

Towards Testable Neuromechanical Control Architectures for Running

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Introduction

Our objective is to provide experimentalists with neuromechanical control hypotheses that can be tested with kinematic data sets. To illustrate the approach, we select legged animals responding to perturbations during running. In the following sections, we briefly outline our dynamical systems approach, state our over-arching hypotheses, define four neuromechanical control architectures (NCAs) and conclude by proposing a series of perturbation experiments that can begin to identify the simplest architecture that best represents an animal's controller.

From Description to Prescription of Motor Control

Descriptive neuromechanical studies of the last decade have achieved a broad consensus that Bernstein's (Bernstein, 1967) "degrees of freedom" problem finds its resolution in a hierarchy of coordinated synergies. There is widespread biomechanical evidence of kinematic reduction in a diversity of mammalian motor patterns such as reaching (Lacquaniti et al., 1983), body segment coordination (Balasubramaniam and Turvey, 2004), and walking (Grasso et al., 2000; Ivanenko et al., 2002). Similarly, dynamical motor behaviors offer longstanding (Blickhan and Full, 1993) and accumulating (Full and Farley 2000) evidence for collapse of dimension in vertebrate and invertebrate running and, more recently, climbing (Goldman et al., 2006). Discoveries from vertebrate (Burke, 1999, 2002; Saltiel et al., 2001) and invertebrate (Pearson, 1993) neuroscience suggest that neural activation results in precise, kinematically selective synergies of muscle activation. A consensus view has emerged for a hierarchical description of animal motion control architecture in which a modular (Mussa-Ivaldi, 1999) complex of motor functions combines distributed (Burke, 1999) feedforward

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pattern generating units (Grillner, 1985) mediated by local feedback (Pearson, 1995) with influence from, rather than domination by conventionally posited “higher” centers of function (Bizzi et al., 1989).

The next challenge in motor science is to move from this broad consensus regarding description to the point of prescription. This latter term denotes computational models that might tie the widely accepted accounts of biological structure to their function in the production of empirical motor behavior, thereby producing testable predictions of motor control architecture. Our use of the term “architecture” underscores our larger interest in how the components of motor control are put together under various circumstances. The descriptive consensus supporting a modular hierarchy encourages the expectation that this should now be possible. Namely, prescriptive computational models capable of accounting for a diverse variety of animal activity ought to incorporate some hierarchical decomposition into motor primitives (Schaal and Schweighofer, 2005).

In the contemporary literature such models take divergent form and seem to vary widely even concerning their scope. For example, several decades of advances in the primate reaching and grasping literature have achieved the textbook (Shadmehr and Wise, 2005) consensus that a kinematic task-oriented reference trajectory “leads” the compliant musculoskeletal system through a representative motion around which the necessary stabilizing torques and forces are generated at the joint level. However, elements of controversy (Jaric and Latash, 2000) still surround the extent to which such feedforward signals (Domen et al., 1999) are “pre-processed” by the nervous system using learned internal models to compute the inverse dynamics (Kawato, 1999) as would be required to insure asymptotically exact tracking in the equivalent rigid body mechanism and as observed in humans (Hinder and Milner, 2003). Moreover, the very question of how such a library of feedforward signals is constructed, deployed, and potentially mediated by the animal’s immediate or longer term mechanical experience remains uncertain.

In reaching tasks, the endpoints of the reference trajectory are presumably driven by perception. Various optimality criteria have been proposed to explain how the resulting interpolating curve is constructed (Biess et al., 2006; Nakano et al., 1999; Todorov and Jordan, 1998). Within this framework, the tradeoffs between feedforward and feedback influences can be determined by stochastic optimal control theory (Kording and Wolpert, 2006; Kuo, 2002). Recent evidence (Schaal et al., 2004) suggests that such discrete motor acts may be initiated and organized differently from rhythmic behaviors such as steady running.

It is worth noting that notions of optimality do not always offer broad prescriptive power. For example, the composition of optimal trajectories is typically not optimal. The appeal to optimality may confound the development of more fundamental compositional principles. For example, arguments for the “power law” (Richardson and Flash, 2002; Todorov and Jordan, 1998), and, more particularly, that the observed episodic power law trajectories constitute the

alphabet of a “motor language” have been shown to be equally well explained as artifacts of nonlinear kinematics (Schall and Sternad, 2001; Sternad and Schaal, 1999).

In contrast, we find the framework of dynamical systems particularly attractive because it permits a malleable but precise means of exploring the composition of modules respecting both their spatial arrangement and temporal sequencing. Dynamical representations of mechanical modules are familiar, and the utility of “collapsed” abstractions of such models has a growing tradition in biomechanics (Blickhan, 1989; Full and Koditschek, 1999) and robotics (Koditschek and Bühler, 1991; Raibert, 1986) – a bouncing spring mass system being one such model or template. Physiologically meaningful dynamical models of neurons (Hodgkin and Huxley, 1952) can be reduced to two (Fitzhugh, 1961; Morris and Lecar, 1981) or three (Ghigliazza and Holmes, 2004b) dimensional dynamical systems in principled ways that retain the salient physiological dependencies with very few lumped parameters. In turn, these can be assembled as physiologically representative (Pearson, 1976) modules, in a network of coupled oscillators that admits further mathematically principled reduction in dimension via phase variables (Ghigliazza and Holmes, 2004a).

Dynamical Systems Approach to Neuromechanics

Adopting a dynamical systems approach to the study of steady state rhythmic activities such as running has led to several general hypotheses regarding the structure of neuromechanical control (Koditschek et al., 2004). For ease of exposition we state these hypotheses within the framework of deterministic dynamical systems theory, although it is clear that a far more subtle treatment of the inevitable variability in real data, for example along the lines presented in (Riley and Turvey, 2002), would be required to handle the results of physical experimentation.

