generates no net mechanical power during simulated running cycle. (**B**) Mechanical work for muscle 179 (dashed line). Muscle 179 absorbs mechanical energy during a simulated running cycle. Arrows represent the direction of the work loop, while (+) and (−) signs indicate net generation or absorption of mechanical energy, respectively. From Ahn et al. (2006).

technique (Josephson 1985) to investigate the functional role of muscle 179, using activation and strain patterns determined *in vivo* during running. Ahn et al. (2006) subsequently examined the work loop, force–velocity and force–length properties of muscle 178 in comparison with muscle 179, again based on activation and strain patterns observed during running. Results showed that muscle 178 generates mechanical work during one part of the cycle and absorbs an equal amount of mechanical work during the other part of the cycle (Fig. 1). Thus, muscle 178 generates no net mechanical work or power output during a cycle ($1.79 \pm 4.58\,\mathrm{W\,kg^{-1}}$; Ahn et al. 2006). In contrast, muscle 179 mainly absorbs mechanical work during a cycle ($-25.4 + 22.9\,\mathrm{W\,kg^{-1}}$, Full et al. 1998; $-19.1 \pm 14.1\,\mathrm{W\,kg^{-1}}$, Ahn and Full 2002).

Although *in vivo* activation and length-change patterns are identical, the strain amplitude differs slightly (18.5% for muscle 178 and 16.4% for muscle 179). This difference in strain amplitude, however, does not account for the difference in mechanical output. Even when the imposed strain is identical (15% strain amplitude), muscle 178 generates mechanical work ($10.1 \pm 11.5\,\mathrm{W\,kg^{-1}}$) whereas muscle 179 absorbs it ($-14.7 \pm 13.1\,\mathrm{W\,kg^{-1}}$; Ahn et al. 2006). Although muscles 178 and 179 are positioned similarly, stimulated identically, and possess similar basic contractile properties, their mechanical functions during dynamic contractions differ considerably.

Not only can different muscles innervated by the same nerve exhibit different functions during movement, but *different muscle segments within a single fascicle* may also exhibit different mechanical output
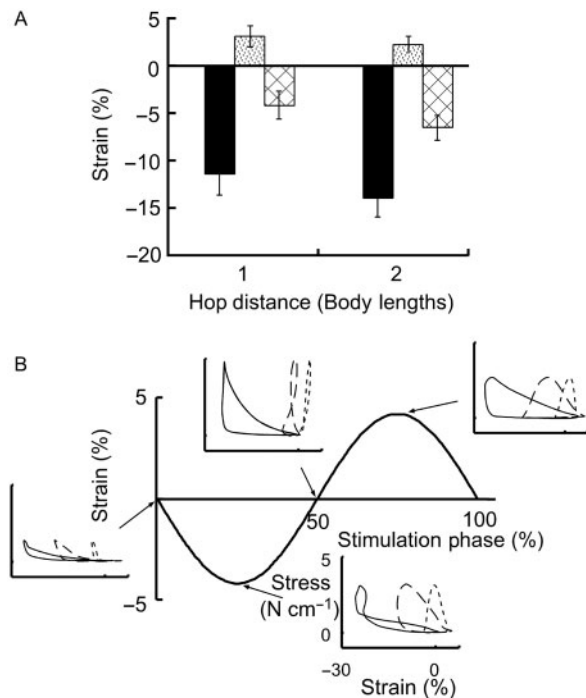
Fig. 2 *In vivo* and *in vitro* segment strain heterogeneity in the toad semimembranosus muscle. (**A**) Average peak *in vivo* segment strain at two hop distances. The central segment of the toad semimembranosus muscle only shortened during hopping (solid bars). In contrast, the distal segment lengthened first (positive stippled bars), then shortened (negative cross-hatched bars), but to a lesser magnitude than the central segment during hopping. Values are means $\pm$ S.D. (**B**) Representative *in vitro* segment work when stimulated at various phases. Work loops are shown for adjacent central (solid lines) and distal segments (dashed lines) as well as the muscle-tendon unit (dotted lines). The axes for the inset work loop plots are identical. From Ahn et al. (2003).

during a single contraction (Ahn et al. 2003). The semimembranosus muscle of the American toad, *Bufo americanus*, is a simple, parallel-fibered muscle positioned to generate extensor moments about the hip joint during hopping (Kargo and Rome 2002). *In vivo* muscle activation patterns in adjacent segments (central and distal) of the semimembranosus show no differences in electromyogram (EMG) onset, duration or amplitude during hopping (Ahn et al. 2003). Length changes, however, differ between central and distal segments. As the central segment shortens during hopping, the distal segment simultaneously lengthens before shortening (Fig. 2A). When the toads hop a distance of one or two body lengths, the magnitude of shortening of the central segment ($-14.0 \pm 4.9\%$) always exceeds shortening of the distal segment ($-6.5 \pm 3.2\%$; Fig. 2A; Ahn et al. 2003).

This strain heterogeneity of adjacent segments observed during hopping *in vivo* is also observed

during cyclical contractions *in vitro*, suggesting that adjacent segments along the length of this single muscle perform different mechanical functions (Fig. 2B). *In vitro* percentage heterogeneity, or the percentage of a sinusoidal cycle during which adjacent segments strain in opposing directions, differs from that of passive cycles at all stimulation phases except phase 0, when the muscle is stimulated halfway through shortening (Ahn et al. 2003). Maximal percentage heterogeneity occurred when the muscle was stimulated at phase 50, or halfway through lengthening ($34.0 \pm 9.2\%$). A small tendinous inscription, where the muscle attaches to the tibia near the knee, corresponds to the region of heterogeneity observed in the whole muscle. Despite the gross simplicity of the semimembranosus muscle, differential expression of protein isoforms and/or the architecture of linkages between muscle fibers and intramuscular connective tissues may influence the pattern of strain during dynamic contractions (Edman et al. 1988).

These studies demonstrate that a single neural signal can produce variable mechanical outputs, not only in adjacent muscles but also in adjacent segments within a single muscle. The mechanical output of skeletal muscle depends on many factors, some of which we understand well (i.e., anatomy, kinematics, neural stimulation, contraction kinetics, force–velocity characteristics, and force–length relationships), but many of which we do not yet understand. Some of the more poorly understood factors that may influence the mechanical behavior of skeletal muscle include submaximal stimulation, muscle architecture, history-dependent properties, interfilament spacing, and variable expression of protein isoforms. We are only now beginning to understand these less frequently studied parameters, even though they may substantially influence the mechanical output of a seemingly simple neuromuscular system. As a device for translating a neural signal into a mechanical output, muscle is clearly a remarkable material that has not yet yielded all its secrets.

Muscle as a smart material with intrinsic self-stabilizing properties

In addition to generating force and producing or absorbing energy, muscles also play important intrinsic, self-stabilizing roles during movement due to their force–velocity, force–length, and viscoelastic properties (Loeb et al. 1999; Richardson et al. 2005; Lappin et al. 2006). For example, when subjected to a higher force, the force output of skeletal muscle

increases automatically to resist the imposed load. Similarly, if a muscle is suddenly unloaded, its rate of shortening increases and its force production decreases (e.g., Rassier and Herzog 2004). This self-stabilizing behavior results from the inverse force–velocity relationship exhibited by all striated muscles, as was first described by A. V. Hill (1938).

The force output of striated muscles is also well known to depend on sarcomere length (Gordon et al. 1966). This length dependence also means that, when operating on the ascending portion of its length–tension curve, a muscle's intrinsic force capacity will increase to resist further stretch when it is stretched to a longer length. Hence, the intrinsic force–velocity and force–length properties of striated muscle provide *immediate* impedance responses that help to stabilize movement in response to perturbations, prior to the subsequent action of force-dependent and length-dependent reflexes that incur time delays and are known to modulate motor recruitment during ongoing tasks. Several recent studies demonstrate that these intrinsic musculoskeletal properties, including force–length and force–velocity behavior, can stabilize movement and simplify control (Brown and Loeb 2000; Jindrich and Full 2002; Aoyagi et al. 2004; Richardson et al. 2005).

Recent studies by Lappin et al. (2006) demonstrate that the viscoelastic properties of active muscle also provide self-stabilization during perturbations in load and contribute to active motor control. Using ballistic mouth opening in toads (Fig. 3A), they investigated elastic recoil in skeletal muscle and associated connective tissues. During ballistic mouth opening, transfer of momentum from the rapidly opening jaws to the tongue is used to project the tongue from the mouth to capture prey (Mallett et al. 2001). Prior to mouth opening, the muscles contract slowly for 50–250 ms as they store elastic energy in connective tissues at their origin and insertion, as well as in series elastic elements within the muscles themselves (Lappin et al. 2006). Lappin et al. (2006) modeled the toad jaws as a damped mass-spring system. In their model, muscle (Fig. 3A, red) is represented as a force generator (i.e., cross bridges) in series with a spring (i.e., series elastic component in the muscle). Extramuscular connective tissues at the origin and insertion are represented together as a separate spring in series with the muscle (Fig. 3A, blue). These muscle and connective tissue springs are attached to the cranium and suspend an external load.

Muscles themselves have been thought to contribute relatively little to the power of fast movements because they shorten rapidly only under very low loads (Alexander and Bennet-Clark 1977; Burrows 2003). This argument follows directly from Hill's (1938) force–velocity curve: the velocity of muscle shortening increases hyperbolically with decreasing load. Lappin et al. (2006), however, demonstrated that muscles can produce an order of magnitude more power during elastic recoil than during isotonic contractions at the same load. Compared to stiffer external connective tissues, such as tendon or cuticle, muscles themselves can contribute more in terms of strain (Fig. 3B) and, via elastic energy stored in their intrinsic connective tissue components, nearly as much in terms of energy, to animal movements.

The apparently low power output of muscle is an artifact of Hill's (1938) after-loaded isotonic paradigm for generating the force–velocity curve. During natural movements, muscles can begin to shorten after relatively long periods of activation. In Hill's (1938) isotonic paradigm, however, not only does the load moved by the muscle vary, but the duration of muscle stimulation prior to movement also varies with the load. At the smallest loads, the muscle is stimulated for very short durations prior to shortening (as little as 10–15 ms) whereas at the largest loads the muscle is stimulated for much longer durations (>250 ms). For natural movements of humans and animals, particularly those with time varying patterns of force and length change and variable periods of activation prior to shortening, a muscle's isotonic force–velocity behavior may well not be relevant.

During active shortening, muscles behave as springs in which displacement increases and stiffness decreases nonlinearly with the change in load (Lappin et al. 2006). When the external load changes unexpectedly, the total stiffness of the mass-spring system adjusts automatically and instantaneously without requiring neural input, due to the load-dependent, nonlinear stiffness of actively shortening muscle (Fig. 3C). The system becomes stiffer when the external load increases, and becomes less stiff when the load decreases (Fig. 3C). Because the stiffness of the extra-muscular connective tissues is relatively constant within the physiological range of movement, the load-dependent, nonlinear elastic properties of the mass-spring system arise from the behavior of muscle during active shortening. Furthermore, because the external load is relatively constant, the forces that develop in the muscles prior to movement determine the elastic properties of the system.

Lappin et al. (2006) suggested that the central nervous control of ballistic movements might be
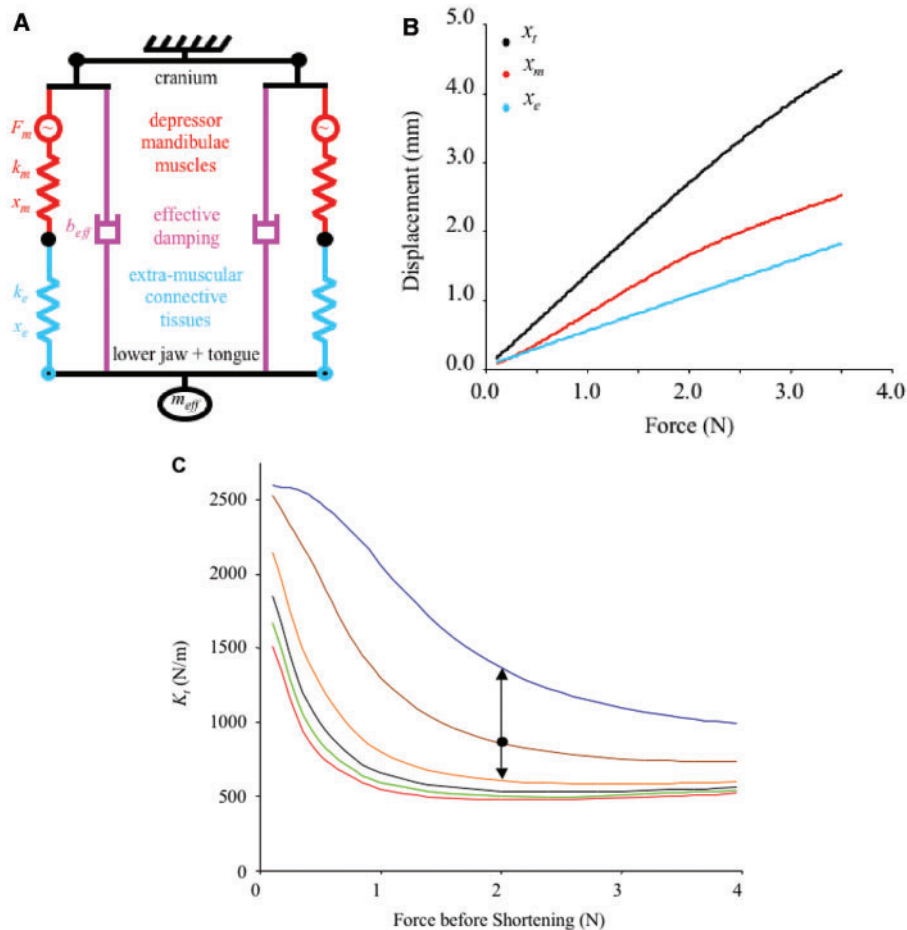
Fig. 3 Elastic recoil model and predictions. (**A**) The elastic recoil model includes the pair of *depressor mandibulae* muscles, which originate on the cranium and insert on the retroarticular processes of the lower jaw. Each muscle (red symbols) is modeled as a force generator (i.e., cross bridges) and a spring (i.e., elastic component) arranged in series. On each side of the cranium, the *depressor mandibulae* muscle is arranged in series with an extra-muscular spring element (blue symbols) that represents the sum of all extra-muscular structures that are strained by contraction of the *depressor mandibulae* prior to movement (i.e., cranium and retroarticular process). The external load is suspended from these springs. Pink symbols represent total effective damping of the mass-spring system. (F_m: muscle force; k_m: muscle stiffness; x_m: muscle displacement; k_e: extra-muscular spring stiffness; x_e: extra-muscular spring displacement). (**B**): Predicted displacement (x_m, x_e, x_t) as a function of the force developed by the *depressor mandibulae* muscles prior to movement. At all but the lowest forces (>0.25 N), the *depressor mandibulae* muscles (x_m) contribute more to total displacement (x_t) than do the extra-muscular spring elements (x_e). (**C**): Dependence of the relationship between *depressor mandibulae* force prior to movement (F_{before}) and total stiffness (k_t) on external load. Loads illustrated include 10 times the *in vivo* load (0.89 N, blue line), 5 times the *in vivo* load (0.45 N, brown line), twice the *in vivo* load (0.18 N, yellow line), the observed *in vivo* load (0.09 N, black line), half the *in vivo* load (0.045 N, green line), and one-tenth the *in vivo* load (0.009 N, red line). Each individual curve shows that, when the external load is constant, displacement increases and stiffness decreases nonlinearly as the force prior to shortening increases. For a given force prior to shortening (e.g., 2 N, black point), the total stiffness increases when the external load increases (upward arrow), and decreases when the load decreases (downward arrow). From Lappin et al. (2006).

relatively simple in principle. The number of motor units recruited, as well as the frequency and duration of their activation, will determine the force attained by a muscle prior to movement (Loeb and Gans 1986). Due to its nonlinear, load-dependent stiffness, the force attained by a muscle prior to movement will determine both the total displacement (i.e., of both extramuscular connective tissues and the muscles themselves) and the total effective stiffness of the mass-spring system. The force attained by

antagonistic muscles will resist movement and may also influence elastic properties. By activating a trigger at the appropriate time, the nervous system can specify the timing of rapid unloading. In principle, it appears that the nervous system could control ballistic movements simply by specifying the forces attained by muscles prior to movement and the timing of rapid unloading. The distance and speed of the resulting movement will be determined by the intrinsic, load-dependent, nonlinear elastic

properties of the mass-spring system (including muscles, tendons, and skeletal elements).

Part II. Contributions of sensory processing to motor control

It has long been appreciated that sensory feedback to muscles from force sensors and length sensors of muscles, as well as from other sensory inputs (e.g., vision, balance, proprioception), acts to provide appropriate changes in muscle activation and force to control and stabilize motion (e.g., Eccles et al. 1957). Such feedback also serves to reinforce the self-stabilizing properties of skeletal muscle described earlier in this article (and see subsequent text). An important principle of neuromechanics is that the mechanics of the sensors and the neural circuits in which they are embedded affects the timing and dynamics of receptor input. Cellular and network properties of the sensors, interneurons, and motor neurons determine the timing and strength of activation of homonymous muscles, as well as of agonists and antagonists, within the limbs and other motor systems.

