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TEMPLATES AND ANCHORS: NEUROMECHANICAL HYPOTHESES OF LEGGED LOCOMOTION ON LAND

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Abstract

Locomotion results from complex, high-dimensional, non-linear, dynamically coupled interactions between an organism and its environment. Fortunately, simple models we call templates have been and can be made to resolve the redundancy of multiple legs, joints and muscles by seeking synergies and symmetries. A template is the simplest model (least number of variables and parameters) that exhibits a targeted behavior. For example, diverse species that differ in skeletal type, leg number and posture run in a stable manner like sagittal- and horizontal-plane spring-mass systems. Templates suggest control strategies that can be tested against empirical data. Templates must be grounded in more detailed morphological and physiological models to ask specific questions about multiple legs, the joint torques that actuate them, the recruitment of muscles that produce those torques and the neural networks that activate the ensemble. We term these more elaborate models anchors. They introduce representations of specific biological details whose mechanism of coordination is of interest. Since mechanisms require controls, anchors incorporate specific hypotheses concerning the manner in which unnecessary motion or energy from legs, joints and muscles is removed, leaving behind the behavior of the body in the low-degree-of-freedom template. Locating the origin of control is a challenge because neural and mechanical systems are dynamically coupled and both play a role. The control of slow, variable-frequency locomotion appears to be dominated by the nervous system, whereas during rapid, rhythmic locomotion, the control may reside more within the mechanical system. Anchored templates of many legged, sprawled-postured animals suggest that passive, dynamic self-stabilization from a feedforward, tuned mechanical system can reject rapid perturbations and simplify control. Future progress would benefit from the creation of a field embracing comparative neuromechanics.

Keywords

locomotion, biomechanics, modeling, neurobiology, control

TEMPLATES AND ANCHORS: NEUROMECHANICAL HYPOTHESES OF LEGGED LOCOMOTION ON LAND

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Summary

Locomotion results from complex, high-dimensional, non-linear, dynamically coupled interactions between an organism and its environment. Fortunately, simple models we call templates have been and can be made to resolve the redundancy of multiple legs, joints and muscles by seeking synergies and symmetries. A template is the simplest model (least number of variables and parameters) that exhibits a targeted behavior. For example, diverse species that differ in skeletal type, leg number and posture run in a stable manner like sagittal- and horizontal-plane spring-mass systems. Templates suggest control strategies that can be tested against empirical data. Templates must be grounded in more detailed morphological and physiological models to ask specific questions about multiple legs, the joint torques that actuate them, the recruitment of muscles that produce those torques and the neural networks that activate the ensemble. We term these more elaborate models anchors. They introduce representations of specific biological details whose mechanism of coordination is of interest. Since

mechanisms require controls, anchors incorporate specific hypotheses concerning the manner in which unnecessary motion or energy from legs, joints and muscles is removed, leaving behind the behavior of the body in the low-degree-of-freedom template. Locating the origin of control is a challenge because neural and mechanical systems are dynamically coupled and both play a role. The control of slow, variable-frequency locomotion appears to be dominated by the nervous system, whereas during rapid, rhythmic locomotion, the control may reside more within the mechanical system. Anchored templates of many-legged, sprawled-postured animals suggest that passive, dynamic self-stabilization from a feedforward, tuned mechanical system can reject rapid perturbations and simplify control. Future progress would benefit from the creation of a field embracing comparative neuromechanics.

Key words: locomotion, biomechanics, modeling, neurobiology, control.

Introduction

This perspective outlines an interdisciplinary approach to the study of diverse, legged locomotor systems. In so doing, we briefly summarize current hypotheses, explore an approach for generating future models and advocate the creation of a field of comparative neuromechanics. For purposes of clarity, we distinguish between two types of dynamic models for locomotion in animals: templates and anchors (Fig. 1). A template is a pattern that describes and predicts the behavior of the body in pursuit of a goal. It is a model created by 'trimming away' all the incidental complexity of joints, muscles and neurons. A template is not only a simple model but also serves as a guide or target for the control of locomotion. Remarkably general behavior, such as the relative speed at a gait change, can be found by using a template on animals that differ in leg number, posture or skeletal type. Templates do not incorporate detailed mechanisms. Yet the diversity of nature's mechanisms is often the very focus of study, not a 'detail' to be removed. We also seek models of how legs,

joints, multiple muscles and neural networks work together to produce locomotion. Therefore, we define an anchor as a more realistic model fixed firmly or grounded in the morphology and physiology of an animal. An anchor is not only a more elaborate dynamic system, but must have embedded within it the behavior of its templates. Fundamental advances in understanding have been made using simple models of the body or isolated preparations of its parts. The next challenge is true integration. We contend that exploring such relationships as prevail between template and anchor will allow the generation of neuromechanical hypotheses that span levels of organization from neurons to whole-body locomotion.