Hypothesis H_1 – Dynamic Stability

We have proposed that the primary requirement of an animal’s neuromechanical control strategy is to stabilize its motion around orbits or limit cycles – periodic solutions to the equations of motion describing the animal coupled to its environment in whose neighborhood there are no other periodic solutions (Full et al., 2002). In a dynamical systems’ sense, stability can be defined as the tendency of a system to return to a steady state even when perturbed. Perturbations shift the state onto nearby trajectories that are either stable (lead back toward the limit cycle) or unstable (lead away from it). For a locomotor behavior to be effective, the limit cycle must be locally stable and the motion must return to the limit cycle after all sufficiently small perturbations.

Typically, dynamical systems models predict that perturbations to mechanical state variables (positions and velocities) will differ in rate of recovery, be coupled, and will reveal systematic shifts in the relative timing of limb coordination.

Hypothesis H_2 – Collapse of Dimensions

We have proposed that multiple legs, joints and muscles operate synergistically to reduce the number of dimensions permitting the limit cycle to be represented by a simple, low dimensional template (Full and Koditschek, 1999) dynamical system (see Fig. 1). The relationship between the low dimensional template and the higher dimensional anchor models that are more closely tied to the animal's morphology is via a posture principle. The posture principle states that each behavior has a characteristic family of body postures associated with it, and that through maintaining the body in these postures the animal forces the high dimensional anchor dynamics to closely follow those of a lower dimensional template. For example, many animals with diverse morphologies and varying number of legs run in a way that moves the center of mass as though it is bouncing on a single elastic pogo-stick (Blickhan and Full, 1993) (Fig. 1).

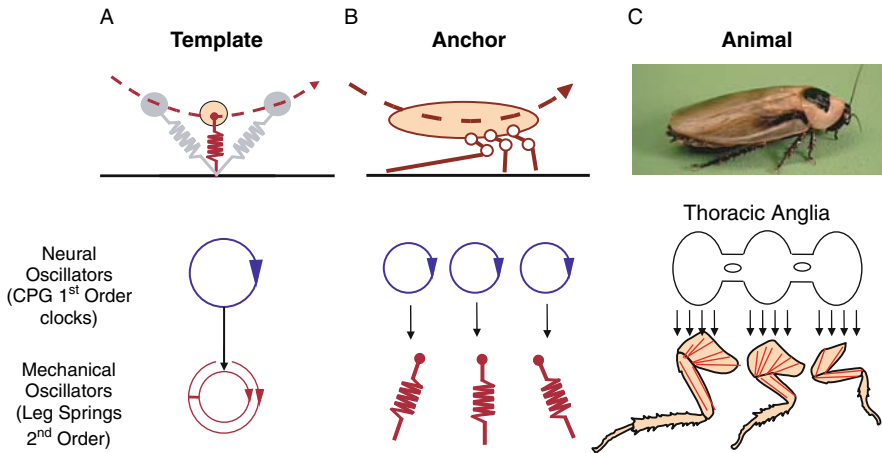


Fig. 1 Representation of animal locomotion as coupled oscillators. Systems are modeled by using two different types of oscillators. The hypothesized thoracic ganglion central pattern generators in arthropods are represented by first order clocks or oscillators (single circles). The musculo-skeletal system is represented by mass-spring systems or second order oscillators. We represent this second order property of a mechanical degree of freedom by means of the double circle icon. **A Template.** The model with fewest parameters is termed the template. **B Anchor.** A model more representative of the animal, the anchor, shows the coupling of three neural and mechanical oscillators. **C Animal.** A modified form of this figure appeared in (Koditschek et al., 2004)

Hypothesis H_3 – Tunable Coordination Control Architecture

We have hypothesized the presence of a tunable coordination control architecture that couples together an “internal” clock or central pattern generator (CPG), whose period is directly controllable, and the rhythmically oscillating mechanical system of the animal’s body, whose period is only controllable indirectly by adding or removing energy. Following the example of (Cohen et al., 1982), we represent the CPGs in animal’s nerve cord as first order oscillators in phase coordinates on the circle. A first order system cannot oscillate without some switching controller unless its state lies on a circle (Winfree, 1980). Because frequency is the control input to the system, we denote a first order oscillator by a single circle (blue circles with an arrow; Fig. 1). We represent an animal’s musculoskeletal system as a body mass atop a leg spring. These mechanical systems function as second order oscillators that have a phase velocity (frequency) altered generally through the intermediary of a power input changing its energy. We represent this second order property of a mechanical degree of freedom by means of the double circle icon (double red circles with arrows; Fig. 1).

The coupling of a neuro-oscillator with a mechanical oscillator substantially reduces the number of feedforward signals required for motion. Paradigms such as Equilibrium Point Trajectory and adaptive inverse dynamics internal models, are yet to explain the construction and organization of the library of feedforward signals necessary for each movement. In a coupled oscillator model, feedforward reference signals arise as the output of a dynamical system – a neural pattern generator equivalent to an explicitly parametrized “library” of trajectories – whose “entries” are parametrized by the dynamical system’s state space or initial condition. Each different initial condition gives rise to a different reference trajectory. Yet, *no independent library of particular trajectories* is stored.

Even more importantly for our present purposes, a dynamical representation of the driving signal or neural clock is not only amenable to hypotheses related to motor “learning” but to the possibility of more immediate influences back from the musculoskeletal system up to the internal clock. Whether modified more or less by feedback a purely feedforward signal generator cannot readily change the timing of events. In contrast, expressing our internal command generator as a clock allows the possibility that the mechanical subsystem might retard or advance its phase. By embracing a dynamical representation of the internal reference signal generator, we will explore in this chapter the extent to which relatively simple mechanical perturbations of an animal’s gait can be used to probe the presence and nature of such feedback influences upon an internal pattern generator by the physical experience of the musculoskeletal system.