A second principle of neuromechanics is that cellular and network properties necessarily introduce timing delays within sensorimotor circuits used to control motor behavior. A robust controller must account for these timing delays, so that interacting components are integrated into an effective control scheme for the system as a whole. These principles are illustrated by the following examples.

Mechanics and function of force sensors and length sensors

Motor coordination results from the interactions among commands from the central nervous system, the mechanical properties and conditions of body and environment, and sensory feedback. Sensory feedback from the muscles, skin and joints provides a critical link that communicates information to the central nervous system about the mechanical and metabolic changes that accompany the evolving movement. Some of this information is utilized for future planning of subsequent movements, and some is used for regulation of the ongoing movement. In the latter case, the fundamental mechanical variables of force, length, and velocity are monitored within muscles by Golgi tendon organs and by muscle spindle receptors, respectively. The corresponding neural signals are returned to the spinal cord, brainstem, or (in animals that possess one) somatosensory cortex to adjust patterns of motor neuron activation.

The adequate stimulus for each receptor is determined by the mechanical arrangement of the receptor and the muscle fibers, namely, in-series connections for the Golgi tendon organs and in-parallel connections for the muscle spindles (Fulton and Suner 1928). It has been argued that combining length and force feedback together at the motor neuron could regulate muscular stiffness (Matthews 1959; Houk 1972; Nichols and Houk 1976) and thereby promote stability and mechanical performance. Indeed, neural feedback does appear to regulate muscular joint and limb stiffness, but understanding how these receptors contribute to this regulation requires a deeper knowledge of their response properties and the synaptic distributions of the pathways emanating from them.

Golgi tendon organs can detect small contractile forces in motor units (Houk and Henneman 1967) and as a population, they provide a measure of total muscular force (Crago et al. 1982). There is some disagreement about the extent to which firing rate is linearly related to force (Jami 1992), but the relationship appears not to depend on previous movement history (Haftel et al. 2005). In contrast, the responses of muscle spindle receptors are related nonlinearly to changes in muscle length. First, these receptors are more sensitive to stretch than to release of muscle (Houk et al. 1981). Second, muscle spindles are responsive to small, rapid changes in length (Matthews and Stein 1969; Hasan and Houk 1975) and as such are particularly sensitive to vibration (Matthews and Watson 1981). Third, an assessment of sensitivity to velocity reveals a fractional power relationship between discharge rate and velocity. Finally, the responses of muscle spindles are influenced by prior mechanical history (Haftel et al. 2004). When the muscle is subjected to three sequential stretches, which take the form of triangular trajectories, the receptor responds with an initial burst followed by a dynamic response. For subsequent stretches delivered with little or no delay, no initial burst is present and the dynamic response is characterized by a reduced firing rate.

All the aforementioned nonlinear properties of the length sensors can be attributed provisionally to the mechanical properties of intrafusal fibers, the special muscle fibers within the spindle capsule that are associated with the sensory nerve endings (Matthews 1972). The response properties of the receptor therefore reflect the passive and active stiffness of the intrafusal fibers, which can be modified by the motor innervation of these fibers. The amplitude sensitivity follows from the tendency of cross-bridges to detach during stretch and from the velocity

sensitivity to the effect of movement on detachment rate. The history dependence also reflects the influence of prior movement on the rate constants for attachment and detachment (Nichols and Cope 2004). The significance of these complexities is that the responses of muscle spindle receptors, rather than linearly representing muscle length and velocity, reflect the *mechanical behavior (i.e., force–length, force–velocity and history-dependent properties) of the muscle itself*. Intrafusal mechanics essentially constitute a model of the properties of the parent muscle. One important implication of these findings is that any signal in the central nervous system that represents length (or joint angle) or velocity must extract this information from the nonlinear responses (Cordo et al. 2002) of a population of diverse receptors.

The functional consequences of the nonlinear properties of muscle spindles can be appreciated by comparing the mechanical properties of muscles in the presence of and in the absence of reflex action. Under resting conditions, group Ia fibers from muscle spindles have a strong and excitatory effect on motor neurons (the stretch reflex), whereas group Ib fibers from tendon organs have relatively weak effects (Nichols 1999). When an active muscle is stretched, the response consists of the mechanical response of the motor units active prior to stretch (i.e., the intrinsic response) plus a component due to motor unit recruitment from the stretch reflex. The intrinsic response is an essentially instantaneous and spring-like change in force that is amplitude-limited (Joyce et al. 1969). The muscle then yields to a varying extent depending on the dominant motor unit type (Huyghues-Despointes et al. 2003a). It is at this point that the forces generated by additional motor units develop and the yield is compensated. Furthermore, the asymmetric properties of the muscle spindle receptors (see earlier text) are complementary to those of the muscle itself, so the net effect of reflex action is to provide for a response that is more spring-like and more symmetrical (Nichols and Houk 1976).

The compensatory actions of the stretch reflex can adapt automatically when the properties of muscles change. Movement tends to linearize the properties of muscle (Kirsch et al. 1994), most likely by accelerating the cross-bridge cycling rate (Nichols et al. 1999b). If muscle is stretched after a period of shortening, the intrinsic response is more spring-like and less amplitude-dependent (Campbell and Moss 2002; Huyghues-Despointes et al. 2003b). Under these conditions, the response of the spindle receptors is also modified (see earlier text), and a smaller and

more delayed signal is sent to the spinal cord. The result is a spring-like response that is now dominated by the intrinsic properties of the muscle rather than by the stretch reflex. The reflex component is automatically timed and graded to maintain a spring-like muscular response (Huyghues-Despointes et al. 2003b), based on the complementary nonlinear properties of muscle and receptor. Reflex action, therefore, compensates for muscle nonlinearity through a predictive mechanism (Houk et al. 1981).

During locomotion, excitatory force feedback via a sensorimotor pathway mediating autogenic (i.e., to and from the same muscle) feedback is established (Guertin et al. 1995; Pearson 1995) and muscular stiffness increases (Ross et al. 2002). The action of force feedback, however, is simply to increase muscular stiffness, not to compensate for muscle nonlinearity, since tendon organs do not contain intrafusal fibers. Because the response properties of the muscle have already been compensated by the stretch reflex, the action of force feedback simply changes the stiffness of the muscle. Therefore, the contributions of length and force feedback are quite different. The former compensates for nonlinearity while the latter modulates the "spring constant".

Not surprisingly, length feedback is distributed locally to muscles that contain the muscle spindles and to closely synergistic muscles (Eccles et al. 1957; Nichols 1994). A group of synergists would tend to undergo similar mechanical changes and require similar extents of compensation. Excitatory force feedback, which is expressed during locomotion, also appears to be distributed mainly to the parent muscle and increases the stiffness and force output of the muscle. It may be speculated that this excitatory feedback is particularly important during tasks requiring large forces, such as walking up a slope (Gottschall et al. 2005). In contrast, *inhibitory* force feedback is distributed to muscles other than the muscle containing the tendon organs. These inhibitory pathways are present both during rest and during stepping (Ross et al. 2003). The rule consistent with the known distribution of this feedback is that force-related inhibition links muscles crossing different joints and different axes of rotation (Nichols et al. 1999a). From this organization, inhibitory force feedback is inferred to promote interjoint coordination and influence limb stiffness.

Timing is everything

In neuromechanical systems, time delays are inevitable (Fig. 4A). They occur in the acquisition of
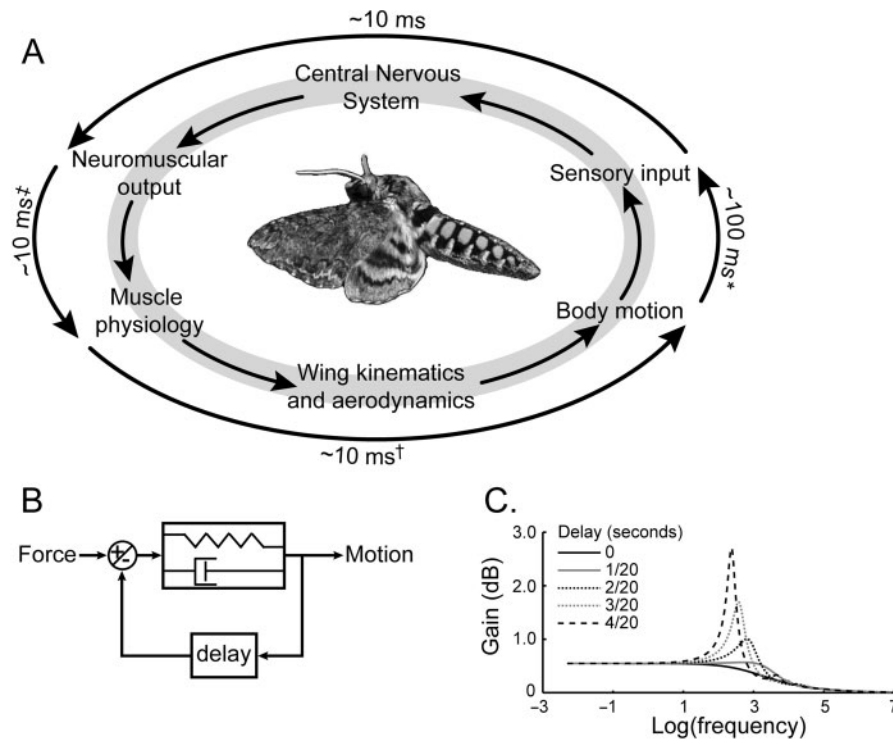
Fig. 4 (**A**) Simplified diagram illustrating operational flow for hawkmoth flight along with measured or estimated delays along both neural and mechanical linkages. Delays are unavoidable in both the neurological and biomechanical portions of the loop. (**B**) Diagram of a single input/single output spring and dashpot delayed feedback system. (**C**) Frequency domain gain response for a spring and dashpot system operating with a variable feedback delay. *Sprayberry and Daniel (2007). †Time constant for motion decay due to drag. ‡Tu and Daniel (2004).

sensory information as well as in the processing of such information for modulating motor output. Even the sensors that encode motion information have lags in their response, which are prior to—and often much greater than—the lags in central nervous system processing (e.g., insect visual systems) (Harris et al. 1999). Some of these sensors—particularly mechanosensory structures—have inertial and viscous behaviors that lend additional delays to a system. There are further delays in the time between the stimulus provided to a muscle and the occurrence of peak force in that muscle. Because biological systems have damping and inertial components, additional time lags arise from their dynamic behavior. Thus, the time at which peak forces occur does not correspond to the time at which peak motion (speed or position) occurs, at least for very rapidly moving systems.

A key problem is to understand the consequences of inevitable delays for control of neuromechanical systems. To explore these consequences, consider a "simple" neuromechanical system with feedback and delay: a spring and a dashpot with a delayed feedback sensor (Fig. 4B). At first glance, delay would seem to be a bad thing—compromising the

ability of the system to respond to rapid perturbations. A plot of the gain (emergent motion divided by driving force) against the frequency of forcing, however, shows that delay actually increases the gain, giving a resonant-like behavior—much like the behavior of a spring-mass-dashpot system. Indeed, feedback delay acts very much like mass in forced oscillatory systems (Fig. 4C). This simple model illustrates three key points: (1) delays in neuromechanical systems can follow either from neural processing times or from the dynamics of the mechanical system; (2) delays can yield resonant behaviors; and (3) the overall dynamics of the system are understandable only in the context of information about all the delays as well as about the set of transfer functions that describe the system.

Expanding this simple control theoretic model to encompass a biological system with multiple inputs (many sensors) and multiple outputs (many actuators), each with potentially different delays, raises enormous challenges. Constructing such systems in a purely control theoretic framework requires knowledge of all the delays and a preconceived model linking specific actuators and actuator combinations to dynamic responses; this information is rarely

available for biological systems. Moreover, there may be many distinct control models that maintain adequate performance under a particular set of conditions. Consideration of just one such model may not reveal the range of possible responses when conditions change, i.e., with the introduction or removal of delays from the system.

To explore the issue of delays in a neuromechanical system, Hedrick and Daniel (2006) focused on an inverse problem in the control of flight in the hawk moth *Manduca sexta*. Their study asked the following questions. (1) Are there multiple ways to control the wings for successful hovering? (2) Does delay in the controls of this system reduce the number of successful solutions to hovering? (3) Are there particular aspects of the feedback system for which delays are more critical than for others? Examining the effects of delay via an inverse rather than forward problem allows simultaneous consideration of its impact on the set of adequate models, as opposed to one specific control model.

The inverse problem was addressed using a micro genetic algorithm (μGA) coupled to a discrete-time, forward-dynamics simulation of flight (Hedrick and Daniel 2006). The algorithms sought sequences of wing beats that were adequate to the task of maintaining the moth's position and orientation within a small region of space, approximating hovering flight. The flight simulation followed from a set of coupled differential equations for the balance of forces and moments in the sagittal plane of the animal. A blade element wing model with experimentally derived force coefficients was used to predict the aerodynamic forces generated by wing motions (Hedrick and Daniel 2006). The resulting forces and torques were applied to a dynamic center of mass (CoM) to compute the resulting linear and angular accelerations. Wing motions for each stroke were specified as three angles: elevation, sweep and long-axis rotation. The time course of each of these angles was modeled as fixed-frequency (single component) sinusoids whose amplitude, mean frequency, and phase offset were determined by nine wing-motion parameters. A final parameter controlled the angle between the thorax and abdomen, allowing the simulated moth to change the location of the CoM relative to the wing hinge.

A genetic algorithm was used to search within the ten-dimensional space represented by the aforementioned control parameters. μGAs are a particularly effective method for searching widely within a rugged parameter space, such as that represented by the set of possible wing beats (Krishnakumar 1989). In practice, the μGA switched randomly between adequate controllers with every wing beat and, due to its stochastic nature, eventually failed to find an adequate controller and the simulated moth left the region of acceptable position and orientation.

The discrete time nature of the model adds an implicit one-wing-beat delay to all operations. The effects of delay on the simulated moth's performance were explored by adding additional delays to particular pieces of sensory information. We found that the inverse model operating under only the implicit one-wing-beat time delay due to the discrete time nature of the model can maintain steady hovering flight using a wide variety of control strategies (Fig. 5A and http://faculty.washington.edu/danielt/movies/gamoth.mov). Adding an additional one-wing-beat delay to all sensory inputs greatly reduced the number of adequate solutions and the model quickly reached failure conditions due to the stochastic noise inherent in the genetic algorithm approach (Fig. 5Aii). Restoring specific sensory inputs expanded the number of adequate solutions to the point where the model once again maintained steady hovering flight, albeit with reduced positional accuracy. The model was most sensitive to pitch rate and vertical velocity, and removing the delay in both these parameters had a multiplicative effect on the number of solutions.

An inverse approach coupled with genetic algorithms capable of broadly searching a rugged parameter space allowed an understanding of the consequences of time delays in feedback controls of complex systems. Rather than focusing on how delay particularly determines the performance of a highly specified control system, genetic algorithms were used to uncover how delays may determine the range of reasonable solutions to a given task (in this case hovering). In a low-delay case, the results demonstrate that many controllers are capable of maintaining hovering flight in the simulated hawk moth. The existence of such diverse solutions for hovering follows from two points: (1) neuromechanical systems may accomplish a task effectively via multiple methods and (2) a behavior is specified as adequate, as opposed to being exactly determined, as it would be in a control model. Delays in the dynamics of the system on the order of one-wing-beat to all sensory systems (∼40 ms) greatly reduced the number of adequate controllers. The fact that the number of successful controllers declines, however, does not necessarily imply that they are poorer controllers. The final outcomes might be "better" because of the emergent resonance properties that follow from delays in feedback control.