Templates: addressing the challenge of a complex, redundant system

Contemporary natural and engineering science are unable to

specify the design plans to build a rapid-running, maneuverable animal such as an arthropod. Why? There are many reasons, but one is foremost. Locomotion results from complex, high-dimensional, non-linear, dynamically coupled interactions between an organism and its environment (Table 1; H₁). Biologists cannot simply borrow explanatory mechanisms from engineers and mathematicians. Appropriate models are available directly from eighteenth century classical mechanics (Arnold, 1989), but their fundamental intractability has been established for more than a century (Diacu and Holmes, 1996). Compounding the difficulties, multiple ion channels and receptors in each neuron, multiple neurons, multiple neuronal connections, multiple sensors, multiple muscles and numerous multi-joint appendages all operating in a time-varying environment complicate any analysis. Most generally, Bellman's (1957) curse of dimensionality could be no more apparent. The number of data points needed or the computational effort increases exponentially with the number of dimensions. In the strict engineering sense, animals appear to be over-built, or at least over-complete (Brown and Loeb, 1999), for the task of locomotion alone. Animals show kinematic redundancy for locomotion because they have far more joint degrees of freedom than their three body positions and three body orientations (i.e. six 'payload' dimensions). Animals show actuator redundancy for locomotion because they often have at least twice as many muscles as joint degrees of freedom. Animals show neuronal redundancy for locomotion because they have more participating interneurons than necessary to generate the observed motor neuron signals. An evolutionary approach to redundancy, complexity, safety factors and adaptation can be enormously revealing, but is outside the scope of this perspective (Lauder, 1996).

Creating a template using synergies and symmetries

One solution to the challenge of complexity is easy in principle, but difficult in practice. The curse of dimensionality may be broken by the introduction of a template – a formal reductive model that (1) encodes parsimoniously the motion of the body (i.e. a task termed 'payload' behavior) with respect to the minimum number of variables and parameters, and (2)

advances an intrinsic hypothesis concerning the high-level control strategy underlying the achievement of this task (Fig. 1). Alexander (1988, 1990, 1992, 1995) and others (Blickhan, 1989; Cavagna et al., 1977; McGeer, 1990; McMahan, 1990) have championed the power of a simple model in discovering the essential features of sagittal-plane, legged locomotion. Alexander (1984) asserted that, 'The advantage of such an approach is to reveal basic principles that do not depend on the fine details of body structure.' In the absence of a principled understanding of a simple model, no firm grasp of any more detailed model is likely. We will do well to view with due curiosity, but deep suspicion, the sort of complex and high-dimensional computational models that computing power allows. In some sense, the 10 000-state computer simulation of ion channels, nerves, muscles and skeletal parts is a less satisfactory model than the animal itself. The real data suffer from noise, but nonetheless contain valuable information. We argue that higher-dimensional anchors are indeed required to reveal how mechanisms work, but can best advance our understanding of neuromechanical integration when informed by an underlying template.

To create a template, redundancies in legged locomotion can be resolved in large part by searching for synergies and symmetries. By synergies, we mean the literal definition of parts working together in combined action or operation. Groups of neurons, muscles, joints and legs can work in concert as if they were one (see, for example, Full, 1993; Raasch et al., 1997; Raibert and Hodgins 1993). As early as 1935, Bernstein recognized the importance of embedded neuromotor synergies in reducing redundancy. By symmetry, we refer to the correspondence of parts on opposite sides of a plane through the body. For example, Cruse et al. (1995) have exploited bilateral and segmental symmetries to design a robust neuro-control model based on one leg of the stick insect. The design by Raibert et al. (1986) of two- and four-legged hopping robots was reduced in complexity because they capitalized on symmetries in their template. Recently, extensive use of symmetry greatly simplified the first horizontal-plane mechanical models of a many-legged runner (J. Schmitt and P. Holmes, in preparation; Kubow and Full, 1999).