The Neuromechanical “Operating Point”

Within a coupled oscillator framework, we adopt the classification of (Klavins et al., 2002; Koditschek et al., 2004), organizing the range of variation of

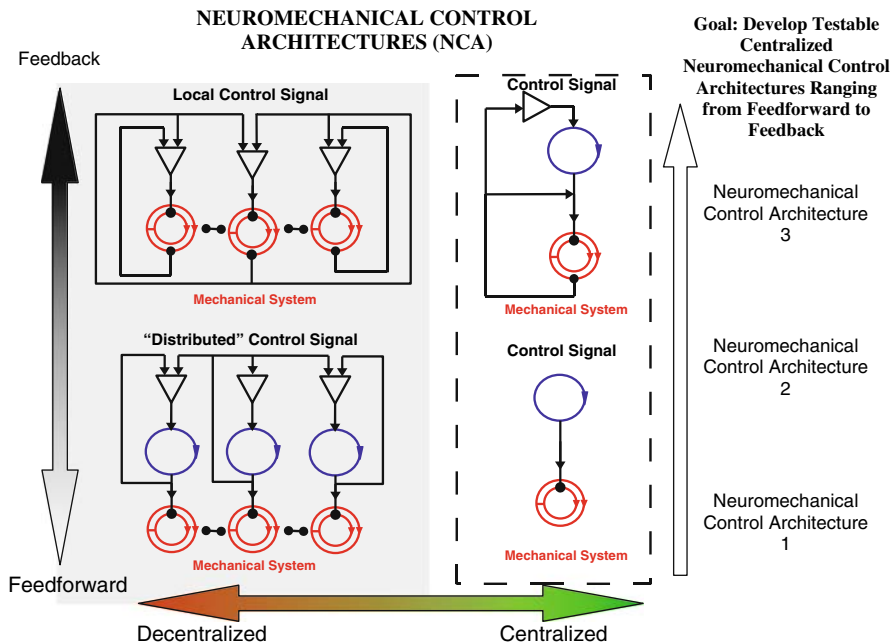


Fig. 2 Neuromechanical control architectures (NCAs) can be classified by broad properties that include the degree of centralization and the extent feedback information can affect the feedforward signals the controller produces. In this chapter we describe three control architectures with a central pattern generator that utilize increasing levels of feedback processing (as indicated by the white arrow) and compare them with an architecture NCA0 that has no CPG

neuromechanical control models into a plane of designs (Fig. 2) available for selection by the animal’s nervous system. We posit that the choice of operating point in this plane selects the coordination coupling the dynamics of internal neural oscillator and musculoskeletal force production. The axes of this plane can be characterized by the balance between feed-forward and feedback control, and the degree of centralization of the information flow.

No single operating point in the plane seems to characterize exclusively the behavior of any animal model. For example, at the more extreme “feedback, decentralized quadrant” of the two axis design plane (Fig. 2) lie decades of careful empirical study on invertebrate walking (Cruse, 1990) that have yielded algorithmic prescriptions less familiar to optimal control theory, but readily studied using the tools of dynamical systems theory (Calvitti and Beer, 2000; Klavins et al., 2002) and demonstrably capable of coordinating complex multi-limbed locomotion in physical (Chiel et al., 1992) models operating in the quasi-static regime. Yet recent experiments have identified (Büschges and El-Manria, 1998) and simulation studies confirmed the important role of feedforward pattern generators in the walking behavior of this animal model (Ekeberg et al., 2004). In contrast, early models of rhythmic vertebrate behavior suggested the prominence of a strongly centralized

feedforward CPG signal (Grillner, 1985), whereas recent studies (Guan et al., 2001) have revealed a more nuanced balance between feedforward and feedback influences. It seems increasingly clear that animal locomotion strategies span the entire neuromechanical architecture plane (Fig. 2).

Surely, one contributing factor to the difficulty of prescribing motor behavior is that the theoretical underpinnings of different regions in this design plane manifest different levels of maturity. Whereas the theory and practice of adaptive inverse dynamics reference tracking controllers for rigid body manipulators, was worked out two decades ago (Sadegh and Witz, 1987; Slotine and Weiping, 1986; Whitcomb et al., 1993), the dynamics of coupled nonlinear oscillators underlying the complete architectural design space of interest remains an active area of mathematical research. Similarly, while there is a three hundred year old literature on Lagrangian mechanics, neural models admit no appeal to physical first principles at the comparable level of universality and methods of abstraction. Nevertheless, the last two decade's intense effort put into both the mathematical formalism and the modeling applications of CPG theory (Holmes et al., 2006) supply us with a two important concepts: the notions of phase and phase response curves.

A large literature on locomotion oriented coupled-oscillators, following on the seminal Cohen-Holmes-Rand Lamprey CPG model (Cohen et al., 1982), enjoys a ubiquity guaranteed by "isochron theory" (Guckenheimer, 1975; Winfree, 1980). This model of coupled first order oscillators has been successfully applied to numerous rhythmic applications ranging from human hand manipulations (Sternad et al., 1992) to robotic juggling (Klavins and Koditschek, 2002) and running (Weingarten et al., 2004). One subsequent effort toward integrated neuromechanical (in the sense of a second order dynamical generator) modeling of the coupling between internal pattern generators and the mechanical body working in its environment, the Haken-Kelso-Bunz model (1985) has stimulated rhythmic studies in humans (Kelso et al., 2001) that support the predicted appearance of certain bifurcations. Moreover, recent efforts (Peper et al., 2004) to ground this model in more detail seem to give the promise of further insight into the mechanisms of human coordination. But the model hypothesizes a fundamentally fixed architecture, occupying a particular point in the feed-forward/feedback and centralized/decentralized plane of motor coordination.