A

B

Example flight paths
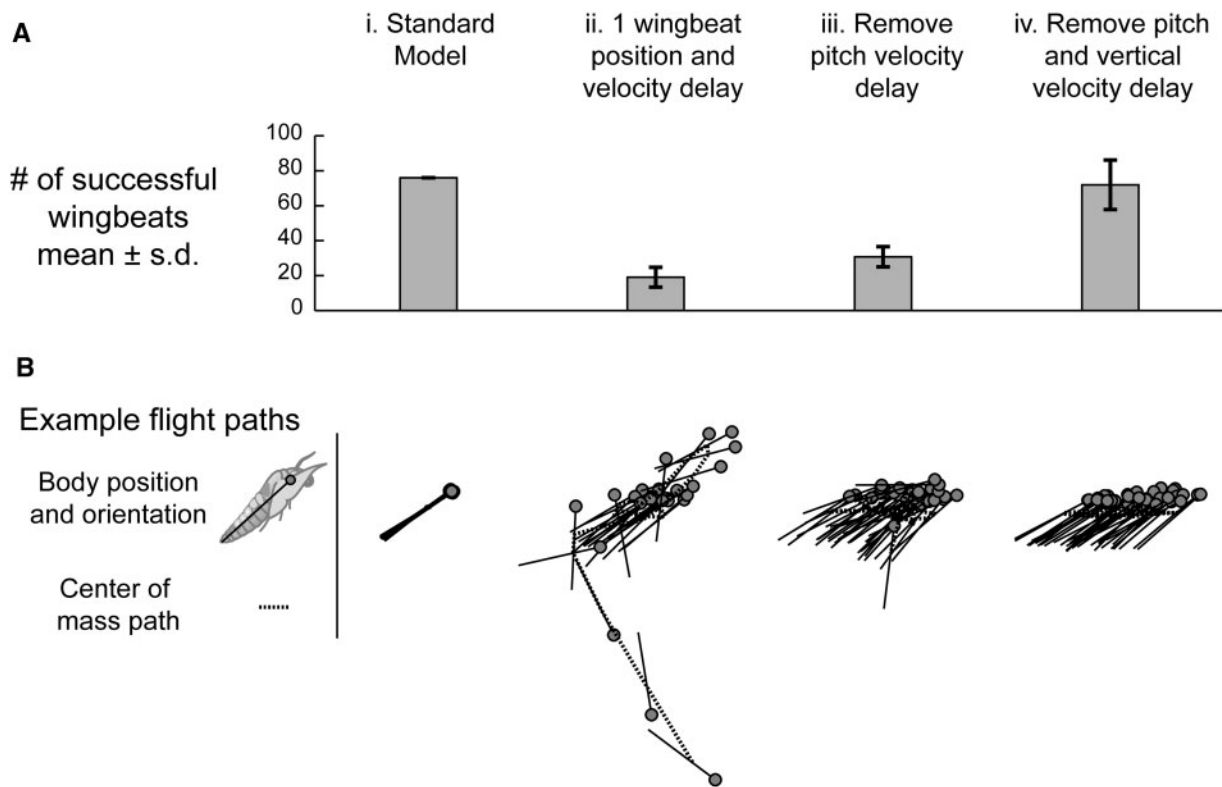
Fig. 5 Effects of imposed delays on different sensory modalities in the simulated hawkmoth. (**A**) Mean number of wing beats completed under four different delay conditions (12 trials per condition). (**B**) Schematic flight paths of the first 40 wing beats from one trial. Differing delay conditions appear in columns i–iv. Columns iii and iv represent successive restoration of sensory information removed in column ii. The complement to column iii, removing the vertical velocity delay, results in similar overall performance.

It is likely that such controllers are more tightly tied to the exact delays in the system.

Part III. Contribution of central networks to motor control

Central nervous control of basic oscillatory movements, as occurs in locomotion and feeding, involves CPGs. CPGs are networks of interneurons that are located within the central nervous system. These interneurons receive input from sense organs and send commands to motor neurons that activate the muscles. The frequency and timing of motor output are determined by the interaction between sensory inputs to the CPG network and intrinsic cellular and network properties of CPG interneurons (Grillner 1975). Investigation of the cellular and network properties of motor circuits is a major subdiscipline of neuroscience. In contrast, many fewer studies attempt to investigate CPG function *in a neuromechanical context*. Within the context of neuromechanics, the goals are to understand (1) how cellular and network properties contribute to the emergent mechanical behavior of the animal and (2) how these properties are tuned to less flexible

system parameters (e.g., body mass and shape, or neural delays that arise from conduction velocities and distances).

An understanding of these issues requires knowledge of the rules of operation that determine the behavior of CPGs in a sensorimotor circuit, as well as of what variable(s) are controlled via neural input. A major principle that governs the operation of CPGs is the idea that these circuits may be reconfigured to change their output. In other words, the population of interneurons that comprises the CPG may change, depending upon sensory input or other factors, and the pattern of neural output of the CPG changes with the population of participating neurons (Morton and Chiel 1994; Pearson 1995, 2000; Pearson et al. 1998). In this section, we present three examples to illustrate these points. The first example illustrates how the CPG for a swimming pteropod mollusk, *Clione*, is reconfigured to modulate swim frequency, and addresses the question of how the variable CPG output contributes to the emergent mechanical behavior during swimming. The second example investigates how neural (i.e., reconfiguration of shared interneuronal circuitry) and mechanical subsystems (i.e., reconfiguration of

mechanical constraints) contribute to multifunction-ality, or the use of evolved structures for multiple functions. This example also illustrates the principle that the function of motor neurons depends upon the mechanical configuration of the periphery. The third example discusses techniques using genetics and molecular and developmental biology to investigate the neuromechanics of swimming in zebrafish. Both spontaneously occurring mutants and genetically modified organisms have been useful for determining the roles of specific hindbrain interneurons in startle behavior and the effects of cell duplication on startle-circuit organization and function.

Central Control of Swimming Speed in *Clione*

In the pteropod mollusk *Clione limacina*, the parapodia are lateral, wing-like structures that produce relatively symmetrical dorsal and ventral bending movements to provide forward propulsive forces during swimming (Satterlie et al. 1985). The wings are flexible, and bend due to contraction of intrinsic sheets of muscle bundles found in their dorsal and ventral surfaces. Two sheets of oblique muscle bundles run across the entire dorsal face of each wing, just under the epithelium, at near-right angles to each other (Satterlie et al. 1985; Satterlie 1993). These striated muscle sheets co-contract to bend the wing dorsally. This organization is repeated on the ventral side, and bends the wing ventrally. The hemocoelic space between the dorsal and ventral muscle bundles functions as a hydrostatic skeleton for the wing, and contains three additional, less-dense layers of muscle. Two of these, the longitudinal and transverse retractor muscles, pull the wing into the body during protective withdrawal. The dorso-ventral muscles, which run from the dorsal epithelium to the ventral epithelium, serve to decrease wing thickness and, presumably, to increase wing stiffness by pressurizing the hemocoel.

The swim musculature is striated whereas the other muscles are smooth. Within each swim muscle bundle, two types of muscle fibers are present. These are segregated into a slow-twitch fatigue-resistant group, which makes up the outermost one-third of each bundle, and a fast-twitch fatigable group, which forms the inner two-thirds of each bundle (Satterlie et al. 1990). This organization is repeated in all bundles of each muscle layer, and in each layer of the wings. The wing muscles are controlled almost exclusively by motor neurons within a pair of pedal ganglia. The pedal motor neurons innervate the ipsilateral wing via a stout wing nerve.

Slow versus fast swimming

Clione are negatively buoyant, so normal slow swimming consists of either "treading water" or slow forward (upward) movement. Wing beat frequencies during slow swimming are approximately one cycle per second, and if they produce forward movement, they do so at a rate of less than one body length per second. When the animal is stimulated mechanically on the tail or body wall, the wings respond with a dramatic increase in frequency (up to five cycles per second) and an increase in contractile force of the swim musculature. In addition, twisting of the flexible wings (pronation and supination) during swimming increases. Fast swimming can propel the animal forward at rates up to eight body lengths per second. The change from slow to fast swimming involves not only an increase in CPG cycle frequency, but also an increase in the force of wing-muscle contractions through recruitment of the large motor neurons that activate fast-twitch, fatigable swim musculature and enhance the contractile activity of the slow-twitch muscle.

Central control of swimming frequency

The CPG for slow swimming is comprised of two groups of antagonistic interneurons (dorsal and ventral swim interneurons—named for the bending movements they control), connected by reciprocal inhibitory synapses (Arshavsky et al. 1985a; Satterlie 1985; Satterlie and Norekian 2001). These neurons are found in the pedal ganglia and each one sends an axon branch across the pedal commissure to the contralateral ganglion. Neurons of each ipsilateral group are electrically coupled to each other and to their contralateral counterparts (Arshavsky et al. 1985a; Satterlie and Spencer 1985). Thus, dorsal swim interneurons and ventral swim interneurons form a "half-center"-like CPG in which simple alternation of activity forms a two-phase locomotor rhythm. Each interneuron fires a single broad action potential during its phase of activity and receives a single inhibitory post-synaptic potential (IPSP) from the antagonistic group during the contralateral wing contraction.

The increase in cycle frequency observed during the transition from slow to fast swimming is accomplished through a combination of cellular and circuit level modulatory changes in the swim CPG (Satterlie et al. 2000; Pirtle and Satterlie 2004). At the cellular level, swim interneurons exhibit a baseline depolarization, enhancement of post-inhibitory rebound, and spike narrowing, all of which contribute to the increase in firing frequency. At the circuit level, a contralateral pair
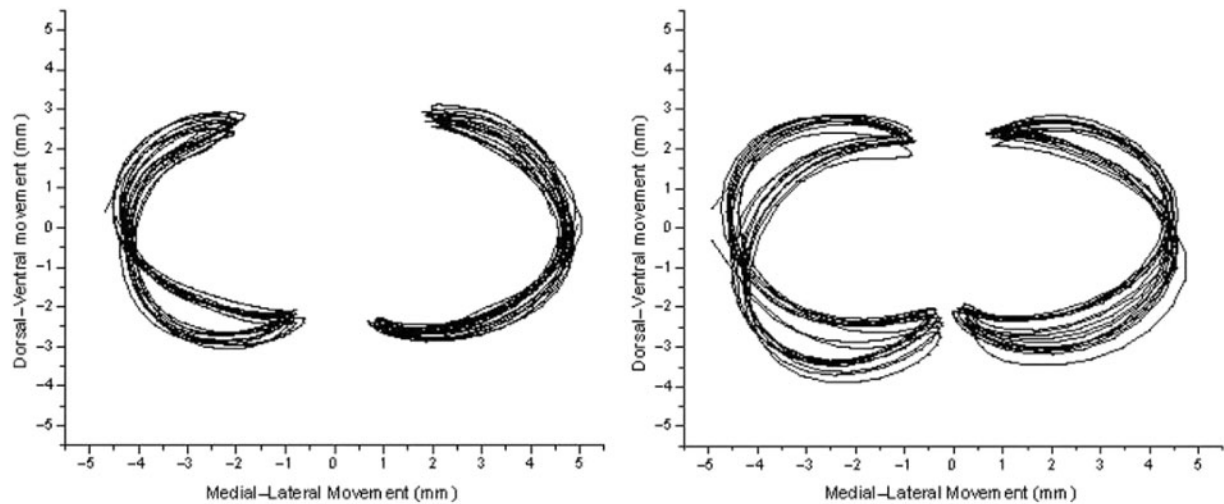
Fig. 6 Plots of wing tip positions through ten successive wing beats as viewed from above in a tethered animal. The plots are two-dimensional representations taken from three-dimensional information collected with two-camera high-speed video filming. Left: Activity associated with slow swimming. Right: Activity associated with fast swimming. This animal exhibited a slightly asymmetrical wing beat in both swim modes.

of pleural interneurons is recruited into the swim CPG (Arshavsky et al. 1985b, 1989). Through synaptic connections between these interneurons and the CPG interneurons, the pattern generator is reconfigured to contribute to, and reinforce, cellular changes involved in increasing CPG cycle frequency. Two clusters of cerebral, serotonergic neurons have been found to produce all of the observed cellular changes in CPG interneurons that accompany the slow-to-fast transition, as well as reconfiguration of the CPG through recruitment of the pleural interneurons (Satterlie and Norekian 1995; Satterlie et al. 1995).

Neuromuscular control of swimming frequency

The swim CPG controls two groups of pedal swim motor neurons, one producing dorsal flexion of the wings, the other producing ventral flexion. This organization is duplicated in each pedal ganglion. Two types of motor neurons have been identified within each group of pedal neurons (Satterlie 1991, 1993). A single, large motor neuron (cell body diameter up to 80 μm) innervates the entire dorsal surface of the ipsilateral wing and a ventral counterpart innervates the entire ventral surface. The remainder of each group consists of small motor neurons (cell body diameter up to 30 μm), each of which has a restricted innervation field in the ipsilateral wing. Dual recordings from large and small motor neurons indicate that both receive similar monosynaptic inputs from CPG interneurons but the small motor neurons produce spikes in the appropriate half-cycle in both slow and fast swimming. In contrast, the large motor neurons show

only sub-threshold synaptic activity during slow swimming and are "recruited" to the spiking mode during fast swimming (Satterlie 1991, 1993). Neuromuscular recordings confirm that small motor neurons innervate the slow-twitch, fatigue-resistant musculature monosynaptically, while the large motor neurons innervate both types of swim muscle monosynaptically.

Swimming mechanics

High-speed digital kinematic analyses of slow and fast swimming (Fig. 6) in both tethered and free-swimming *Clione* reveal differences in swimming mechanics at different swimming speeds. For example, the angle-of-attack changes from 42° to 52° in slow and fast swimming, respectively. The change in angle-of-attack is likely related to the innervation pattern of large motor neurons and the relative conduction times throughout the various parts of the wing. In addition, the wing-tip excursion does not appear to change from slow to fast swimming—the wing tips either nearly touch, or slightly overlap at each extreme of wing contraction at both speeds. This observation implies that the wings must be stiffer at higher swimming speeds in order to resist the increasing hydrodynamic forces acting upon them.
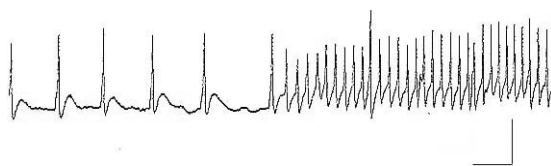
Two groups of muscles appear to contribute to increasing wing stiffness at higher swimming speeds. During fast swimming, a small proportion (5–10%) of slow-twitch muscle cells change from swim-related phasic activity to high-frequency tonic firing (Fig. 7). The tonic firing appears to be associated with

summation of post-spike depolarizing after-potentials, and can be triggered through serotonergic modulatory inputs to the musculature. In addition, a dense "grid" of dorsoventral muscles is present in the wings (Fig. 8), and these dorsoventral muscles appear to fire tonically rather than in phase with swimming movements. The motor neurons that innervate these muscles have not yet been identified, so their activity during slow and fast swimming remains to be measured. Together, these mechanisms likely increase wing stiffness during the change from slow to fast swimming.
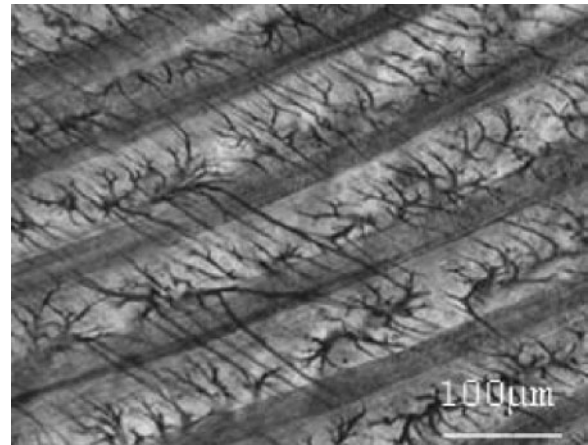
These studies demonstrate that modulation of swimming frequency in *Clione* involves a combination of central and neuromuscular alterations. Upon mechanical stimulation, both cellular and network-level changes in CPG configuration contribute to an increase in cycle frequency of central motor output. The increase in frequency of CPG output in turn increases swim-muscle contractility, the angle-of-attack of the wings, and wing stiffness. Together, these mechanical effects produce an increase in the speed of forward movement during swimming.

Neuromechanics of multifunctionality: feeding in *Aplysia*

Engineered devices are usually constructed deliberately to perform a single function. A piston within an internal combustion machine, a subroutine within a software package, or a supporting cable within a bridge, all play fixed roles. Creating devices that are functionally decomposable has great utility because designing the entire device is easier, individual components can be replaced rapidly, and it is

Fig. 8 Whole mount immunohistochemical staining of dorsoventral muscles with an antibody against a vertebrate hyperpolarization-activated cation channel (HCN_2; Sigma). The dark "stripes" are dorsal swim muscle bundles, separated by lighter stripes in between the muscle bundles. Only the upper halves of the dorsoventral muscle cells are evident in the photo plane. The cell bodies of the dorsoventral muscles are located in the center of the hemocoelic space. Their multi-branching processes run from the cell body to insert on the basement membrane under the epithelium on each side of the wing.

Fig. 7 Intracellular recording from a slow-twitch, swim muscle cell. Initially, each spike-like response corresponds to a single dorsal wing contraction, and they occur at 1 Hz. Note the prominent depolarizing after-potential. In the middle of the record, the animal initiates a transition to fast swimming. The muscle cell fires at a higher frequency (up to 6 Hz), which does not correspond to the swim frequency (2 Hz in this part of the record). Similar periods of out-of-phase fast firing were observed in 5–10% of intracellular recordings from slow-twitch muscle cells during fast swimming. They typically lasted for the duration of fast swimming, and likely represent a mechanism for increasing wing stiffness. The initial spike-like responses are 50–55 mV in amplitude (resting potential = − 63 mV). Scale bars: 25 mV, 1 s.

possible to predict the effects of adding or removing a component. To create an engineered device that is multifunctional, multiple components (each of which can perform one well-defined function) are packaged together. A classic example is the Swiss Army knife. It can be used as a knife, scissors, awl, or screwdriver, among other functions. An engineered multifunctional device, however, has some drawbacks. Only one tool can be used at a time. Furthermore, if a tool has not been specifically designed, it is difficult to adapt an existing tool to a completely new function.

Evolved devices are usually capable of switching rapidly among multiple functions. The human hand can switch from pounding a stake into the ground, to unscrewing the lid of a jar, to playing piano. Turtles use their legs to paddle, walk, or scratch (Earhart and Stein 2000). The human tongue participates in swallowing, breathing, and speaking (Gestrau et al. 2005). Thus, evolved devices tend to show much greater adaptability and flexibility than engineered ones. They can be adjusted to perform new functions if the environment changes but may not perform any one function as well as an engineered device. Because evolution works on neural control and biomechanics simultaneously, it is also unlikely that evolved devices can be functionally decomposed as simply as engineered devices.