Table 1. *Hypotheses of diverse, legged, locomotor systems*

H ₁ :	Locomotion results from complex, high-dimensional non-linear, dynamically coupled interactions between an organism and its environment
H ₂ :	Diverse species that differ in skeletal type, leg number and posture walk stably like sagittal-plane inverted-pendulum systems
H ₃ :	Diverse species that differ in skeletal type, leg number and posture run stably like sagittal-plane spring-mass systems
H ₄ :	Diverse species that differ in skeletal type, leg number and posture run stably like horizontal-plane, laterally directed, spring-mass systems
H ₅ :	Maneuvers require minor neuromechanical alterations to straight-ahead running
H ₆ :	Control strategy is dependent on the precision, rhythmicity and speed of locomotion
H ₇ :	Joints moments are minimized by ground reaction force vectors aligning along the leg axially
H ₈ :	Differential leg structure and function in sprawled-posture runners permits greater stability and maneuverability
H ₉ :	Passive, dynamic feedback from a 'tuned' mechanical system allows rapid response to perturbations and can simplify control
H ₁₀ :	Feedforward control, as opposed to continuous neural feedback, sets the basic patterns during rapid locomotion
H ₁₁ :	Neural feedback may function more in a state-event-dependent manner during rapid locomotion
H ₁₂ :	Distributed, reflexive mechanisms at the level of the muscle and skeleton can allow rejection of rapid perturbations and simplify control

In this perspective, we focus on versions of two templates, the spring-loaded inverted pendulum (SLIP) and the lateral leg spring (LLS; Fig. 1). After describing the tasks they encode, we will explore the control hypotheses they imply. Although simple, dynamic models of legged locomotion have proved to be valuable, construing them as templates implying specific high-level control hypotheses has received far less attention (McMahon, 1990; Raibert, 1986).

Evaluating a template by refutation

There are many different simple models that might be imposed upon the same underlying behavior, and it is incumbent upon a champion for any one or another to compare its relative efficacy. To this end, templates instill the conceptual advantages of simple models with the methodological imperatives of refutable hypotheses. Articulating the distinct control strategy any one of them prescribes addresses the natural question as to how they might be compared with each other. In general, templates yield empirically refutable hypotheses, and their relative ability to withstand the light of data represents the primary means of discriminating efficacy.

Walking by vaulting – inverted pendulum template

The mechanics of walking in bipeds and quadrupeds has been characterized by a template referred to as the inverted pendulum (Cavagna et al., 1977). This model is simple, consisting of only a point mass atop a stiff rod, yet capably represents the underlying task of translating an animal's center of mass – the 'payload' of locomotion behaviors. The model has just one degree of freedom and can serve as an anchor to no lower-dimensional mechanical behaviors. It is a candidate template because it has both prescriptive as well as descriptive power (Fig. 1). For example, it predicts that kinetic energy will be exchanged with potential energy as the body vaults over a stiff leg. As much as 70% of the energy that would otherwise be supplied by muscles can be conserved by this mechanism in humans, birds and dogs. Blickhan and Full (1987) showed the model to be general and not restricted to systems with upright postures when they discovered that eight-legged crabs employ four distributed pendulums which function simultaneously as one (Table 1; H₂). Farley and Ko (1997) found 51% energy exchange in sprawled-posture walking lizards. Interpreting even more literally its prescriptive aspect, McGeer (1990), inspired by the double and triple pendula of Mochon and McMahon (1980), built a novel family of bipedal robots that walk in a stable manner down slight inclines without assistance from sensors, actuators or any computer control.

Given its simple and prescriptive form, the inverted pendulum template enjoys the further virtue of supporting specific predictions about the details of body movement that can be refuted by data. For example, Lee and Farley (1998) have recently shown that the motion of the center of mass in human walking departs significantly enough from the trajectories of the inverted pendulum template that it is unlikely

to be a literal control target for the musculo-skeletal system. Similarly, Full and Tu (1990, 1991) found no evidence for the use of the inverted pendulum mechanism in insects.