Still missing are broadly applicable behavioral assays such as perturbation experiments that might help pin down at what operating point in this "design space" (Klavins et al., 2002; Koditschek et al., 2004) any specific motor activity is maintained, much less a *prescriptive* view of how some specific environmental condition or particular task might dictate (or at least constrain) that selection. This chapter places particular emphasis on the feedforward/feedback axis of the design space for more centralized controllers (right side of Fig. 2). We do so within the framework of coupled oscillators where we couple a single neural pattern generator to a single mechanical oscillator rather than focusing on the decentralized coupling of individual neural pattern generators to each other (Golubitsky et al., 1999) or mechanical oscillators to one another (Haken et al., 1985).

Neuromechanical Control Architectures

Here we compare four classes of neuromechanical control architectures (NCA0 through NCA3, illustrated in Fig. 3). NCA1 through NCA3 embody increasing levels of feedback influence on pattern generated by the nervous system, and NCA0 offers an alternative with no CPG. These explore the operating points in the neuromechanical control architectural space that go from more feedforward to greater feedback within a centralized architecture (Fig. 2). Our choice of architectures is strongly influenced by the biological literature and by analogies to controllers of legged robots built by one of the authors (Koditschek, et al., 2001) and robots built by other collaborators.

Our architectural classes sample a range of possible couplings between the sub-systems of Fig. 1. The simplest instance is one where only the mechanical state of the animal is of importance and processing is minimal, whereas the most complex is one where a neural controller uses feedback to stabilize the mechanics and internally represents the phase of the mechanical system with bidirectional coupling to a CPG. Two more architectures of intermediate complexity and processing ability are described.

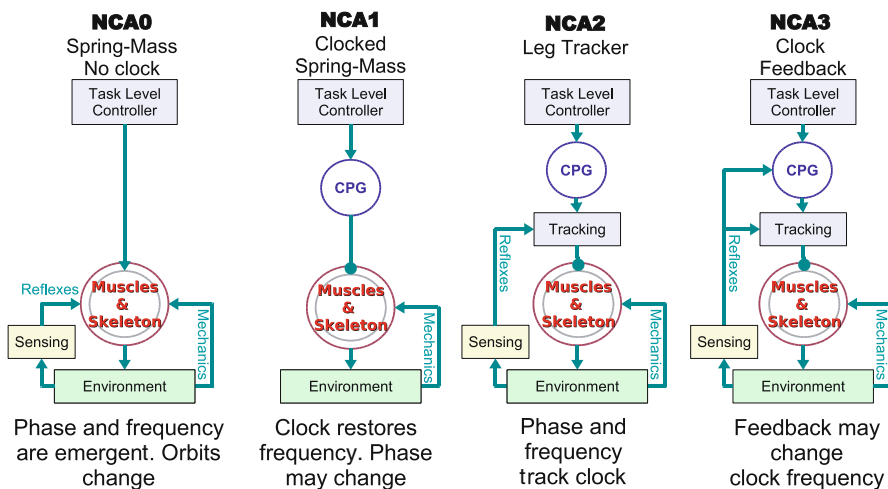


Fig. 3 Columns represent the control architectures NCA0 through NCA3. The **Task Level Control** block generates a constant setting of parameters for the behavior (e.g. “use tripod gait at 15 cm/sec”). **CPG** plays out a scheduled periodic signal at the frequency selected by the task level control and possibly modulated by feedback. **Tracking** compares actual and reference trajectories in a time-invariant way to generate a force activation. **Muscles and Skeleton** interact mechanically with the **Environment** and also modify the representation of the environment returned by **Sensing**

In proposing these architectures we do not suggest that any one of them describes the structure of the neuromechanical control system in any given animal, or corresponds in a direct way to morphology. Rather, we propose these as parsimonious and testable models for control used in specific behaviors. A conclusive experimental outcome – one that rejects simpler feedback architectures in favor of more elaborate ones – enables us to say that during a specific task or behavior a control architecture as simple as the one we find is sufficient for explaining the outcome, and is functionally equivalent to the animal’s controller within this restricted context. An animal may use controllers from all of these classes in different behavioral contexts, or when dealing with extreme perturbations in the same behavioral context.

The exact outcomes possible with models belonging to each architecture class are sensitive to the details of the equations of motion. Nevertheless, some conclusions can be drawn if we assume two properties: asymptotic stability of the periodic motion, and structural stability of the dynamical system. The former property implies that any initial state sufficiently close to the periodic orbit governing the locomotor behavior moves onto the orbit. The latter property implies that the dynamics remain unchanged (in a topological sense) if the equations of motion are modified by small changes.

While both these assumptions may not hold for some models of locomotion, we feel they are justified for practical reasons. Persistent locomotive behaviors seem to have a periodic structure that animals revert to even when perturbed by the environment. Asymptotic stability expresses this reversion in mathematical language. Structural stability expresses the fact that properties of the animal’s body and environment are variable, and to maintain a behavior, the equations of motion must be effectively insensitive to this variability.