Multifunctionality in animals arises from both biomechanics and neural control. Musculoskeletal systems (e.g., limbs of vertebrates or insects), hydrostatic skeletons (e.g., worms), or muscular hydrostats (Kier and Smith 1985) have many more than the minimum number of degrees of freedom necessary to move throughout their workspace. As a consequence, there are multiple ways in which they may exert force or reach a particular endpoint. Similarly, neural circuitry shows great flexibility. Neural circuits may reorganize: connections may change or neurons may enter or leave a circuit, rapidly generating multiple motor synergies (Morton and Chiel 1994). Studies of stick insects, cats, and lampreys suggest that differential activation of pattern generators for individual joints underlies multi-limbed locomotion and allows local sensory input to shape and modify ongoing locomotor activity (Buschges 2005). Recent studies of hypoglossal neurons and motor neurons that control tongue musculature during breathing, coughing and swallowing (Gestrau et al. 2005) and of spinal interneurons during multiple forms of fictive scratching (Berkowitz 2005) suggest that shared interneuronal circuitry contributes to multifunctionality.

Feeding in *Aplysia*

To understand the neural and mechanical mechanisms of multifunctionality in a biological system, we studied three qualitatively different feeding responses in the marine mollusk *Aplysia californica*. The feeding apparatus, known as the buccal mass (Fig. 9), controls a central grasper. The grasper consists of a muscular structure, known as the odontophore, which is covered by a flexible toothed sheet of cartilage, known as the radula. The grasper can open or close and it can move toward the jaws (protract) or move toward the esophagus (retract). Protraction is mediated by the I2 muscle (Hurwitz et al. 1996), retraction is mediated by the I1/I3/jaw complex (Morton and Chiel 1993), opening is likely mediated by the I7–I10 muscles (Evans et al. 1996), and closing is mediated by the I4 muscle (Morton and Chiel 1993).

By combining the elementary motor components (i.e., protraction and retraction, opening and closing) in different ways, the buccal mass can generate three qualitatively different feeding responses (biting, swallowing and rejection) (Fig. 10). During biting, the animal opens and strongly protracts the grasper, closes the grasper just prior to the peak of protraction, and then retracts the grasper weakly. During swallowing, the animal pulls food that it
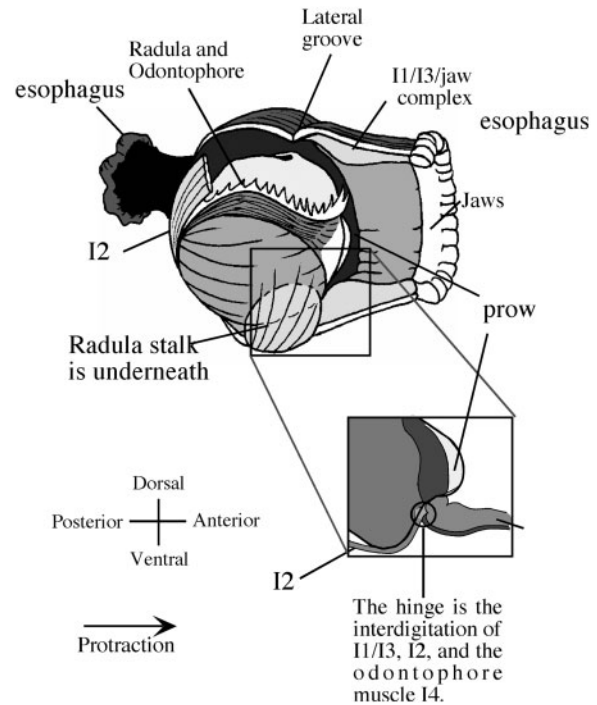

Fig. 9 Anatomy of the buccal mass. A lateral cutaway view of the anatomy is shown, along with an inset that illustrates the hinge (drawn by Dr Richard Drushel). The radula is a thin, flexible sheet of cartilage-like material covered with fine teeth. The underlying odontophore consists of a mass of muscles, the largest of which is I4, that can open and close the radula. The radula/odontophore is referred to throughout this review as the grasper. The I1/I3/jaw complex is anterior to the grasper when it is at rest, and the I2 muscle is posterior to the grasper at rest.

has successfully grasped into the buccal cavity by opening and weakly protracting the grasper, positioning the grasper further forward on food without pushing the food out of the buccal cavity, and then closing and strongly retracting the grasper. During rejection, the animal moves inedible material out of the buccal cavity by closing the grasper on the inedible material, protracting the grasper, and then opening and retracting the grasper.

Mechanical control of swallowing

Swallows fall into two categories (Ye et al. 2006a): (1) smaller amplitude swallows and (2) larger amplitude swallows that are associated with rotation of the ingested material. In the smaller amplitude swallows, the different elementary motor functions are associated with specific muscles (Figs 11 and 13A). In contrast, during the larger amplitude swallows, the I2 muscle is activated for a longer duration and protracts the grasper farther forward than it does in a small-amplitude swallow. The new position of the grasper allows two new degrees of freedom to be expressed. First, the grasper is now
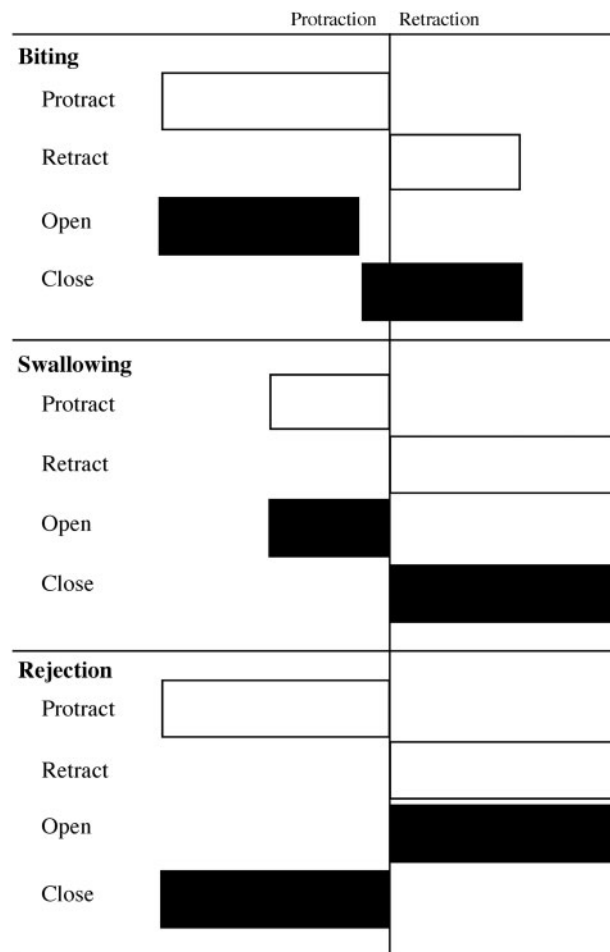
Fig. 10 Schematic summary of the construction of biting, swallowing and rejection from the elementary motor behaviors of opening, closing, protraction, and retraction.

tilted ventrally relative to the food to be ingested. Thus, when the grasper closes, it not only grasps the food, but also rotates the food ventrally while pulling it inward between the grasper halves. Second, the anterior rotation of the grasper stretches a muscle at the grasper's base (the ''hinge'') (Fig. 9, inset). When the hinge is activated, it retracts the grasper and rotates it dorsally, so that food is pulled farther inward as it rotates dorsally (Fig. 11B).

These biomechanical changes alter the function of the identified neurons that control these degrees of freedom. The B8 motor neuron, which activates the I4 muscle, mediates grasping in a small amplitude swallow and also mediates ventral rotation and retraction in a large amplitude swallow. The B7 motor neuron, which activates the hinge muscle, has no overt behavioral effect during a small amplitude swallow, but contributes to retraction during a large amplitude swallow. Thus, by preparing the periphery differently (i.e., protracting the grasper weakly or

strongly), new degrees of freedom can be expressed (Ye et al. 2006a; Fig. 11B). These results also suggest that the function of motor neurons depends on the mechanical context in which they are activated (see also Ahn and Full 2002).

Mechanical control of rejection

During rejection, the grasper closes on inedible material as protraction begins (in contrast to swallowing and biting, during which the grasper opens as it protracts). When the grasper opens or closes, it changes shape. The I4 muscle, which is horseshoe-shaped, surrounds the radular stalk, the position of which is controlled by the muscles of the odontophore. When the halves of the radula are open, the radular stalk is between the radular halves and is surrounded by odontophore musculature, so that the grasper assumes a roughly spherical shape. When the radular halves close, the radular stalk is pushed out of the ventral part of the odontophore musculature, so that the grasper assumes a roughly ellipsoidal shape (Neustadter et al. 2002a, b). Because the buccal mass is a soft-tissue structure, the change in grasper shape alters the lengths and positions of the surrounding muscles; we refer to this as mechanical reconfiguration. By using magnetic resonance imaging to obtain *in vivo* views of the buccal-mass musculature in intact, behaving animals (Neustadter and Chiel 2004), Novakovic et al. (2006) observed that the changing shape of the grasper elongates the I2 protractor muscle during the protraction phase of rejection.

Using a kinetic model of the buccal mass, Novakovic et al. (2006) have shown that the closed odontophore both enhances the mechanical advantage of I2, and lengthens it, increasing the force it can generate due to its length/tension property (Yu et al. 1999). They also observed that the onset of activation of the I1/I3/jaw complex must be delayed for two reasons. First, the I1/I3/jaw complex cannot retract the grasper until the grasper's widest extent is posterior to the I1/I3/jaw complex. Second, because the halves of the grasper must open to release inedible material at the peak of protraction, activating the I1/I3/jaw complex would act to close the grasper halves, or antagonize the grasper muscles. This contrasts with swallowing, during which the grasper closes near the peak of protraction and the I1/I3/jaw complex acts as an agonist to enhance grasper closure.

For these reasons, activation of the hinge initiates the retraction phase of rejection and there is a significant delay from the end of activity in the I2
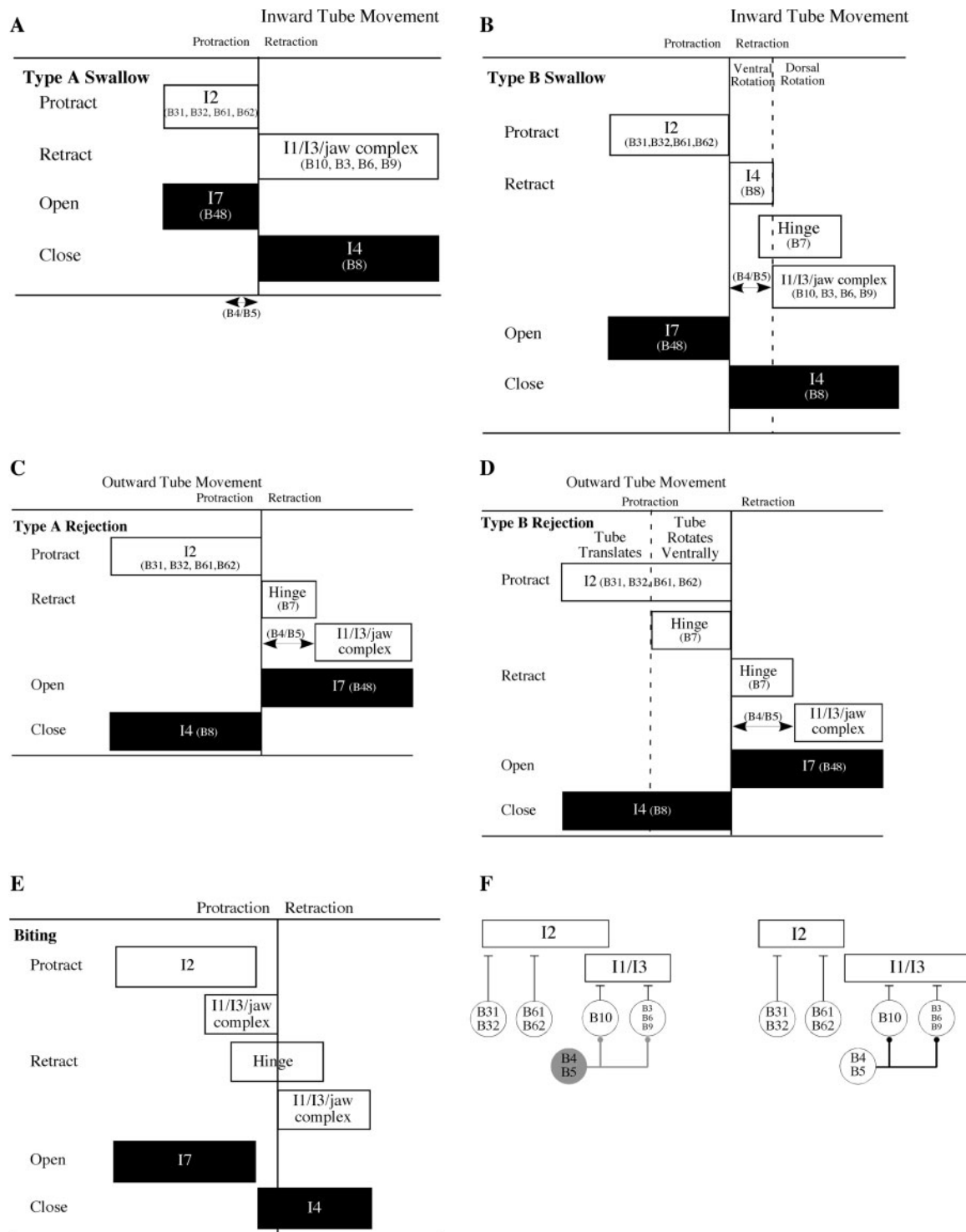
Fig. 11 Schematic summary of the implementation of Type A and Type B swallows, rejection, and biting.

protractor muscle to the onset of activity in the I1/I3/jaw complex. Predictions of the model have been confirmed both *in vitro* and *in vivo* in a recent study (Ye et al. 2006b). In larger amplitude rejections, food is not only pushed outwards, but rotates about the hinge, and this larger protraction is associated with an even larger delay before the onset of activity in the I1/I3/jaw complex (Fig. 11C and D; Ye et al. 2006b). Thus, mechanical reconfiguration alters the efficacy of the I2 protractor muscle, and the change in timing of the opening of the grasper alters the functional role of the I1/I3/jaw complex

from agonists in swallowing to antagonists in rejection (Fig. 11C and D).

Mechanical control of biting

During bites, unlike swallows, the grasper protracts very strongly as it attempts to grasp food, and then retracts weakly. Using magnetic resonance imaging to examine biting in intact, behaving animals, we observed that near the peak of protraction, the I2 muscle shortens far more than it does during swallowing (Neustadter et al. 2007). A kinetic model (Sutton et al. 2004b), based on *in vitro* biomechanical studies of the I2 muscle (Yu et al. 1999) and of the hinge (Sutton et al. 2004a), demonstrates that the I2 muscle becomes very weak near the peak protraction of biting, both because it loses mechanical advantage and because its short length reduces its ability to generate force. Unless the I2 muscle is either strongly neuromodulated or assisted by another muscle, I2 is unlikely to be able to fully protract the grasper (Sutton et al. 2004b; Neustadter et al. 2007; Fig. 11E).

The model also suggests that the forces generated by the posterior region of the I1/I3/jaw complex are context dependent (i.e., the direction of the net force exerted by the muscle changes with mechanical context): when the I1/I3/jaw complex is anterior to the midline of the grasper the I1/I3/jaw complex exerts retractive forces, but when the I1/I3/jaw complex is posterior to the midline of the grasper it exerts protractive forces. Our modeling studies suggest that the I1/I3/jaw muscle, which acts as a retractor during swallowing and rejection, may act as a protractor muscle near the peak protraction of biting. Moreover, the timing of neural activity in I2 and in the I1/I3/jaw complex is consistent with this hypothesis. During biting, activity in the I1/I3/jaw complex begins before the end of activity in the I2 protractor muscle.

Interneuronal mechanisms underlying multifunctionality

Previous studies have suggested that cerebral buccal interneurons, activated in different patterns, may underlie the switch from ingestion to rejection by altering the timing of activation of the grasper-closer motor neurons (the B8 motor neurons) relative to the neurons responsible for the protraction/retraction cycle (Jing and Weiss 2001, 2002). In *Aplysia*, B4/B5 neurons make extensive inhibitory connections to the motor neurons of the I1/I3/jaw complex (Gardner 1993) so that intense firing in the B4/B5 neurons could delay the onset of activity in

the I1/I3/jaw complex motor neurons (Fig. 11F). The B4/B5 neurons are active at the border between protraction and retraction and the intensity of their activity varies with the behavioral response: they are least active during biting, more active during swallowing, and most active during rejection (Warman and Chiel 1995; note length of arrows marked B4/B5 in Fig. 11A–D, and note that B4/B5 is not active during biting, Fig. 11E and F, left; B4/B5 shown in gray). Stimulation of the B4/B5 neurons during rejection-like *in vitro* responses delayed the onset of activity in the I1/I3 motor neurons (Fig. 11F, right side; B4/B5 shown in black), whereas inhibition of the neurons shortened the delay to onset of activity in the same motor neurons (Ye et al. 2006b). Stimulation of the B4/B5 neurons during swallowing induced a switch to rejection, whereas stimulating them during biting induced a switch to swallowing-like responses (Chestek et al. 2004).