Running by bouncing – spring-loaded inverted pendulum template

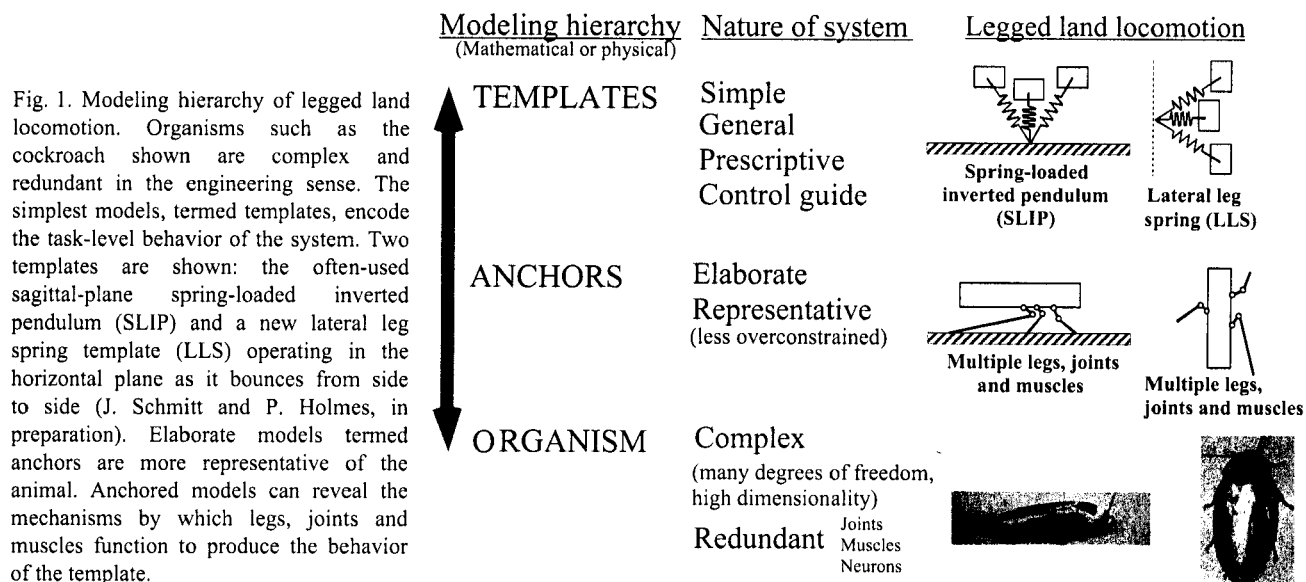
Diverse species that differ in skeletal type, leg number and posture run in a stable manner like the sagittal-plane spring-mass system (Table 1; H₃; for references, see Full and Farley, 1999) depicted in Fig. 1 that we call the spring-loaded inverted pendulum (SLIP). In humans, dogs, lizards, crabs, cockroaches and even centipedes, the center of mass falls to its lowest position at midstance as if compressing a virtual leg spring and rebounds during the second half of the step as if recovering stored elastic strain energy. The virtual leg spring of insects consists of a tripod of legs on the ground simultaneously working as if they were one leg of a biped or two legs of a trotting quadruped (Full and Tu, 1990, 1991). Relative leg stiffness is surprisingly similar in six-legged trotters (cockroaches), four-legged trotters (dogs, rams), two-legged runners (humans, birds) and two-legged hoppers (kangaroos; Blickhan and Full, 1993).

This simple model of running was used as a template by Raibert and colleagues (Raibert, 1986), who built spectacularly successful running machines in the form of physical pogo sticks actuated by air-springs and stabilized by controllers that managed appropriately the total mechanical energy of the center of mass. In the light of this example, it is natural to inquire whether the SLIP is merely a descriptive simple model or represents a true template for animal locomotion in the sagittal plane. Preliminary numerical study (Schwind, 1998) suggests the latter. Namely, when the Lagrangian equations of motion of the SLIP model are fitted to center-of-mass trajectories from human runners, appropriately calibrated spring laws yield surprisingly accurate cross-validation predictions. Much more extensive study of this kind across various animal species will be required before refuting the general conclusion that the SLIP is a template for steady-state animal running in the sagittal plane.

Running by ricocheting – lateral leg spring template

J. Schmitt and P. Holmes (in preparation) developed a three-degrees-of-freedom model analogous to the sagittal-plane SLIP, but with the spring compressed along a leg placed laterally in the horizontal plane (Fig. 1). The lateral leg spring (LLS) represents the behavior of one or more legs and is flung out ahead of the center of mass as the body bounces from side to side. The LLS model has three degrees of freedom, adding body yaw to the planar translations of the center of mass, because maneuvers such as turning entail the coordination of a body's orientation with its heading (i.e. the direction of the center of mass velocity vector).

The LLS is energetically passive in the sense that the leg spring is governed by Hooke's law. The body motion arises from the rigid body mechanics of the compression and decompression phases of the leg as it swings freely around a



fixed ground contact point located in a fixed manner relative to the body frame at the beginning of each new stance phase. The model is actively controlled by state-event feedback, taking the form of a signal for the leg to release its ground contact point and instantaneously to change sides to the next contact point exactly when the decompressing spring has recovered its original rest length. Surprisingly, despite the absence of any modeled energy losses, J. Schmitt and P. Holmes (in preparation) show that, when the LLS is attached to the body behind the center of mass, the mechanics of the model produces stability in both heading and body orientation. No equivalent of continuous neural feedback is required to respond to a perturbation.