NCA0 – Spring Mass with no Clock

The simplest class of architectures we propose is outside the feedforward – feedback axis of Fig. 2, in that it contains no CPG at all and thus the extent of feedback to CPG is immaterial. The behavior of NCA0 systems is governed almost entirely by mechanical dynamics. As the block diagram in Fig. 3 illustrates, once the task level goals are set all dynamics are mediated by the mechanical interaction alone. The defining property of NCA0 systems is this lack of “internal” non-mechanical state, allowing equations of motion to be written solely in terms of instantaneous mechanical state variables. By observing the mechanical state of a NCA0 system one may predict its future course, and so mechanically identical “snapshots” of a behavior should reliably lead to similar motions over multiple cycles of motion. What little control there is occurs at the transition between mechanical regimes. Like the lateral leg spring model (LLS) (Schmitt and Holmes, 2000) and the spring

loaded inverted pendulum model (SLIP) (Blickhan, 1989), running NCA0 systems stabilize by virtue of how the posture of the body evolves from ground contact to ground contact.¹ For example, in the simplest model presented in (Schmitt and Holmes, 2000) it is shown that after a perturbation by a lateral impulse, the angle between the body heading and the direction of motion becomes smaller from step to step by virtue of the leg force acting on the body. The instantaneous mechanical state of the model is sufficient to make such an argument, and predict future cycles of motion.

NCA1 – Clock Driven Spring Mass

The second class of architectures is a family of driven mechanisms with variable stiffness. These and all subsequent architecture classes we consider differ from the previous class by the introduction of a clock that “keeps internal time” via its phase θ . In this second architectural class, the clock is uncontrolled. It runs at a constant frequency ω and sets the mechanism’s stiffness using a periodic function (a “schedule”) $\psi(\theta)$. No reciprocal influence from the mechanical state modifies either the clock frequency or the stiffness imposed at any particular phase (see second column of Fig. 3 for a block diagram).

It is convenient to imagine NCA1 systems as compliant-legged clockwork toys. A snapshot of the kinematic state of a clockwork toy does not tell us whether the internal spring is wound-up or not, but after observing its motions for a few cycles – they are completely predictable, and they do not vary except in so far as external forces directly hinder or aid them. The motions themselves cannot be predicted directly from the mechanical state, but they are predictable periodic functions of time, and changes to these motions are accomplished only by mechanical means.

Many actual toys are built with NCA1 architectures, as are the fastest running legged robots – the Sprawl robots Bailey et al., 2001.

NCA2 – Tracking Leg Controller

The third class of architectures also contains a feed-forward (dynamically uncoupled) driving clock. The clock schedule interacts with the body mechanics by inducing the generation of forces. These forces are not a scheduled pattern of activations – instead they are infinitesimally generated² by comparing the actual

¹ The LLS and SLIP models would fall into the NCA0 category – except for the technicality that they are not fully asymptotically stable and thus do not satisfy our H_1 Hypothesis.

² We use the phrase “infinitesimally generated” to represent the fact the trajectories are defined in terms of an ordinary differential equation, which is an equation relating infinitesimal quantities.

trajectory of a leg and a reference schedule driven by the clock. The comparison is carried out by a filter³ which in robotics applications would be referred to as a “tracking controller” because it would cause a leg to track any reference signal. In that sense, the filter realizes an internal representation of the mechanical dynamics of a leg.

Reflecting this view, our depiction of the **Tracking** block in Fig. 3 incorporates a feedback channel that reaches “up” to a level mediating the clock output but not as “high up” as to affect the internal dynamics of the clock itself.

We constrain the filter to be time invariant, so that the feedback it generates can depend on the form of the reference trajectory and of the actual trajectory – but cannot depend directly on time. The filter encodes the mechanical dynamics in the sense of being able to anticipate what force is necessary as a function of tracking error and state to drive this error to zero, thereby making the mechanical trajectory converge to the reference.

Unlike NCA1 systems, NCA2 systems react to mechanical perturbations using non-mechanical means that require some form of neural sensing. As forces are exerted by the musculoskeletal system of the animal, the kinematic changes induced by these forces are compared with the reference provided by the clock and forces are adjusted according to discrepancy detected with the sensory information. The adjustment is time-invariant – it does not depend on “when” in the cycle of motion a particular kinematic discrepancy occurs, only on the difference between the actual and reference trajectories. Like the stiffness of the clockwork NCA1 systems, the “desired” reference trajectory is a predictable, periodic function of time, and by knowing this function, the reaction to an external perturbation is predictable – but unlike NCA1 systems, this prediction is not purely a mechanical outcome.

Examples of NCA2 systems include most commercially available robots, and the first generation of controllers for the RHex robots (Saranli et al., 2001). In the RHex robots, each leg has a “proportional-derivative (PD) controller” attached to its driveshaft motor. These PD controllers read the state of the driveshaft, compare it to the desired reference angle for that leg and cause the motor to exert a force proportional to the size of the error (“Proportional” gain) and the rate of change of that error (“Derivative gain”). In the sense of Fig. 3, each leg has its own **Tracking** block that knows nothing about the state of other legs, and brings that individual leg into conformance with the clock signal.

The filter as set out here bears some correspondence to the classical notion of an “Equilibrium Point Hypothesis” controller. The major distinction to be drawn here is the origin and meaning of the reference signal itself. Proponents of the Equilibrium Point Hypothesis (Jaric and Latash, 2000) and of the more detailed internal model architecture (Kawato, 1999) and its associated

³ The term “filter” refers to the feedback laws being specified by a function of the tracking error *and its derivatives* rather than merely a function of instantaneous tracking error.

optimization literature posit a kinematically (and, possibly, dynamically) particular reference signal that encodes in detail space-time information sufficient for the specific motor act being indexed, presuming the mediating feedback will correct the minor imperfections of the internal model as well as the potentially major perturbations of the un-modeled external world.

In contrast, the reference signal issued by NCA2 works primarily as an infinitesimally generated “clock” arising as the output of a (typically simple) dynamical system. It may well have space-time detail grafted on — for example, as in Saranli et al. (2001) and Weingarten et al. (2004a,b), where the piecewise constant vector field is not simply a constant — but its primary purpose is to time the onset of the different repeated phases of the rhythmic locomotion cycle.