These studies of multifunctionality in *Aplysia* demonstrate that there is a remarkable functional flexibility in the muscles of the buccal mass. Muscles and motor neurons may change their function due to changes in their mechanical context, whether this is due to expression of new degrees of freedom, mechanical reconfiguration, or context dependence. In some feeding responses, muscles act as agonists, whereas in others they act as antagonists. Thus, understanding the functional role of an interneuron may require a deeper understanding of the biomechanical functions of the motor pools it controls, as well as the biomechanical context in which it is activated.

It is likely that flexibility of function underlies multifunctionality in other systems as well. For example, a study of the buccal masses of several cephalopod mollusks demonstrated that the function of posterior mandibular muscle could close or open the beak depending on whether lateral mandibular muscles were contracted, a form of reconfiguration that has been termed "muscular articulation" (Uyeno and Kier 2005). Similar flexibility of function is also observed in vertebrates. For example, the epaxial muscles of the snake mediate swallowing if an animal's body is straight, and locomotion if the body is curved (Moon 2000).

In addition to providing insights into the neuromechanics of multifunctionality, these studies serve as the basis for designing biologically inspired multifunctional robots. A gripper device, modeled on *Aplysia*'s buccal mass, has been constructed. The device can be used to ingest slippery, compliant materials (Mangan et al. 2005). A small change in the gripper's control, based on the mechanisms

elucidated in *Aplysia*, would allow the gripper to be used for egestion as well. Such devices might be useful for harvesting or manipulating slippery and compliant materials, potentially including medical applications.

Using genetic manipulations to investigate central control of swimming in zebrafish

Larval zebrafish have become a model system for experiments on motor control of locomotion. The transparency of the larval zebrafish body makes it possible to image neuron morphology and physiology in intact, live animals. Complementary to imaging approaches, visually guided electrophysiology provides physiological data with fine resolution of the timing and pattern of neuron or muscle activity. Recent kinematic descriptions of swimming and startle behavior in larval zebrafish (e.g., Budick and O'Malley 2000; Muller and van Leeuwen 2004; Thorsen et al. 2004) provide a foundation for integrating morphology and physiology with mechanics and function.

Research on motor control in zebrafish has benefited greatly from studies of developmental genetics and associated techniques. The timing and extent of expression have been determined for many genes, and their roles in patterning the body have been examined. Manipulating gene function has made it possible to modify the locomotor system and dissect the functions of its parts in precise ways.

Such approaches have been used to examine the startle behavior, a focus of work on motor control in zebrafish. Of particular interest have been the Mauthner cells, a pair of large neurons in the hindbrain that drives the startle response (reviewed by Zottoli and Faber 2000). The M-cells' cell bodies are located in rhombomere (r) 4 of the hindbrain, just medial to the otic capsules. Their axons cross the midline of the hindbrain and descend the length of the spinal cord synapsing with elements of the segmentally repeated spinal cord circuits along their lengths. A single action potential generated by a Mauthner cell can drive an initial C-shaped body bend of the startle, although it is now known that other reticulospinal cells also are involved in the response (e.g., Gahtan et al. 2002; Liu and Fetcho 1999).

Many mutants are available with aberrant startle morphology. Neural mutants including *deadly seven* (*des*) (Gray et al. 2001) and *space cadet* (*spc*) (Granato et al. 1996) possess altered startle neural circuits, with changes including duplicate Mauthner cells (*des*) or loss of an excitatory cell that provides input to the Mauthner cells (*spc*). Other mutations affect the musculoskeletal system. For example, the *fused somites* mutant loses some myosepta and axial muscle fibers extend across several adjacent segments (van Eeden et al. 1996). Although mutants may have a wide range of altered characters in addition to the one of interest, with careful controls such lines have provided valuable insights into the function of locomotor morphology (e.g., Lorent et al. 2001; Liu et al. 2003) by determining, for example, functions of startle circuit neurons and effects of changing the startle circuit on cell physiology and behavior.

Other approaches to altering the nervous system involve developmental manipulation of wild-type fish. Neurons can be added or removed by increasing or decreasing the production of specific proteins. For example, Mauthner cells can be added to the hindbrain by modifying rhombomere identity with addition of mRNA from *hoxb1a* or *hoxb1b* genes (Fig. 12A; McClintock et al. 2001). In contrast, morpholino antisense oligonucleotides block translation and can be used to decrease expression of a particular gene (reviewed by Corey and Abrams 2001). Morpholinos to *hoxb1b* decrease expression of this gene in rhombomere 4 (r4), resulting in loss of normal Mauthner cells (McClintock et al. 2002). Cell-specific ablations (Fig. 12B) provide the most direct test of the function of a given neuron, and the transparency of the larval zebrafish makes it possible to use lasers to finely focus on an individual cell for ablation (e.g., Liu and Fetcho 1999).

Both addition and deletion of specific neurons can be used to address questions of motor control. An example is research on the function of ectopic neurons (added, misplaced cells) in the startle response (Hale et al. 2004). The addition of ectopic r2 Mauthner cells provided an opportunity to examine how modifications to neural circuit structure affect locomotion and, more broadly, mechanisms by which neural circuits and behavioral systems may evolve.
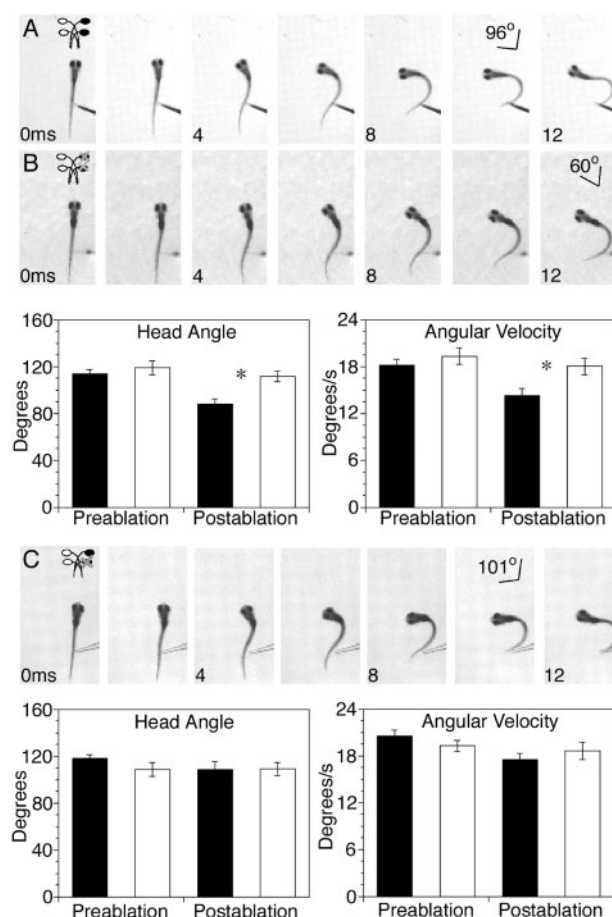
Initial behavioral observations on fish with duplicate Mauthner cells showed that the addition of ectopic cells did not affect performance of the startle response (Fig. 13A). This result suggested three alternative hypotheses for the role(s) that ectopic cells may play in the startle response: (1) they have no function; (2) they work with the normal Mauthner cells to generate normal behavior; or (3) they are functionally redundant copies of the normal cells.

In order to examine what role ectopic Mauthner cells might play in behavior, the effects of ablating the r4 M-cell, the r2 M-cell, or both r2 and r4 cells
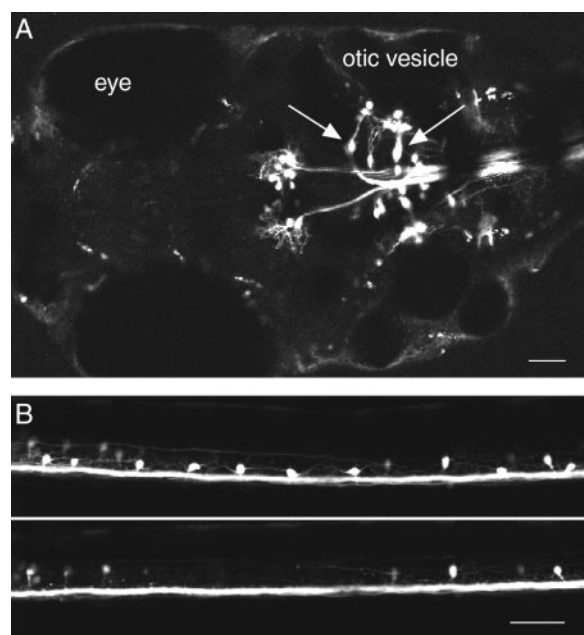
Fig. 12 Imaging and manipulating brain and spinal cord neurons in living larval zebrafish. (**A**) Midbrain and hindbrain reticulospinal interneurons labeled with fluorescent dye (10 kDa fluorescein dextran, Molecular Probes). The normal Mauthner cells are labeled (closed arrows). A duplicate Mauthner cell is shown on the upper half of the image in rhombomere 2 (open arrow). (**B**) Lateral view of an array of multipolar commissural descending (MCoD) spinal interneurons (Hale et al. 2001) before laser ablation and the same region of cord after ablation. Note that after ablation of the MCoDs, other cells in the image remain as does the Mauthner axon that runs below the targeted cells. Images modified from Brainerd and Hale (2005). Scale bar = 50 μm.

Fig. 13 Ectopic Mauthner cells appear to be functionally redundant to normal Mauthner cells in fish that over-express *hoxb1b*. Modified from Hale et al. (2004). (**A**) Behavior of fish with duplicate Mauthner cells. (**B**) Ablation of both r2 and r4 Mauthner cells results in a decreased angle of head movement and peak angular velocity. Black bars represent turns toward the side of the body that were controlled by the ablated Mauthner cells; white bars are turns toward the intact side. This result is comparable to the decrease in performance when the r4 Mauthner cell is ablated in normal fish. (**C**) Ablation of the r4 Mauthner cell decreased neither head angle nor peak angular velocity, suggesting that the ectopic cells in rhombomere 2 are functionally redundant to those in rhombomere 4. For scale, the fish pictured are approximately 3.9 mm TL.

on startle kinematics were examined. This study focused on two parameters analyzed in studies of Mauthner cell function: the angle of head movement and the peak angular velocity of the initial startle bend. These escape metrics have been shown to decrease in response to tail stimulation when the Mauthner cell is ablated (Liu and Fetcho 1999), and are key to models of motor control of escape (Foreman and Eaton 1993). In fish with ectopic Mauthner cells, ablation of both r2 and r4 M-cells resulted in a decrease in performance of the startle response comparable to that seen when the r4 M-cell is removed from the normal animal (Fig. 13B). In *hoxb1b* over-expressed fish, there was no significant decrease in performance when one of the r2 or r4 M-cells was ablated (Fig. 13C). These data indicate that the ectopic (r2) and normal (r4) M-cells are, at least in some respects, functionally redundant and support the idea that morphological duplication may provide substrate for the evolutionary generation or modification of neural circuits (Hale et al. 2004).

The strong base of knowledge of swimming and startle behaviors and their neural control provides an excellent opportunity to examine the interaction between neurobiology and biomechanics in aquatic locomotion. The approaches discussed earlier in this article for motor control can also be applied to sensory systems, making it possible to address how sensation of internal and external forces on the animal shapes behavior. By examining not only feedforward control of locomotion via descending commands from the brain and spinal cord, but also

feedback control via sensation of body dynamics and the physical environment, a broad understanding of sensorimotor integration in vertebrate aquatic locomotion can be developed.

Part IV. Interplay among brain, sense organs, muscles and the environment

Animal movement emerges from the complex interplay among descending output from the brain, sensory input from the body and the environment, muscle dynamics, and the emergent dynamics of the whole animal. From the complex mechanical interactions between legs and the ground during walking, to the dynamics of feeding, reaching, running, flying, swimming, and other movements, neural systems must necessarily contend with or take advantage of the static and dynamic properties of the mechanical systems with which they interact (Chiel and Beer 1997; Nishikawa 1999; Dickinson et al. 2000). The interplay between neural and mechanical systems occurs at all levels of biological organization, from the tuning of the properties of the muscles of a fly's thorax (Pringle 1949) or a toad's tongue (Lappin et al. 2006), to the dynamics of legs, wings, fins, and whole bodies and their interactions with the medium against which they act. The examples presented in this section focus on the interplay among these components. The first example addresses the interplay between sensorimotor properties of the nervous system and mechanical properties of the musculoskeletal system during locomotion. Specifically, neuromuscular and mechanical control for stability, associated with unexpected changes in terrain height, is examined in a running avian biped (guinea fowl). Within this animal model, a proximo-distal gradient of muscle function and neural control is hypothesized that reflects differences in muscle-tendon architecture along the limb. The second example argues that broad, evolutionary patterns of motor control may emerge simply by comparing kinematic patterns of movement (in this case, bipedal versus quadrupedal walking of bonobos) as the collective output of the neuromuscular and skeletal systems. A related example uses a modeling approach to investigate how physical properties of the environment influence neuromuscular features of swimming versus jumping in frogs.

### Feedforward, feedback, and intrinsic control of the limbs during locomotion

Terrestrial animals regularly encounter rough terrain with variable substrate properties. This requires time-varying neuromuscular control to adjust to changing conditions when running. Feedback from proprioceptive and visual sensory information must be integrated with descending feedforward motor output to adjust muscle force, length and work production to changing limb and body dynamics. As noted earlier in this article, timing delays in feedback circuits are important to how an animal's motor response is mediated, and because of them, animals may also rely on intrinsic stabilizing force–velocity and force–length properties of their muscles when perturbed from a steady movement path (Brown and Loeb 2000). Such stabilizing responses occur immediately, prior to subsequent sensory-motor feedback control, and likely continue as neural feedback subsequently modulates motor activation to stabilize the animal.

A proximo-distal gradient in muscle function and motor control

The interplay between reflex feedback and muscle mechanics influences how animals achieve dynamically stable movement. Studies of limb muscle architecture (Biewener 1998) and function (Roberts et al. 1997; Daley and Biewener 2003; Gillis et al. 2005), suggest the possibility of a proximo-distal gradient of muscle function during running, in which long-fibered proximal muscles modulate limb and body work, whereas short-fibered distal muscles (many with longer tendons) favor more economical force generation and elastic energy savings (Biewener and Roberts 2000). Along with this functional and architectural gradient, there may also be a proximo-distal gradient in motor control of muscles involved in the stance phase of running (Daley et al. 2007). In such a gradient, proximal limb muscles are under feedforward control, driven by central (spinal) pattern generating neural circuits, and relatively insensitive to changes in loading during stance. In contrast, being the first to interact with the substrate, distal muscles are inherently more sensitive to loading, resulting in greater force–length and force–velocity effects and more rapid proprioceptive feedback regulation.

There is evidence that reflex feedback can rapidly adjust muscle activation within a perturbed step and recent evidence suggests that reflexes also contribute substantially to muscle activity in steady locomotion (e.g., Grillner 1975; Nichols and Houk 1976; Pearson et al. 1998; Pearson 2000). However, the relationships between muscle-tendon architecture, function and neural control within the limb are not yet clear. A proximo-distal gradient in neuromuscular control would allow the proximal joints to produce
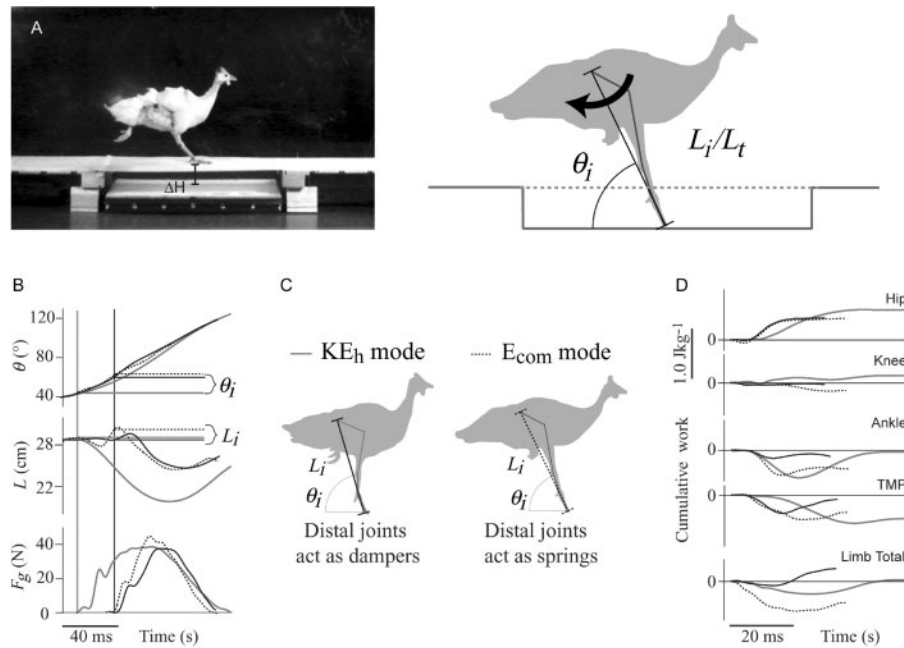
Fig. 14 A Guinea fowl encounters an unexpected drop in substrate height during running. (**A**) An 8.5 cm drop in terrain was camouflaged by tissue paper stretched tightly across the gap (image from Daley et al. 2006). Body and limb dynamics were quantified using CoM energy analysis and inverse dynamics (Daley et al. 2006, 2007; Daley and Biewener 2006). Black lines indicate KE_h mode, dashed lines indicate E_{com} mode, see part (**C**) and text. Gray lines in (**B**) and (**D**) depict control patterns. (**B**) Limb retraction did not change substantially from level running, resulting in a steeper limb angle at the point of contact (θ_i). Limb extension varied during the perturbation, resulting in variable relative leg length at contact (L_i/L_T) (figure modified from Daley and Biewener 2006) (**C**) Limb posture at contact determined the bird's energy response mode, due to the sensitivity of distal joint function to changes in limb loading (**D**). Parts C and D modified from Daley et al. 2007 and Daley and Biewener 2006, respectively.

consistent limb cycling, while the distal joints rapidly adjust their force and work output to meet changing locomotor demands.