The LLS appears to be a candidate template because it is not merely simple but hypothesizes a high-level control policy for the virtual leg whose resulting dynamics exhibits behavior qualitatively consistent with biological measurements. For example, ground reaction forces and translational velocities predicted by the LLS are consistent with data on sprawled-posture runners such as cockroaches (Full and Tu, 1990). Perhaps, diverse species that differ in skeletal type, leg number and posture run in a stable manner like horizontal-plane, laterally directed, spring-mass systems (Table 1; H4). Direct fitting to measured center-of-mass trajectories of the Lagrangian equations for the LLS model will either refute its utility or reinforce the suggestion that it is a literal control target for running in the horizontal plane.

If the LLS model plays the role of a template, it should be general enough to admit virtual control policies that achieve maneuvers. Turning, for example, requires that the animal's heading must be deflected and the body axis rotated to match the heading. The degree of deflection in heading is proportional to the magnitude of the laterally directed impulse from a single virtual leg and inversely related to the body's forward momentum. Jindrich and Full (1999) found

that a single virtual leg's effectiveness at generating a turn was a function of the leg's placement. A leg placed laterally just ahead of the center of mass requires no fore-aft component to align the body axis with the heading. A leg placed closer to the body and well behind the center of mass requires large fore-aft forces to align the body axis with the heading. J. Schmitt and P. Holmes (in preparation) have found that the LLS can generate turns by adjusting leg stiffness, leg length, touchdown angle or the leg attachment position. If the leg attachment point is briefly moved ahead of the center of mass, the template is destabilized and turns. The change of the leg attachment point is analogous to a shift in the center of pressure. We hypothesize that maneuvers in general may require minor neuromechanical alterations to straight-ahead running (Table 1; H5).

Anchors: addressing the need for neuromechanics

Anchors reveal mechanisms

Templates define the behavior of the body that serves as a target for control. But, by their very purpose, they cannot provide causal explanations of detailed neural and musculo-skeletal mechanisms (Fig. 2). This requires the elaboration of minimal models into progressively more morphologically and physiologically grounded details. One can only introduce neurons into a muscle group; one can only introduce muscle groups into a joint; one can only introduce joints into a leg.

Anchors are elaborated models with greater complexity than templates. Anchors afford a more faithful correspondence to the animal's structure and function and are a useful point of departure if we are to reveal the mechanisms that give rise to the template behavior. Even the simplest anchors encourage integrative hypotheses of joint, musculo-skeletal and nervous system function. The lack of synthetic, anchored models in comparative biomechanics is striking. Isolated system