NCA3 – Clock Feedback Controller

The fourth and final class of architectures extends the previous class by allowing the clock dynamics to be affected by the mechanical state, rather than merely having the clock output filtered. We restrict the NCA3 architecture to systems where the clock feedback is “small” in the sense that the clock never stops or reverses direction. We also require that the signal generated by the clock remains the same except for changes in frequency, and that changes to the clock are slow with respect to the gait cycle time and thus take a step or longer to become noticeable.

It is convenient to think of a NCA3 system as assessing overall “difficulty” and adjusting its desired frequency accordingly. Depending on the task and the perturbation, the system might speed up or slow down, always “trying” to accomplish the goals set by the task level control. NCA3 systems are similar to those with simpler architectures in that they express a one-dimensional loop of “desired” states – the reference trajectory – in a predictable cyclic order. The forces exerted are a time invariant function of the difference between the reference and actual trajectories. Yet, unlike simpler architectures, the rate at which this sequence of “desires” is expressed depends on sensory information.

An example of a NCA3 device is the RHex robot with the new generation controllers described in (Weingarten, 2004b).

The succession of architecture classes just introduced may reveal to the reader that we do not posit the clock as the source of kinematic or dynamic “space-time” detail (although it might be used for that purpose as well by appropriately detailing the vector field or the feedforward component as exemplified by (Weingarten, 2004b) as much as viewing it as a time-keeper. Our point of view is so agnostic about the “true function” of the internal reference signal that we may just as readily embrace the interpretation that it is the body’s internal state estimator for the mechanical phase and beyond, as suggested for example in Kuo (2002).

Kinematic Phase – A Window into a Dynamical System

The challenge of testing neuromechanical control architectures (Fig. 3) and determining the operating point of an animal in an architectural design space (Fig. 2) is considerable. Perturbations to a system and its subsequent response are necessary to reject architectures. Recovery responses must be measurable. Ideally, the approach taken should allow a window into the dynamical system. Both the global responses at the level of the template or system as well as more local responses at the level of the anchor (the detailed joint and appendage motions that result in a characteristic posture) should be identifiable. Recovery of the center of mass to its original limit cycle or to a new one should be detectable. It should be apparent whether and how perturbations of joints collapse back to a representative posture.

Measuring the recovery of the center of mass from perturbations during running has proved difficult. Support for the lateral leg spring model (most similar to NCA0) has come from perturbations using a jetpack on running cockroaches (Jindrich and Full, 2002). Cockroaches recover within a step using the intrinsic properties of their tuned musculo-skeletal system. Evidence for spring-loaded, inverted pendulum behavior has been found when helmeted guinea fowl recover from a step perturbation when running along a track with a false top (Daley and Biewener, 2006) and when humans run on surfaces of various compliance (Ferris et al., 1998). More common are detailed kinematics responses to perturbations that add to our intuition about a control hypothesis, but do not reject a neuromechanical control architecture (Kohlsdorf and Biewener, 2006).

Here, we propose a kinematic approach based on phase analysis that can be used by experimentalists to test neuromechanical control architectures. Biomechanists have long employed gait diagrams and phase response curves for the study of rhythmic locomotor tasks. In the study of terrestrial locomotor gaits, the repetitive motions of the limbs are partitioned into cycles based on foot landing and liftoff events. Phase within a step is typically defined in terms of the fraction of time elapsed since the last footfall relative to the interval ending with the next footfall. These techniques have been used effectively in many studies, such as those characterizing inter-leg influences in stick insect walking using phase response curves (Cruse 1985a,b; Cruse and Epstein, 1982).

This standard approach is dependent on a distinguished footfall event. It is often difficult, if not impossible, to define phase when perturbations significantly change or even destroy the event altogether, such as when locomoting on a rough terrain where footfalls can be missed entirely. Low time resolution makes it difficult to differentiate both perturbations and recoveries. For example, a delay in the motion of a limb induced in early swing may not be resolved from one induced in late swing. More generally, in such classical methods, frequency is defined by the time elapsed between footfalls – meaning that frequency is only “measured” once a step, and it is difficult to deduce at what point in time frequency actually started changing.

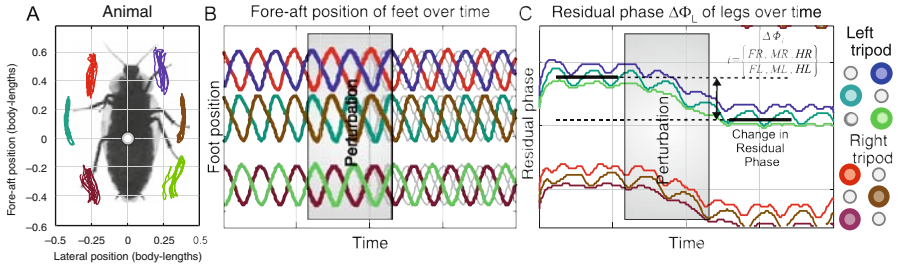


Fig. 4 Relationship between foot or tarsal paths, their periodic coordinates and phases for a running cockroach. **A** Paths of feet relative to the body in constant speed running (experimental data); **B** Periodic fore-aft positions x_i $i = FL, ML, \dots$ of feet in the body frame (model). The grey lines indicate extrapolated positions of the feet consistent with motions before the perturbation; **C** Residual phase of the feet in **B** ($\Delta\Phi_i$) relative to a putative constant frequency model ($\hat{\Phi}_{ext}$). The π phase difference between the two tripods and the constant frequency are clearly apparent. Each tripod comprises the front and hind legs on one side of the body together with the middle leg of the other side, as illustrated by the color-coded circles on the right of the figure