This hypothesis can be tested by examining the body, limb, and muscle dynamics of an animal that must stabilize in response to an unexpected perturbation to steady running. Under feedforward control, little change in the motor output and mechanical function of proximal muscles would occur when the limb and body are perturbed. However, the distal muscles would exhibit rapid changes in contractile performance and activation pattern in response to changes in limb dynamics. The altered performance of the distal muscles would allow rapid changes in muscle work performance within the perturbed step. This expectation differs from the observed limb and CoM responses of cockroaches subjected to an explosive impulse perturbation (Jindrich and Full 2002), which exhibited little evidence for 'within-step' sensorimotor feedback.

Testing control hypotheses through sudden perturbations in substrate height

Following from this novel experimental approach in cockroach locomotion (Jindrich and Full 2002),

investigation of running dynamics in guinea fowl exposed to sudden perturbations reveals control strategies for negotiating unpredictable terrain. Guinea fowl experienced two different perturbation types: (1) an unexpected drop in substrate height while running ($\Delta H = 8.5$ cm; Fig. 14A), or (2) regularly encountered obstacles on a treadmill ($\Delta H = 5$ cm and 7 cm; Fig. 15A). These experiments offer a means for revealing the dynamic interplay between mechanics and control by studying the animal's temporal response for adjusting to unexpected changes in terrain. The first experiment investigated the interplay between joint, limb and body dynamics through CoM energy and inverse dynamic analyses based on force plate and high-speed video recordings (Daley et al. 2006, 2007). The second experiment explored the relationship between limb and joint dynamics and muscle contractile performance through simultaneous high-speed video and *in vivo* recordings of muscle force, length and EMG activity (Daley 2004, 2005). These experiments show that animals are able to adjust rapidly, and achieve remarkable stability. In particular, limb posture adjusts immediately, prior to the shortest reflex latencies of their neuromuscular
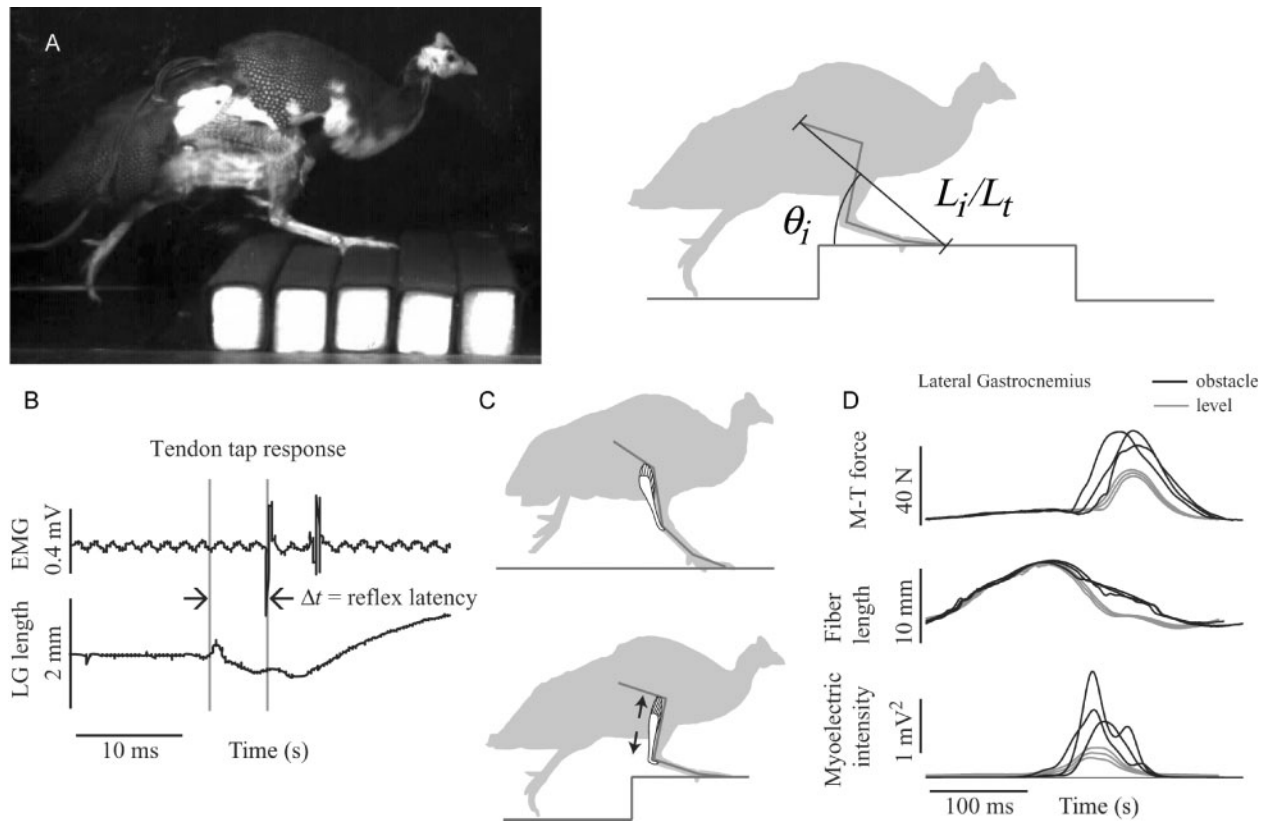
Fig. 15 A Guinea fowl runs over repeated step obstacles. (**A**) *In vivo* contractile performance of the lateral gastrocnemius (LG) was recorded while birds negotiated 5 and 7 cm obstacles while running (Daley et al. 2004, 2005). (**B**) A tendon tap method was used to measure the stretch reflex latency of the LG. (**C**) In association with the more flexed, crouched posture during obstacle steps, the LG was stretched and operated at longer lengths. (**D**) The change in limb posture and muscle-tendon operating length was associated with increased recruitment intensity and force development during obstacle steps. Black lines indicate steps directly onto an obstacle (as shown in A), and gray lines show the mean ± 95% confidence interval for level running steps.

system (Fig. 15B). This occurs as an intrinsic mechanical response when the limb's interaction with the ground suddenly changes, due to the feedforward activation of limb muscles in anticipation of ground contact. In running guinea fowl, however, active motor feedback modulation of distal limb muscles reinforces this immediate, passively stabilizing response after only a 5–8 ms reflex latency (Fig. 15B).

A simple spring-mass system accurately describes the CoM dynamics of steady running animals (Cavagna et al. 1977; McMahon 1985; McMahon and Cheng 1990). What happens when animals are faced with a sudden loss in potential energy (PE) after unexpectedly breaking through a false floor? One possibility is that guinea fowl maintain their level running CoM trajectory by extending their limb to accommodate the change in substrate height, similar to human runners upon encountering an extremely compliant surface (Moritz and Farley 2003, 2005). Alternatively, guinea fowl must either convert lost PE into kinetic energy (KE) and speed

up, or absorb (and lose) CoM energy through limb muscles.

When confronted with this unexpected challenge, guinea fowl proved remarkably stable, falling in only 2 out of 72 trials over the course of three separate studies. In most cases, the animals managed their energy dynamics and stabilized their running by converting lost PE to KE (KE_h mode), with the remainder of cases involving energy absorption by the limb (E_{com} mode) (Daley et al. 2006). Whether the animal adopted a KE or E_{CoM} stabilizing mode depended on limb dynamics during the time between anticipated and actual ground contact (Fig. 14B and C). The limb followed the same retraction trajectory as during level running, despite dramatically altered loading as it broke through the tissue paper, resulting in a steeper limb angle at contact (θ_i) compared to steady running (Fig. 14B). The limb also extended to varying degrees during the perturbation (L_i/L_T; Fig. 14B). The resulting ΔPE was 43% less than if they made no adjustment in limb posture following the sudden drop in height.

These results suggest feedforward motor activation of muscles for limb retraction and weight support in anticipation of the stance phase of steady running. Consistent with feedforward control, proximal muscle work at the hip was unaffected by the breakthrough perturbation for either energy mode (Fig. 14C). The angle of the limb at contact (θ_i) was altered, however, and, together with relative differences in limb extension (L_i/L_T) (Fig. 14D), dictated the limb loading and energy response (Daley and Biewener 2006; Daley et al. 2007). When the limb landed at a steeper angle and more flexed posture (lower L_i/L_T), the distal joints acted as springs and, due to positive hip work, the limb as a whole did net positive work, increasing KE (KE_h mode; Fig. 14C and D). When with the limb landed at a shallow angle and more extended posture, the distal joints absorbed energy, as did the whole limb, to absorb the lost PE of the animal's CoM (E_{CoM} mode; Fig. 14C and D). These results suggest differences in proximal versus distal limb muscle responses, but leave unresolved whether modulation of distal muscle function reflects changes due to intrinsic force–length and force–velocity properties, or by reflex feedback.

Study of distal limb muscle function in the lateral gastrocnemius (LG) when guinea fowl encounter a rectangular step obstacle on a treadmill (Fig. 15A) reveals the inherently intertwined roles of intrinsic mechanical and proprioceptive feedback responses in distal muscle performance. Guinea fowl step on the obstacle with a more flexed, crouched posture (Fig. 15B), resulting in longer muscle fiber lengths in LG (Fig. 15D) at the onset of stance-phase activity. Longer fiber length at the onset of stance is correlated with higher peak-force and mean-force during stance (Fig. 15D). The stretch reflex response, however, has a latency of only 4.7–8.5 ms in this muscle, rapid enough to modulate muscle performance within the perturbed step, which is 120–170 ms in duration. Consistent with this, the longer length of the LG upon obstacle contact is associated with more intensive motor recruitment (EMG intensity; Fig. 15D). These results demonstrate that both intrinsic mechanical and reflex feedback contribute to altered distal limb muscle performance during terrain height perturbations. Furthermore, the time-course of each overlaps substantially. Consequently, more sophisticated analyses (such as dynamic modeling) may be required to quantify the contribution of each to rapid changes in muscle mechanical performance.

The posture-dependent changes in the distribution of limb muscle work during terrain height perturbations suggest that a proximo-distal gradient of neuromuscular control may improve the stability of running in rough terrain. In such a gradient, the hip extensors are relatively insensitive to load and are controlled in a feedforward manner by spinal motor circuits. In contrast, more distal ankle extensors and digital flexors are highly load-dependent, responding immediately to changes in loading via intrinsic muscle stabilizing properties, followed by proprioceptive feedback to modulate their contractile activity. Consequently, limb cycling remains constant, but limb posture, loading and energy performance are interdependent, allowing rapid adjustments during locomotion in uneven terrain.

Ecological morphology, evolutionary biology, and the influence of the environment

Understanding the relationship between an organism's appearance and the way it performs or functions in its environment is a fundamental aim of ecological morphology. Insight into both the process of adaptation by natural selection as well as the factors that constrain evolution are crucial and require integration of many biological disciplines and approaches (Aerts et al. 2000a, 2002; Van Damme et al. 2003). Arnold (1983) developed a useful conceptual approach for such an integrated analysis, based on quantifying how well individual organisms *perform* ecologically important functions (e.g., sprinting, maneuvering, climbing, biting, singing). Starting from the established variation in performance (defined in terms of an ecologically relevant function such as one of the aforementioned), the effect on fitness (a measure of an individual's survivorship and/or reproductive success) must be estimated. The larger the fitness differences that result from small shifts in performance, the steeper the *fitness gradient*. It is also important to examine the links among phenotypic variation, genotypic variation, and performance. The larger the performance differences that result from slight changes in 'design', the steeper the *performance gradient*.

For many ecological functions, the musculoskeletal system plays a key role. Searching for correlations between variations in design (e.g., inertial properties, linear dimensions) and performance (e.g., sprint speed, maneuverability) is a first step, but does not explain the selective mechanism(s) behind the established relationship. Insight into the causal aspects can be gained either from a broad comparative approach or from further in-depth research. For the musculoskeletal system, this most often requires biomechanical analyses and modeling.

In ecological morphology, an important but often overlooked 'design' feature of the musculoskeletal system is concealed in its temporal dimension: what are the spatiotemporal aspects and patterns of coordinated movement? Similar 'designs' can yield diverging performance when operated differently, or alternative morphologies may result in comparable performance when appropriately controlled. It is the interaction between the nervous system and the mechanical properties (e.g., shape, structure, dimensions) of the body and the environment that determine the musculoskeletal performance of an organism in its natural habitat (Enoka 2002).

Consequently, studies of motor control in the context of eco-morphological analyses may lead to a better understanding of adaptation and evolution. However, because variation in individual performance requires the study of large numbers of specimens (and many observations per specimen), this makes experimental neurophysiological approaches extremely challenging to carry out in this context. A more tractable approach may be to study the kinematics of an animal's movement as representative of the *collective output* of the interaction of the nervous system, body mechanics, and physical environment and as an overall indicator of performance.

Consider the control of a motor task with an obvious range in performance (e.g., slow to fast running, small to large jump distance, gentle to hard biting) (Fig. 16). A simple, graded "intentional" drive (i.e., intensity is related to the required performance level), subject to proprioceptive and peripheral feedback, descends from a higher brain center to activate a central network at a lower level (e.g., coupled CPGs). This network transforms the simple command into coordinated muscle-tendon actions distributed over different limbs and joints. Feedback can tune the coordinated activity, but it is the interaction with the intrinsic dynamics of the system and with the environment that ultimately determines the appearance of the collective output of the neural controller (i.e., the spatiotemporal aspects and patterns of coordinated movement).

The level of performance is the measure for the graded drive. Running faster, jumping higher, or biting harder is associated with greater activation (whatever the actual nature) of the lower level network. Borrowing further from terminology of *dynamic equilibrium theory* (Kugler and Turvey 1987; Thelen and Smith 1994; Latash 1998), the level of performance is the *control variable* of the system. In the proper biomechanical and functional morphological context, evaluation of how the collective
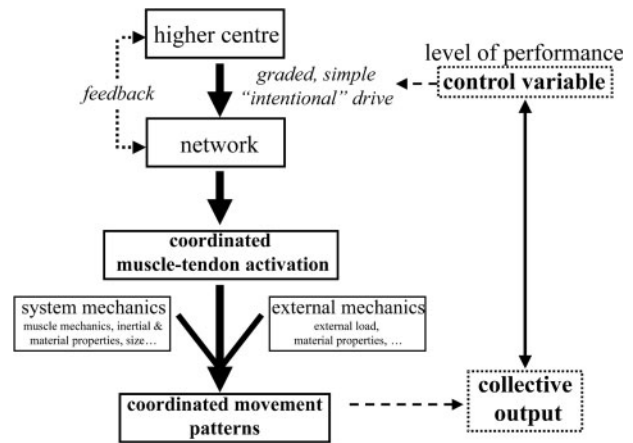
Fig. 16 Schematic diagram for control of a simple, graded "intentional" drive, subject to proprioceptive and peripheral feedback, descends from a higher brain center to activate a central network at a lower level. The network transforms the simple command into coordinated muscle-tendon actions distributed over different limbs and joints.

output adjusts to changes in the control variable might reveal details of the interplay between the fundamental neural and mechanical components of control, which might otherwise remain hidden (Fig. 16). The following examples illustrate this concept.

Evolution of bipedality in hominoids

For many reasons, bonobos (*Pan paniscus*) are assumed to resemble the common ancestor of chimpanzees and humans (Aerts et al. 2000b; D'Août et al. 2002). Therefore, the bonobo is a suitable model for studying "early steps" in the evolution of bipedal locomotion, starting from an obligate quadrupedal condition. In order to gain insight into how the neural control of hind limb movement may differ, and have evolved, between these locomotor modes, quadrupedal and bipedal kinematics (in terms of spatiotemporal gait variables and movement patterns: i.e., the *collective output*) can be gathered for a number of specimens (n = 9) and compared to each other as a function of walking speed (the *control variable*).