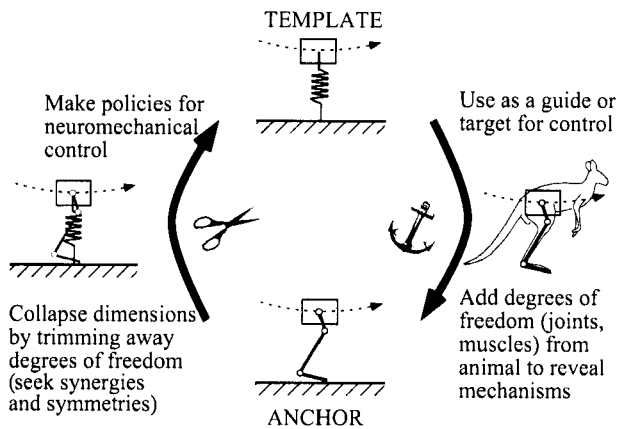


Fig. 2. Relationship between the template and anchor. A template is a pattern that describes and predicts the behavior of the body in pursuit of a goal. A template, such as the simple pogo stick or spring-loaded inverted pendulum (SLIP) shown here, serves as a guide or target for the control of locomotion. Since we also seek models of how legs, joints, multiple muscles and neural networks work together to produce locomotion, we can also add degrees of freedom to better represent the animal of interest such as a kangaroo. The resulting anchor is a more realistic model fixed firmly or grounded in the morphology and physiology of an animal. An anchor is not only a more elaborate dynamic system, but must have embedded within it the behavior of its template. A template is created by 'trimming away' all the incidental complexity of joints, muscles and neurons. Using this process, we can hypothesize new neuromechanical control policies that span levels of organization. The relationship between template and anchor offers a specific solution to Bernstein's (1935) 'degrees of freedom problem' by advancing a specific hypothesis concerning the manner in which the template's behavior emerges from the morphological and physiological details. The anchor's 'lower-level' within-stride control policy actuates the ankle, knee and hip joints to 'trim' the motion of its mass center down to that of a SLIP. The 'higher-level' stride-to-stride control policy regulates the task-level behavior of the template, such as fore-aft speed, hopping height or duty factor, essentially 'driving' the virtual SLIP. Such specific models of hierarchical control generate empirically refutable hypotheses.

function, albeit now in more natural regimes, is still the rule. Templates should be anchored so as to reveal underlying mechanisms. These mechanisms represent the channels along which neuromechanical integration can be attempted. We now assess the difficulties in this undertaking, introduce the notion of an anchor as a specific grounding hypothesis and explore its utility in reducing these difficulties.

Mechanisms require control

In proceeding from the animal as a body or point mass to one with jointed legs, we confront immediately Bernstein's historical (1935) 'degrees of freedom problem'. The musculo-skeletal system has many degrees of freedom, even if it is simplified to a linkage of rigid bodies. Locomotion entails coordinating these many degrees of freedom, meaning that the system restricts itself to a low-dimensional subset of its high-

dimensional space of possible motions, presumably in different ways when coordinating different behaviors. In other words, there is a 'collapse of dimension' that occurs in regulating locomotion. It is the job of the integrative biologist to hypothesize empirically refutable control strategies that can achieve this simplification. We believe the most direct path towards such hypotheses begins with a view of empirically unrefuted templates (of the kind described above) as literal control targets, and then seeks specific control principles that will suffice to embed them in the surrounding mechanism. Identifying and analyzing the control activity that achieves this coordination cannot fail to shed some light upon the manner in which the nervous system and the musculo-skeletal system interact. At the very least, understanding the coordination of the elaborated mechanical system in expressing template behavior should produce prescriptions of the form 'the nervous system must at least be doing ...' or, contrarily, proscriptions of the form 'the nervous system could not possibly be doing ...'

Anchors – a strategy for embedding templates in elaborated models

The coordinated recruitment of high-degree-of-freedom physiological mechanisms into the low-degree-of-freedom mechanical template requires significant control activity. Raibert's (1986) work first showed that one might organize quadrupedal locomotion with reference to a single virtual leg conceived as a SLIP. Later, he introduced an ankle joint into the model to produce a one-legged hopping robot, a monoroo. Recently, Saranli et al. (1998) have proposed algorithms that coordinate the running of an ankle-, knee- and hip-actuated monopod by reference to a virtual SLIP. The resulting controller takes high-level control commands, such as desired speed, hopping height and duty factor, for a SLIP and produces joint torques that force the center of mass of the ankle, knee and hip monopod to behave in the prescribed (lower degree of freedom) manner.

In all these cases, the actual morphological details comprising degrees of freedom 'redundant' for the task are 'trimmed away' by a controller under whose influence there emerges a virtual mechanism (Fig. 2). This mechanism is modeled by the dynamics of a template. The template has just enough complexity to encode the task of maneuvering the payload – the body center of mass for running – and no more. The remaining degrees of freedom are used simply to anchor the maneuver in a particular complement of mechanical hardware. We will say that a more complex dynamic system is an 'anchor' for a simpler dynamic system if (1) motions in its high-dimensional space 'collapse' down to a copy of the lower-dimensional space of motions exhibited by the simpler system and (2) the behavior of the complex system mimics or duplicates that of the simpler system when operating in the relevant (reduced-dimensional copy of) motion space. Thus, although Raibert's (1986) quadruped has an entirely different morphology from the ankle-knee-hip monopod, both can serve as anchors for the SLIP template. In other words, these anchors can be endowed with controllers that, within any