Our kinematic phase method enables phase and frequency to be resolved “instantaneously”. In high-speed video-based kinematic measurements, a phase and frequency can be reliably computed for each pair of consecutive video frames. For example, movements of the feet of a running cockroach relative to its body (Fig. 4A) can be plotted as near sinusoidal oscillations as a function of time (Fig. 4B). If a cockroach was perturbed by an obstacle that altered the phase of all its legs, then a phase change should be apparent in the sinusoidal oscillations when the oscillations before the perturbation are compared with those after (Fig. 4B). This can be seen by extrapolating the oscillations before the perturbation into the time after the perturbation (Fig. 4B, grey lines). Our method determines the change in relative phase at every instant in the cycle (Fig. 4C). Cockroaches use an alternating tripod when running fast. The front left, middle right and left hind leg are in phase, but move in anti-phase to the front right, middle left and right hind leg. In our example (Fig. 4C), the relative phase of legs within a tripod is the same. Before the perturbation, there is no change in the phase of the legs. After the perturbation, a phase change has occurred in all legs and both tripod. The phase change can be detected for any leg at any time, even within a step, with readily available kinematic data.

From a theoretical standpoint, our method to calculate instantaneous phase change relies on a dynamical systems view. We assume that a locomoting animal is best represented by a high dimensional dynamical system. Its high dimensional state consists of mechanical quantities such as positions, velocities, strains, etc., as well as myriad non-mechanical quantities representing the state of the nervous system and the animal’s physiology. In steady state, our hypothesis H_1 asserts that its deterministic periodic behavior is manifest as an isolated

cycle embedded in this high dimensional state-space and thus defining a global phase Φ_G . The projection of global phase Φ_G on any subset of coordinates associated with some sub-system specifies a phase consistent with global phase but expressed only in terms of that sub-system. As a consequence we can speak of a “mechanical phase” Φ_M defined in terms of the mechanical state variables alone; “kinematic phase” Φ_K defined in terms of the kinematic state variables alone and “leg phases” $\Phi_{FR}, \Phi_{MR}, \Phi_{HR}, \Phi_{FL}, \Phi_{ML}, \Phi_{HL}$ for the individual legs (front-right, middle-right, etc.) of a hexapedal animal.

A priori, the global phase Φ_G is difficult to estimate, whereas the “kinematic phase” Φ_L of a sub-system such as a leg L can be estimated more easily by some phase estimation function $\hat{\Phi}_L$ (we use the hat $\hat{\cdot}$ to denote estimates of quantities) of its directly observable kinematics. Such an estimate function is a smooth function of kinematic observations of leg L and corresponds to the actual leg phase Φ_L on the cycle itself. For all states sufficiently near the limit cycle, the global phase Φ_G is well defined. The projected phase $\hat{\Phi}_L$ for a sub-system L may be multi-valued because it depends on the state of other sub-systems outside of L. As a consequence, the phase estimate $\hat{\Phi}_L$ for states off the limit cycle will be different from the actual phase of the sub-system Φ_L by a (linearly) small term. Nevertheless, we argue that by using a combination of these estimates that includes all of the sub-systems that may move independently in the behavior (e.g. all legs), we can obtain an estimate $\hat{\Phi}_K$ of the whole kinematic phase Φ_K . In a repetitive and persistent locomotor behavior such as constant velocity forward running, the complete state of the animal is in correspondence with its kinematic state – otherwise the behavior would not persist in a repetitive form – and so the kinematic phase estimate $\hat{\Phi}_K$ is (a posteriori) a reasonable proxy for estimating global phase Φ_G .

Figure 5 illustrates the relationship between a global kinematic phase estimate $\hat{\Phi}_K$ and the kinematic phases of the legs $\hat{\Phi}_{FR}, \hat{\Phi}_{MR}, \hat{\Phi}_{HR}, \hat{\Phi}_{FL}, \hat{\Phi}_{ML}, \hat{\Phi}_{HL}$ from the running cockroach in Fig. 4A,B. We assume that our kinematic phase estimate $\hat{\Phi}_K$ (Fig. 5A) represents the global phase Φ_G . In this example, the kinematic phase estimate $\hat{\Phi}_K$ is constructed from the positions and velocities of the animal’s six feet by treating the centroids of the two tripods as “virtual legs”. We used the relative position of the tripod centroids and its derivative (velocity) to generate a phase estimate by normalizing them to mean 0 and variance 1, and taking them as the X and Y coordinates of a point. The phase estimate is the angle of the point, as plotted in Fig. 5A, relative to the X axis. The cycles of individual feet can be viewed as projections into different sub-systems (Fig. 5B) of our kinematic phase estimate $\hat{\Phi}_K$.

We derived our estimate of the future motions of the animal (Fig. 4B,C) from our kinematic phase estimate $\hat{\Phi}_K$ (Fig. 5A) which we also consider to be a reasonable estimate for global phase $\hat{\Phi}_G$. We used the fact that by construction, global phase Φ_G evolves linearly in time. We “unwrapped” the cycles in our phase estimates so that phase is increasing rather than wrapping around from π to $-\pi$. These instantaneous unwrapped phases as a function of time – global