When walking bipedally, bonobos use smaller strides at higher frequencies compared to when they walk quadrupedally at the same speed (Fig. 17A). This difference is entirely explained by the smaller steps the animals take (distance traveled during limb stance), as duty factors (the fraction of the cycle the foot contacts the ground) change in both modes in an identical way with speed. Remarkably, however, the relationship between speed and stride frequency (or stride and step

length) for both bipedal and quadrupedal walking can be well described by similar power functions ($y = ax^b$) with identical exponents (b) (Aerts et al. 2000b). This means that, irrespective of the actual absolute values of the variables, a gain in speed that requires a doubling or tripling of stride frequency (or similar changes in stride and step length) during quadrupedal walking, requires a similar doubling or tripling for the same speed gain during bipedal walking. Moreover, kinematic analysis reveals that the smaller bipedal steps are due to a decreased range of motion in the hip (knee and ankle patterns do not change), which in turn is likely related to the altered inclination of the trunk (D'Août et al. 2002; Fig. 17B). Taken together, these findings suggest that, despite the large and obvious quantitative differences in quadrupedal versus bipedal locomotion (Fig. 17A), basic aspects of hind limb control are identical. This conclusion is important when placed in an evolutionary context, but it could not be drawn without first establishing the relationship between stride frequency and walking speed.

Mechanics of the environment

Obviously, when comparing conditions (such as locomotor modes, environmental circumstances), the choice of the appropriate control variable is crucial. In the aforementioned example, the use of walking speed is self-evident. This is less true in cases where grossly similar movement patterns are used for clearly distinct tasks. This occurs, for example, when considering level running versus steep climbing in lizards (Van Damme et al. 2003), or swimming versus jumping in frogs (Nauwelaerts and Aerts 2003). How should performance be compared between cyclic swimming (for which speed seems the obvious control variable) versus noncyclic jumping (for which jumping distance seems most appropriate)? This question becomes meaningful in an eco-morphological context when searching for potential evolutionary trade-offs (i.e., when optimization of one function interferes with another function).

In the semi-aquatic frog, *Rana esculenta*, neither a trade-off (i.e., the good swimmers are the bad jumpers and *vice versa*) nor a positive correlation (i.e., the good swimmers are the good jumpers) was detected between swimming and jumping (Nauwelaerts et al. 2005). The absence of correlation might point to independent neural controllers for swimming and jumping. To investigate this question, it is necessary to identify an appropriate control variable (performance measure) for jumping

and swimming. The similarity in gross limb movement patterns of both locomotor modes (forceful kicking with the hind limbs for both swimming and jumping) suggests that a force-related variable may be most appropriate: the more forceful the kick the further the jump and the faster the swimming cycle. Surprisingly, propulsive impulses (time integral of propulsive force) were always considerably lower for swimming than for jumping, even if specimens were chased vigorously to evoke maximal performance (Nauwelaerts and Aerts 2003). Consequently, a comparison similar to that carried out for walking bonobos is impossible, simply because the ranges of the control variable do not overlap. Yet, a new question is generated: which of the components of the control black box (Fig. 16) is responsible for the seemingly inferior aquatic performance?

Analysis of swimming and jumping reveals slight differences in kinematics (Nauwelaerts and Aerts 2003) and muscle activation patterns (Gillis and Biewener 2000). To what extent this reflects basic differences in neural control is difficult to assess because kinematics and activation patterns represent collective output, including the effects of feedback and interaction with the intrinsic dynamics of environment and body. Isolating the magnitude of the potential environmental effect on the propulsive impulse is only possible if frogs could be urged to swim and jump with strictly identical neural control, excluding any feedback. Obviously, this cannot be realized experimentally! Mathematical modeling offers a solution to this problem. Using a simple computer model, consisting of an ellipsoid body with telescopic limbs and plate like feet, and a limb actuator with Hill-type muscle properties tuned so that the model frog achieves realistic jumps, identical stimulation of the actuator on land and in the water results in propulsive impulses similar to those measured *in vivo* (Nauwelaerts and Aerts 2003). This indicates that, although altered neural control cannot be excluded, the animal's interaction with environmental mechanics may suffice to explain performance differences observed during jumping and swimming in real frogs.

Part V. Bio-inspired robots and physical models: the new frontier

The earliest robots were heavy, noncompliant machines programmed for highly specific tasks whose movements were far removed from those of animals. Most robots in current use retain these features. Over the past 20 years, a new generation of robots has been inspired by the design of animals.
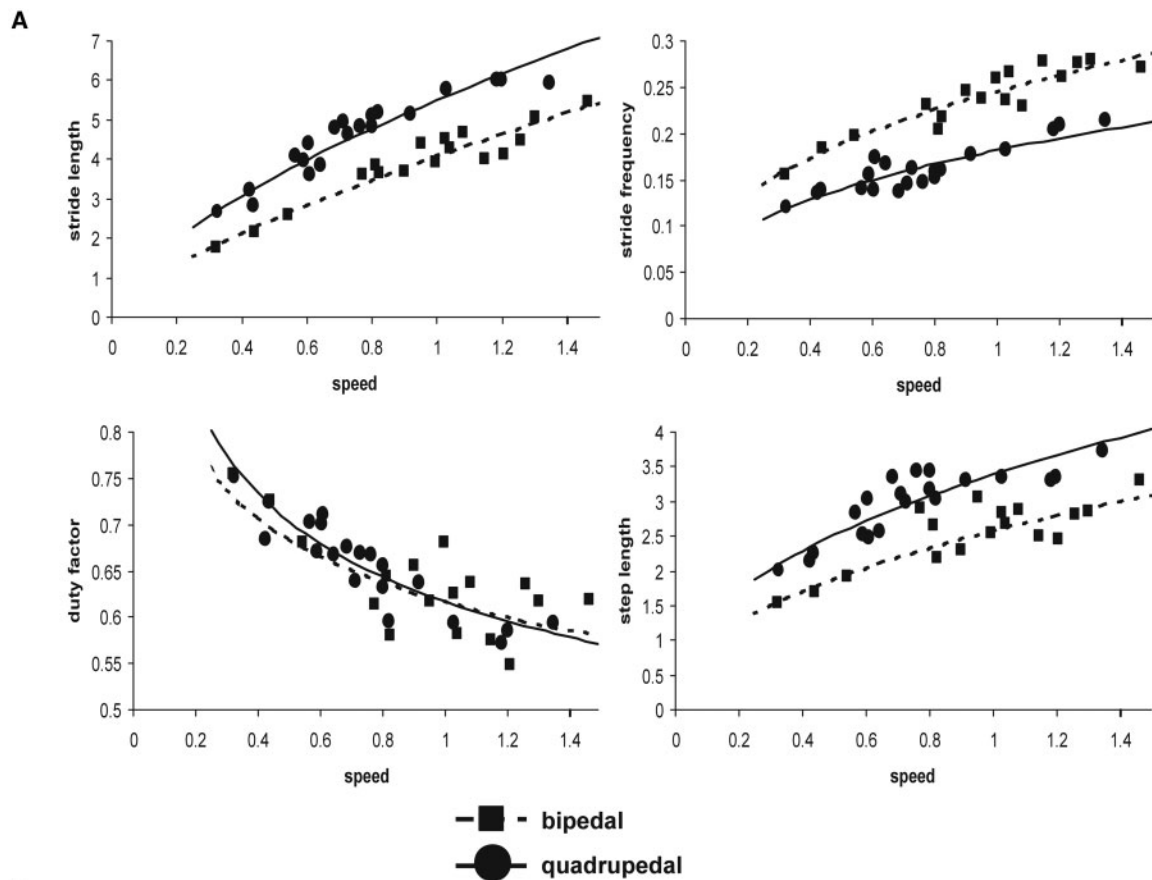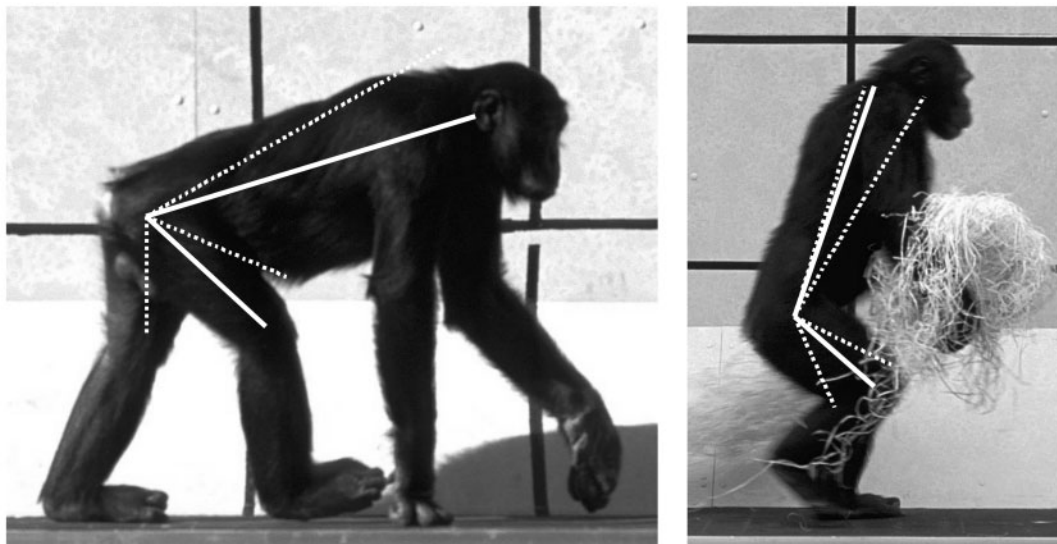
Fig. 17 (**A**) Relationships between dimensionless speed, stride length, stride frequency, duty factor, and step length during bipedal and quadrupedal walking in bonobos (after Aerts et al. 2000b). (**B**) Trunk and thigh orientation in a quadrupedal and bipedal walking bonobo, with approximate indication of their ranges of motion (dotted lines). Data from D'Août et al. 2002. Photographs by K. D'Août.

By *biological inspiration*, we mean the transfer of principles and analogies from biology to other disciplines so as to advance that discipline, such as building robots that can out-perform other designs by using ideas from neuromechanics (Full 2000). Early examples are Raibert's series of breakthrough monopedal, bipedal and quadrupedal hopping machines (Raibert 1986). A robot named *Genghis*

(Brooks 1989) followed, which grossly resembled an insect, but used distributed control principles inspired by insect locomotion.

In the ensuing decades, there has been an explosion of robots that have been inspired by a wide range of animals: from stick insects such as *TUM* (Cruse 1990; Pfeiffer et al. 1994) and the *Lauron* series (Berns et al. 1994; Gaßmann et al. 2001) to hexapods including RHex (Saranli et al. 2001) and Whegs[TM] (Quinn et al. 2003); to *Scorpion* with eight legs (Kirchner and Spenneberg 2001) and *Ariel* (Greiner et al. 1996) and *RoboLobster*, which operate in the near shore environment (Ayers et al. 2001). A recently developed micromechanical flying insect (Wood et al. 2003), based on a scaled hardware model of a fly, generates lift forces using actuator-driven elastic deformations of the wing-hinge, matching the indirect propulsive mechanisms of flying insects.

Soft-bodied animals have inspired the development of robots with compliant structures. A three segment worm-like robot, actuated with shape-memory-alloy springs, crawls around and through obstacles underwater (Vaidyanathan et al. 2000). A three segment inch worm robot, actuated by modified "air muscles" (i.e., pneumatic 'McKibben[TM] actuators'; e.g., Chou and Hannaford 1996), can move through curved tubes while letting fluid pass through its center (Mangan et al. 2002). A robot arm, inspired by the design of octopus tentacles (McMahan et al. 2006), has a large range of motion and can lift payload despite having a soft structure. These examples represent a fraction of the wide variety of robots that have been inspired by living organisms.

Not only can notions of neuromechanics serve roboticists, but robots functioning in a different role, as physical models, can serve neuromechanics. Because neuromechanical systems are often complex and difficult to understand, models of these systems can be useful research tools (Holmes et al. 2006). A robot can serve as a physical model to generate biological hypotheses (Fig. 18). Physical models have advantages over mathematical models because they must necessarily obey physical laws, and it is often easier to visualize results and make comparisons with the animal (Ritzmann et al. 2000; Koditschek et al. 2004; Ritzmann et al. 2004). Robots for this purpose should incorporate the biomechanics of the subject animal at the detail necessary to address particular questions. A physical model of the feeding mechanism of *Aplysia* was developed to illustrate the workings of a soft biomechanical system and to support the biological hypothesis that the function of
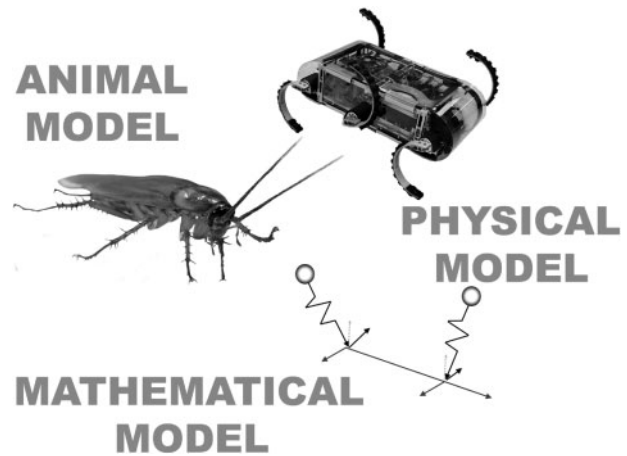
Fig. 18 The field of neuromechanics will benefit from the integration of natural experiments on animals, such as cockroaches, with mathematical and physical models. Both mathematical (a bouncing spring-mass shown here) and physical models (the robot, RHex) provide testable hypotheses for experiments on animals.

the jaw musculature complex depended on its mechanical context (Mangan et al. 2005). The physical model confirmed the biological hypothesis and serves as a teaching tool to visualize the animal's biomechanics. Scaling can be used to ease the development of the model. By matching the Reynolds number, Dickinson et al. (1999) used a large wing-shaped plate moving in an oil bath to model the unsteady fluid dynamics of a fly's wing and identify the aerodynamic forces it generated. Likewise, a robot developed to investigate the sensorimotor control of cockroach legs should have cockroach leg designs with appropriate motors and sensors that provide comparable performance, but if scaled appropriately, it need not be the same size as the animal.

Evolution of a robot model of a cockroach

A series of cockroach-like robots have been developed to understand sensorimotor control in animals with complex multi-jointed legs. Each successive generation of robots incorporates more of the complexity found in cockroach biomechanics. Each robot was developed to address a specific question and, when a discrepancy was noted between robot and animal, new questions were formulated and a new robot was developed to address them.

Robot I (Beer et al. 1992) was developed to test insect-inspired gait controllers, and therefore its design was simplified accordingly. It had six legs, each with two joints driven independently by electric motors. Three different gait controllers were successfully demonstrated. Using the first two of these,
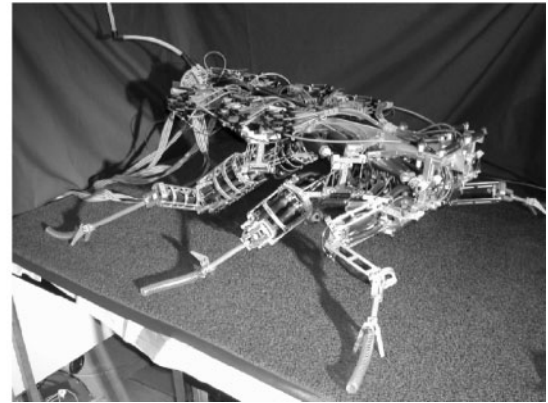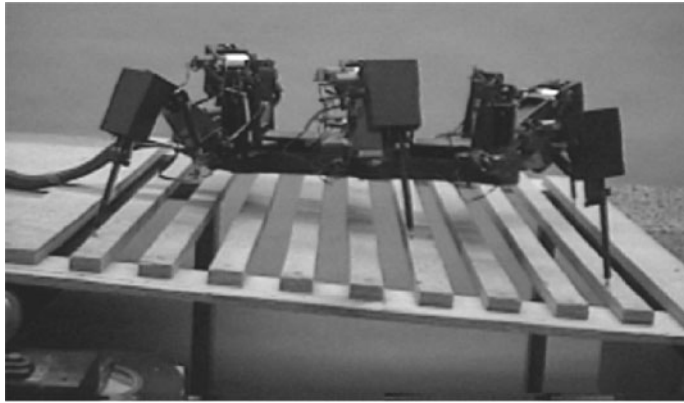
Fig. 19 (**A**) Robot II could walk across a slatted surface using local leg reflexes. (**B**) Robot V is a cockroach robot that uses Festo^{TM} air muscles.

Robot I could walk in a continuum of insect gaits; from the wave gait with one leg swinging at a time, to the tripod gait with three legs swinging in synchrony (Beer et al. 1992). Robot I was one of the first robots to implement and demonstrate the robustness of the Cruse gait controller (Cruse 1990; Espenschied et al. 1993).

Robot II was developed to address the importance of local leg reflexes for turning and locomotion on irregular terrain. Robot II (Fig. 19A) had a distributed control system that included a modified Cruse gait controller and insect inspired local leg reflexes (Espenschied et al. 1996). Its design was necessarily more complex than that of Robot I to enable more animal-like turning. Each of its six legs possessed three independently controlled joints. Using its modified Cruse controller, it walked in a continuum of insect gaits and omni-directionally. Local leg reflexes enabled walking on irregular terrain and over slatted surfaces.