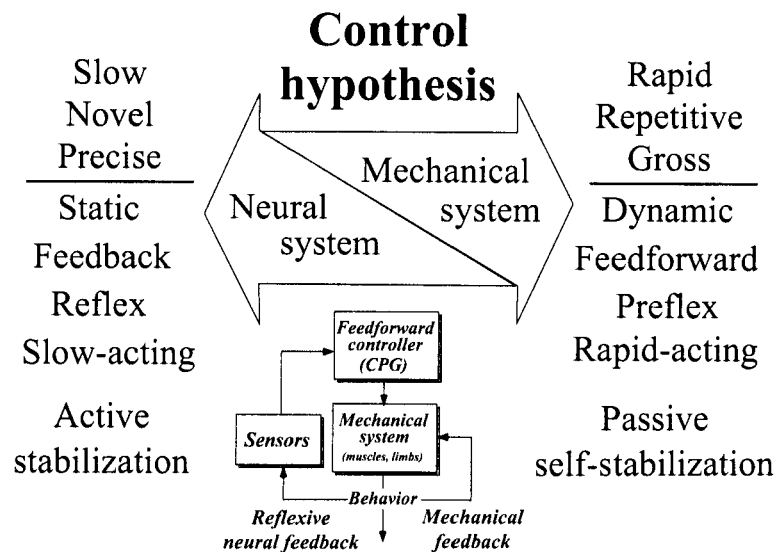


Fig. 3. Neuromechanical control hypothesis. Control may be task- or intensity-dependent. The left side of the figure shows traditional neural control by way of negative feedback during slow, variable-frequency activity. The right side of the figure emphasizes the role of control in a tuned mechanical system operating during rapid, rhythmic activity. CPG, central pattern generator.

single stride, attempt to remove the unnecessary energy or motion from all the legs and joints until they carry the center of mass in such a fashion as to coincide with motion of the SLIP template. From the view of the high-level locomotion task, only the SLIP needs to be controlled from stride to stride once the template is anchored and has a lower-level control policy for the redundant degrees of freedom.

If, when analyzing animal motion data, we are unable to refute a particular template using the evaluation procedures described above, then it becomes tempting to speculate that the template serves as a literal control target. It becomes tempting, in turn, to view the animal's complex body and limb morphology as an anchor for that template. For adopting a template fixes the control target but does not settle the issue of how the various sensors and actuators at the animal's disposal are to be recruited to achieve it. The notion of an anchor represents a specific approach to doing so that may be refuted by careful study of the animal's joint torque control strategies. Since these are governed by the forces exerted in the various muscle groups and the latter, in turn, are recruited by the motor neuron activation patterns, the refutation of an anchor represents the beginning of an inquiry starting from the animal's outside and heading inwards.

Work by Farley and colleagues gives an example of how starting with a template for hopping can lead to very specific hypotheses about which muscles are involved in control. They have discovered that humans accommodate softer surfaces (Farley et al., 1998) or hop higher (Farley and Morgenroth, 1999) by increasing their leg stiffness. Because of the mechanical operation of the leg, overall leg stiffness is most sensitive to changes in ankle stiffness, although it is also sensitive to changes in limb configuration at the instant of foot contact. In both cases, humans alter their leg stiffness by modulating their ankle stiffness. We clearly require an approach that capitalizes on the notion of a template to inform us of where in the animal control originates.

The role of the neural versus mechanical system in control

The role of control has been traditionally reserved for the nervous system. Yet, developing control policies for an anchor will be most effective if we use the mechanical behavior of the template as a guide. Raibert and Hodgins (1993) stated, 'Many researchers in neural motor control think of the nervous system as a source of commands that are issued to the body as direct orders. We believe that the mechanical system has a mind of its own, governed by the physical structure and laws of physics. Rather than issuing commands, the nervous system can only make suggestions which are reconciled with the physics of the system and task [at hand].' Since neural and mechanical systems are dynamically coupled, we must rethink what exactly is being controlled and where the control originates.

Despite pioneering neurobiological research, particularly on arthropods (for reviews, see Wilson, 1966; Graham, 1985; Pearson, 1993; Burrows, 1996; Delcomyn, 1985; Cruse, 1990) as well as in applied dynamic systems theory (Beer, 1995; Collins and Stewart, 1993; Golubitsky et al., 1998), no complete integration of neural and mechanical systems for legged locomotion has occurred (Chiel and Beer, 1997). The reasons are numerous. One major complication is that neural and mechanical phenomena occur at disparate spatial (micro to macro) and temporal scales. Electrophysiological recordings have been made on larger arthropods such as stick insects, locusts, lobsters, crayfish and crabs. Most of these species are very slow locomotors. The nature of the control strategy appears to depend on the precision, rhythmicity and speed of the locomotion task (Table 1; H_6). During slow, variable-frequency locomotion tasks requiring precise stepping, the nervous system probably dominates control by way of continuous feedback (Fig. 3). The effects of the mechanical system beyond what can be approximated by statics are negligible. The dynamics of the mechanical system most probably begins to dominate at intermediate and fast speeds. In general, examining near-

maximal performance can often give more clues to life's design than looking at submaximal performance. Study of more rapid rates of locomotion could hint at design limitations. More specifically relevant to the argument of this perspective, dynamically dexterous animals appear to operate in a regime significantly constrained by physical mechanics.