For all of Robot II's abilities, it did not have the power necessary to accelerate like a cockroach. This was remedied in Robot III by using air cylinders instead of motors. Robot III implemented cockroach leg designs. Its front, middle and rear leg pairs were designed to model more closely the biomechanics of the animal (Full et al. 1991; Watson and Ritzmann 1998). Cockroach leg pairs each have different sizes and ranges of motion. To reflect this, the front legs of Robot III were the smallest, had five independently controlled joints and reached their feet in front of their body joints (Nelson et al. 1997). The middle legs were larger, had four joints, and their feet cycled equally in front and behind their body joints. The rear legs were the largest, had three joints, and their feet cycled behind their body joints. Leg movements very similar to those of the animal were produced and the Cruse controller was shown to be effective for coordinating the legs of this robot with very different leg-pair designs (Nelson and Quinn 2001).

Robot III demonstrated that neuromechanical principles are shared across species. For example, posture control inspired by mammalian research was developed and demonstrated for this cockroach robot (Nelson and Quinn 1999). Furthermore, a comparison of the front leg movements of Robot III, cockroaches, and mammals highlighted similarities in their designs that enable forward reaching movements (Ritzmann et al. 2004). The results show how disparate animals evolve similar solutions because of shared physical constraints.

Robot III did not walk well because it was missing an important component of a neuromechanical system, namely passively stiff joints (Loeb et al. 1999; Jindrich and Full 2002). Its actuators did not have passive properties similar to muscle. Although Robots I and II also lacked artificial muscles, their electric motors reacted quickly enough that their active control systems could mimic the compliance of muscles. Robot III's pneumatic control system was at least as fast as the animal's nervous system, but it needed actuators with passive properties akin to muscle for stability.

Robot IV and Robot V (Fig. 19B) were developed to study the role of various properties of muscle in cockroach sensorimotor control. The leg designs of Robot IV were similar to those of Robot III, except that its joints were actuated by McKibben^{TM} actuators, which share many important properties with muscle (Chou and Hannaford 1996). Their force/weight ratios rival those of muscle, they are structurally compliant, and when they are used in antagonistic pairs to actuate a joint, the joint's passive stiffness can be modulated by a control system (Caldwell et al. 1995; Chou and Hannaford 1996).

Unfortunately, McKibben™ designs of the time were short-lived because they failed in fatigue at high air pressure (Kingsley and Quinn 2002).

Robot V (Fig. 19B) was developed to take advantage of Festo™ air muscles, a new type of McKibben artificial muscle that is more robust. The leg designs of Robot V are similar to those of Robots III and IV (Kingsley et al. 2003). EMGs recorded from cockroach motor neurons are being used to drive robot joint motion (Mu and Ritzmann 2005; Rutter et al. 2007). Optimization is used to tune a neuromuscular model for the purpose of matching robot and cockroach joint motions. The model system serves as a quantitative hypothetical relationship between EMG and joint motion during the observed behavior. It will then be used to predict control of additional types of movement, such as turning and climbing, which have been studied in the insect.

Using general principles of neuromechanics

Understanding neuromechanical systems requires the formulation and testing of hypotheses that integrate from the component to the system level, from the level of individual muscles and neurons, through the biomechanical properties of the body, to the interaction of an organism with its environment. By taking a systems approach, which integrates the analysis of movement, biomechanics, neurophysiology, robotics, analysis of dynamical systems, simulation and modeling, it is possible to address this challenge and to obtain deep insights into the principles of neuromechanical systems in general, and legged locomotion in particular.

The control of a neuromechanical system depends on the task. At one extreme, gross, repetitive, rapid movements are dominated by mechanical feedback where "preflexes", acting before reflexes, play a critical role in control. At the other end of the spectrum, precise, novel and slow movements, in which static forces are dominated by neural feedback, reflexes at both the local and task level are required (Full and Koditschek 1999). Within this framework, testable neuromechanical systems hypotheses can be formulated for locomotion, and the evidence examined concerning the mechanisms by which neuromechanical control emerges from the combination of both mechanical and neural feedback.

During legged locomotion, the primary requirement of a control strategy is to stabilize the body around a steady state pattern of foot and body movement (i.e., a stable gait). A periodic trajectory in the state space of the system (for example,

a periodic pattern of rotational, lateral, and fore-aft velocity of the CoM during a stride) can be considered a limit cycle. If the limit cycle is stable, after small perturbations, the trajectory will return to a steady state periodic trajectory. If the limit cycle is unstable, a small perturbation will lead the trajectory away from the periodic behavior (Full et al. 2002).

A dynamical systems framework for the nature of control differs from that suggested by simple reference trajectory planning. In a dynamical system's view of control, the limit cycle is a target of control determined by the mechanical properties of the animal. The rate of recovery from perturbations demands no preferred phase be restored following perturbation. In contrast, reference trajectory planning postulates that neural controllers command limbs to follow prescribed paths whose origin is unknown. Such control depends upon gains in neural feedback loops to maintain a fixed phase with respect to some internal or external reference.

Although it may be tempting to immediately address these alternatives in a particular experimental animal, the challenge is daunting. As Bernstein (1967) pointed out, neuromechanical systems are characterized by very high degrees of freedom. In a cockroach, for example, there are millions of neurons that may contribute to locomotion control (since it is a whole body movement that is rapidly responsive to environmental changes, and thus may engage most of the sensory, motor and interneuronal circuitry at times), there are two hundred and twenty muscles controlling the legs (Full and Ahn 1995), and there are forty two degrees of freedom in the exoskeleton that contribute to locomotion. Determining the torques or angles that give rise to particular forces or positions at the endpoint of the legs is an ill-posed problem because of the large numbers of degrees of freedom.

To understand systems with many degrees of freedom, the relationship between two types of models, "templates" and "anchors", can help lead to testable hypotheses (Full and Koditschek 1999). A "template" refers to the simplest model of the system behavior used as a target for control. We obtain the template from the biological system by trimming away complexity, collapsing the system's dimensionality. An "anchor" refers to a more representative model of the biological system of interest with its preferred posture (e.g., a cockroach). By adding legs, joints and muscles, a neuromechanical hypothesis can be tested at the desired level of detail.

The *template* for legged locomotion is a spring mass system (i.e., a bouncing pogo stick), subject to

control at the level of its CoM, and responsive, on a cycle-to-cycle basis, to changes in its CoM and that state of the world. Both mathematical and experimental studies have shown that there is a common pattern among two-legged (humans; Cavagna et al. 1977), four-legged (dog), six-legged (cockroach; Full and Tu 1990) and eight-legged running animals (crab; Blickhan and Full 1987), where the vertical force of the virtual leg spring (representing all the legs touching down) increases and fore-aft forces shift from deceleratory to acceleratory. When viewed as a spring mass template, the relative leg stiffness of diverse trotters, runners and hoppers is nearly constant over nearly five orders of magnitude of body mass (Blickhan and Full 1993). The *anchor* for legged locomotion is a sufficiently detailed model of the animal of interest at its preferred posture that allows exploration of the physical control at the leg or joint level to determine within cycle responses to perturbations of the CoM and limbs. Mechanical feedback from the viscoelastic properties of the musculoskeletal system, and joint torques produced by muscles activated by the controller can respond to perturbations restoring the preferred posture. Further evidence of an anchor and preferred posture that collapses to a template comes from a preliminary study of the posture of a cockroach running at its preferred speed. A 42 degree of freedom, rigid segment anchor can be used to model all the leg movements in joint space captured from high-speed video during steady-state running. Surprisingly, one principal component appears to explain nearly 80% of the motion. A simple, preferred posture with all joint angles linearly correlated could be used to characterize the insect's movements as it ran.

Mathematical models at both the template and anchor level have revealed the potential for a remarkable degree of self-stabilization arising from mechanical feedback in legged systems (Holmes et al. 2006). Direct experiments on rapid-running animals have supported these models (Jindrich and Full 2002; Spagna et al. 2007). Control of neuromechaincal systems appears to work with the natural dynamics of the body and limbs. These fundamental biological discoveries, in concert with their mathematical representations, inspired the design of two rapid-running legged robots (RHex; Altendorfer et al. 2000 and Sprawl; Cham et al. 2002). In turn, these robots are serving as physical models allowing manipulation of parameters more easily than in animals and complementing the mathematical models by being subject to real environmental challenges.

A similar approach has yielded deep insights into vertical running. Studies of cockroaches climbing on a glass bead surface (Goldman et al. 2006) and of geckos climbing on a smooth balsa surface (Autumn et al. 2006) have shown that they can move vertically at rates up to $50\,cm\,s^{-1}$ with stepping frequencies up to 15 Hz. The gecko is a four-legged vertebrate that uses van der Waals forces to attach to vertical surfaces, whereas the cockroach is a six-legged invertebrate that uses claws, pads and spines to attach. But both appear to use a similar underlying process: their feet pull down and towards the midline. Their front feet pull the head towards the wall, while their hind feet push away from the wall. This suggests a template for climbing (Goldman et al. 2006), and has served as the basis for creating a dynamic climbing robot (RiSE; Autumn et al. 2005).

Using the template and anchor approach, control architectures that integrate the nervous system with the musculoskeletal system can be tested (Fig. 20). One such architecture couples neural and mechanical oscillators. Feedforward CPGs modeled as first order oscillators can act via muscles and leg springs. Leg springs can be modeled as second order mechanical oscillators providing mechanical feedback through tuned visco-elastic structures. Preliminary support for this model comes from studies of cockroaches running over rough terrain (i.e., obstacles that may be as great as three times hip height) while measuring muscle action potentials (MAPs; Sponberg and Full 2005). No significant difference is apparent in the number of muscle action potentials or in the interspike interval distribution when rough terrain running is compared to running on flat terrain. The largest perturbations, such as complete missteps, do recruit reflex responses, and delay the feedforward CPG signal.

In addition to within cycle preflexes and reflexes that maintain posture while running, task level reflexes appear critical for controlling cycle-to-cycle behavior. To test how these interact with the CPG and mechanical system, senses for self-orientation and navigation can be explored. The role of the antenna of cockroaches is particularly well suited for study (Cowan et al. 2006). A template sensing neuromechancial model has revealed that proportional derivative (PD) feedback is required for stabilization and this was realized in a bio-inspired robot (i.e., SPRAWL) that navigated with a compliant antenna. Preliminary results measuring antennal nerve activity of cockroaches in a virtual turning device support the hypothesis of a phasic velocity response (Sponberg et al. 2006) consistent with PD feedback control.
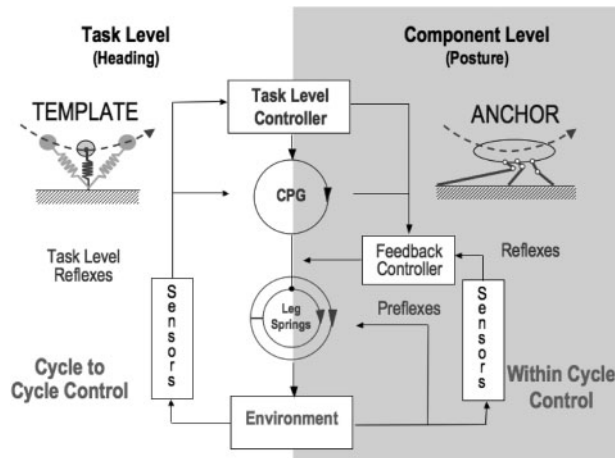
Fig. 20 Neuromechanical control architecture. Animals are modeled as two coupled oscillators. A hypothesized central pattern generator (CPG) is represented by a first order clock or neural oscillator (single circle icon). The musculo-skeletal system is represented by a mass-spring system, or a second order oscillator (double circle icon). A preferred posture of a more anchored or representative model is maintained within a cycle by mechanical feedback from preflexes and neural feedback. The task level navigation of a template or reduced model (e.g., a bouncing spring-mass system) is maintained from cycle to cycle by neural feedback from sensors such as eyes or antenna that adjust the CPG.

The next step is to test a variety of different neuromechanical control architectures for locomotion. Based on experience with successively more instrumented versions of the robot RHex and notions originating from neuronal coupled oscillators, Koditschek et al. (2004) proposed a plane of coordination architectures for controlling movement, which represents trade-offs between feedforward versus feedback control on one hand, and trade-offs between centralized versus decentralized control on the other. As internal signaling within the body runs up against bandwidth limitations—for example, in the face of fast movements or noisy sensors—feedback cannot be as effective and the mechanical system must be increasingly well tuned to its environment so that feedforward, decentralized controls can suffice. In contrast, when internal channels carry adequate data in a timely manner—for example, when the required movements are slower or when the required sensors are more accurate—then more centralized control that relies more heavily on feedback can confer greater stability. This perspective stimulates hypotheses that predict specific behavioral consequences from specific assumptions about the nature of a task and the environment within which it must be performed.

Discussion

Striated muscle is a remarkable material with an extremely high power density, which can be controlled by the nervous system and the contractile dynamics of the muscle itself. Muscles contribute to motor control by translating neural signals into mechanical outputs. In addition, the intrinsic properties of muscle contribute automatically and instantaneously to dynamic stability and control of movement. It is surprising that so little is known about the mechanisms within muscle that determine its mechanical function and intrinsic load-dependent properties during dynamic contractions.

The mechanics of sensors (exteroceptive and proprioceptive) and the neural circuits in which they are embedded affects the timing and dynamics of sensory input. Proprioceptive feedback requires unavoidable delays, reinforcing the importance of and need for automatic, instantaneous self-stabilizing properties of the muscles themselves.

Inevitable time delays are associated with all components of a sensorimotor system, from the sensors that provide information about the body and environment, to the central circuits that process sensory information and send commands to motor neurons, to the muscles that incur substantial lags in force development, and to the inertial and viscous forces that influence the emergent mechanical behavior of the whole organism. These lags may simplify or complicate control. A robust controller must account for *all* the delays that are incurred by the system during movement. Even for robots, tuning of central feedforward control to emergent body dynamics can sometimes be accomplished only by trial and error, or in other words "learning by experience" (Koditschek et al. 2004).

At the level of neuromechanics, the function of central networks is complex. The function of these networks depends upon the mechanical context in which the networks operate. In addition, due to interactions with intrinsic properties of the muscles, a change in frequency of network output may affect more than just the frequency of movement. It may also affect the force output and/or stiffness of the muscles. In this context, both naturally occurring mutants and recent developments in molecular biology provide exciting new tools for integrating studies of neurobiology and biomechanics.

The emergent mechanical behavior of the whole organism, its *collective output*, results from the interplay among brain, sense organs, muscles, and environment. Recent work suggests that feedforward

control may be more important for proximal segments, whereas feedback control may be more important for distal segments of the limbs. Unexpected perturbations are useful to investigate the roles of feedforward versus feedback and intrinsic control in stabilizing movement. Studies employing perturbation approaches to locomotion make clear that self-stabilizing force–velocity and force–length properties of muscles provide an important immediate control response for stabilization prior to feedback via neural reflexes. Neuromuscular control, thus, involves the ongoing dynamic interaction of intrinsic muscle properties with neurally mediated feedback to modulate motor behavior. Studies in soft tissue structures suggest that rapid switching among different behaviors may emerge from flexible coalitions of muscles whose functions may change in different mechanical contexts, controlled by neural circuitry that can rapidly reorganize to exploit these muscular coalitions by changes in phasing, duration and intensity of motor neuronal activation.

Neuromechanics can also inform studies in the fields of ecological morphology and evolutionary biology. The environment shapes the neuromechanics of movement through the processes of natural selection and adaptation. Interaction with the physical environment also influences the collective output of the neuromechanical system. Thus, physical properties of the environment must be considered and integrated into a unified view of motor control.

The field of robotics is naturally allied with neuromechanics. Biologically-inspired robots serve as hardware models for testing biological hypotheses, and principles of neuromechanics inspire the design of faster, more agile robots.

The idea that motor control is carried out by a single subsystem (i.e., the central nervous system) appears overly simplistic. All subsystems contribute to the emergent mechanical behavior of the organism (or robot) as a whole. Networks of interneurons are nevertheless adaptable elements that can be rapidly tuned to changing system parameters. Muscles also exhibit adaptability, albeit to a more limited degree and over a longer time scale than the nervous system. Parameters such as the mass distribution of the body tend to be even less adaptable, at least in adults. Ultimately, the properties of an animal's environment and the laws of physics represent fundamental constraints on the biomechanics of movement and, thus, must be considered to understand the properties of neural control circuits and neuromuscular design in general.

Directions for future work

Neuromechanics is a nascent field that offers many directions for future work. From the foregoing discussion, it is apparent that many questions remain. In the future, there is considerable need to understand what factors determine the mechanical roles that muscles play during movement, as well as what mechanisms confer key intrinsic self-stabilizing properties of muscle. In terms of central networks and sensory processing, systems-level integrative studies need to be performed to elucidate how cellular and network function underlies, and is tied to, emergent mechanics. At the systems level, we know relatively little about the processes through which network output is tuned to system constraints. These challenges of neuromechanical integration *cannot* be met within the domain of biology alone, even if biologists take a multi-level, multidimensional approach. They demand an *interdisciplinary* effort that includes mathematical modeling, numerical simulation, and physical modeling (i.e., robot operations), as well as continuing biological experimentation.

Acknowledgments

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