Feedforward controller with 'mechanical feedback' through morphology

Kubow and Full (1999) explored the advantages and disadvantages of a many-legged, sprawled-posture morphology as opposed to a bipedal or quadrupedal upright stance by producing a feedforward, horizontal-plane model for hexapod running. The ground reaction force patterns of each leg in bipedal runners and quadrupedal trotters are similar. The patterns can differ markedly in many-legged, sprawled-posture morphologies. In insects, the front pair of legs decelerate the insect only during the stance phase, while at the same time the hind pair of legs only accelerate the animal forward. The middle pair of legs first decelerate and then accelerate the body during a step. Large lateral forces have been measured (Full et al., 1991). Despite legs seeming to work against one another, joint moments are minimized by ground reaction force vectors aligning axially along the leg. (Table 1; H₇; Full et al., 1991; Full, 1993). Perhaps, differential leg structure and function in sprawled-posture runners permits greater stability and maneuverability in the horizontal plane (Table 1; H₈). The Kubow and Full (1999) dynamic, cockroach model prescribes leg forces using a feedforward clock analogous to a central pattern generator with no equivalent of neural feedback among any of the components. Surprisingly, the model runs in a stable manner at the animal's preferred speed, rejecting artificially imposed perturbations! The model self-stabilizes. Perturbations alter the translation and/or rotation of the body which, consequently, provides 'mechanical feedback' by altering leg moment arms. In a sense, control algorithms are embedded in the morphology itself. Passive, dynamic feedback from a 'tuned' mechanical system may allow rapid response to perturbations and can simplify control (Table 1; H₉). Feedforward control, as opposed to continuous neural feedback, can set the basic patterns during rapid locomotion (Table 1; H₁₀; Fig. 3). The use of a feedforward clock with mechanical feedback does not exclude an important role for neural feedback in rapid locomotion. However, neural feedback may function more in a state-event-dependent manner (e.g. to signal stance or swing phase) than continuously during rapid locomotion, much as in the LLS template (Table 1; H₁₁). Almost certainly, neural control models of rapid running that do not account for and take advantage of the natural dynamics of the system will be inadequate.

Prelexes

In addition to leg geometry and the properties of the skeleton, musculo-skeletal complexes can play a role in control. Typically, muscles are thought to respond to perturbations by way of active neural reflexes. However, during rapid locomotion, response time is shortened. A more immediate response, before the reflex,

results from the muscle's intrinsic force-length and force-velocity properties. Brown and Loeb (1999) have termed this zero-delay response a 'prelex' (Fig. 3). The mechanical impedances from the stiffness and viscosity of rhythmically active (not neurally reactive) muscle can generate large, immediate restoring forces. Distributed, prelexive mechanisms at the level of the muscle can allow rejection of rapid perturbations and simplify control (Table 1; H₁₂). Unfortunately, the characterization of rapid disturbance rejection during cyclic locomotion that can be directly related to leg or whole-animal perturbations is lacking and should be an active area of investigation critical to the understanding of control and stability.

The time for integration through collaboration

Whether control is asserted *via* mechanical design or *via* neural coordination or almost certainly by some interlocking shared principle, what emerges from these models is the image of the animal 'throwing its motion into the hands of the mechanical template' while merely 'tuning up' the redundant degrees of freedom around the stereotyped posture that supports the template motion. A goal of neuromechanics should be to demonstrate theoretically and attempt to refute empirically such specific hypotheses concerning the collapse of dimension of an anchor down to its template under the animal's control policy.

More specifically, the voluminous kinematic data that can now be collected on particular species should be analyzed with an effort to produce an anchor. Force-platform data should be used to create and test templates. Those proposing templates should look more towards mechanism and suggest anchors. Biomechanics and neurobiologists should suggest more global control policies using a template as a guide. However, to understand how diverse, legged animals locomote on land, a field of comparative neuromechanics must be created that truly integrates both disciplines. This is essential, but not sufficient. To the neurobiologists and biomechanists, we must add engineers and mathematicians. Integration among disciplines and unprecedented collaboration are required if we are to explain complex, non-linear, dynamically coupled interactions between an organism and its environment.

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