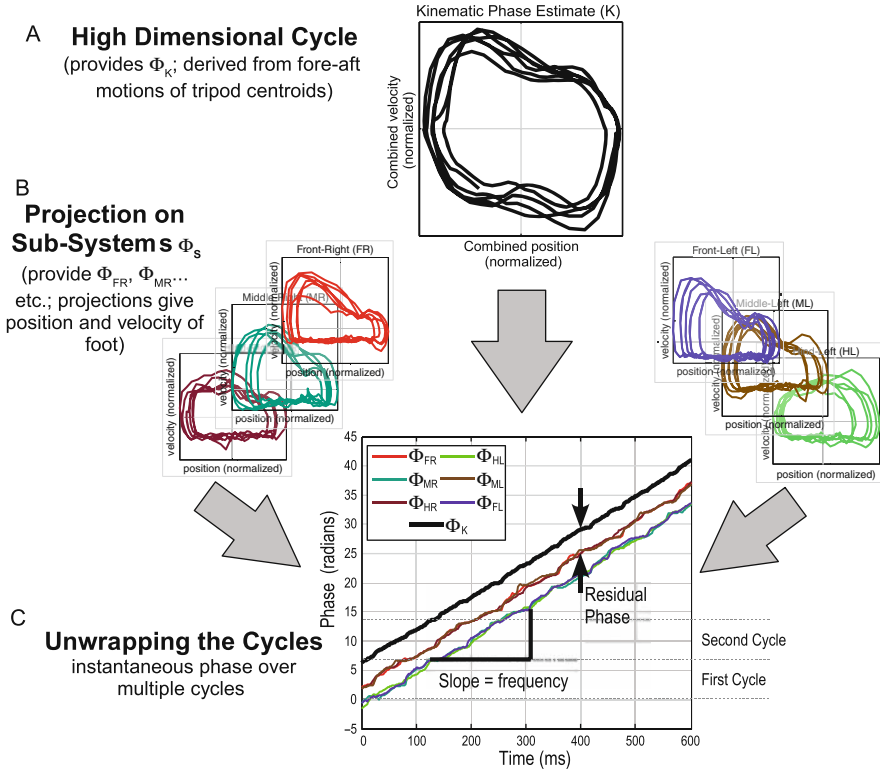


Fig. 5 Determining instantaneous phase change in a running insect using a dynamical systems approach. **A** Plot of kinematic phase estimate $\hat{\Phi}_K$. Kinematic phase estimate represents the global high dimensional dynamical system of a locomoting animal. Kinematic phase estimate $\hat{\Phi}_K$ is constructed from the positions and velocities of the animal’s six feet by treating each tripod as a virtual leg at its centroid. By taking the difference in fore-aft position of the centroids and its derivative we obtain plot of **A**. **B** Plots of sub-system phase estimates $\hat{\Phi}_S$ for individual feet $S = FL, ML, HL, FR, MR, HR$, which may be viewed as projections of our overall kinematic phase estimate $\hat{\Phi}_K$. **C** Instantaneous phase as a function of time for both (global) kinematic phase and leg phases of individual legs. Leg phases fall into two groups, each set representing a tripod of support. The slope of the lines represents cycle frequency. The instantaneous difference of a phase from the trend-line of the kinematic phase estimate $\hat{\Phi}_K$ is used to calculate any phase changes that result from a perturbation as in Fig. 4

and per-leg – are plotted in Fig. 5C. Once we were confident that our global phase estimate $\hat{\Phi}_G$ evolved linearly over extended periods of time when validated with unperturbed motion data, we took pre-perturbation experimental data from a trial and extrapolated a model of the “unwrapped” data with some constant frequency ω and phase intercept ϕ_0 using linear regression:

$$\hat{\Phi}_{\text{ext}}(t) \stackrel{A}{=} \omega t + \phi_0 = \hat{\Phi}_G(t) + \rho(t) \quad (1)$$

$\rho(t)$ regression residual

The model predicts the future behavior that should have occurred without the perturbation. Because of the high temporal resolution of the phase estimate $\hat{\Phi}_G$, a short pre-perturbation interval – potentially an interval as short as a step or two – may be sufficient for extrapolating several strides into the future with $\hat{\Phi}_{\text{ext}}$.

The “(global prediction) residual phase”, in the form of

$$\Delta\hat{\Phi}_G(t) \stackrel{\Delta}{=} \hat{\Phi}_G(t) - \hat{\Phi}_{\text{ext}}(t) \quad (2)$$

and its sub-system analogs for any sub-system S

$$\Delta\hat{\Phi}_S(t) \stackrel{\Delta}{=} \hat{\Phi}_S(t) - \hat{\Phi}_{\text{ext}}(t) \quad (3)$$

can be used to observe how the whole animal is perturbed in timing, and how different sub-systems reestablish their relative phasing. In the present example, Fig. 5C shows that the sub-systems in question – individual legs – exhibit characteristic phase relationships, and that the three legs with similar relative phases are those functioning as a tripod. Moreover, it illustrates that our estimate of global phase – the kinematic phase estimate $\hat{\Phi}_K$ (Fig. 5A and grey line in Fig. 5C) also represents the phase and frequency (i.e. slope of the line in Fig. 5C) of the leg sub-systems when no perturbations are present. The lack of a change in instantaneous phase in Fig. 4C before the perturbation is simply a consequence of a constant difference in phase between the leg phase and our global phase estimate (Fig. 5C). As shown in Fig. 4C, a perturbation may alter the residual phase, i.e. the phase relationship between the extrapolated phase estimate $\hat{\Phi}_{\text{ext}}$ and the actual phase.

The utility of a global phase estimate in the study of non-linear oscillators cannot be over-emphasized. We expect that a global phase estimate will become an invaluable tool for the experimentalist studying biological systems that are, in mathematical essence, non-linear oscillators comprising a neural pattern generator, a musculoskeletal system and their interactions with the environment. The most obvious use of a global phase estimate is to allow the future motions of the animal to be predicted by linear regression of the global phase using its recent motions. This prediction may be compared with the outcome of the animal’s response to perturbations – forming an assay that can be used to test neuromechanical control architectures (Fig. 3).

Perturbation Experiments

We examine several types of perturbations that can assist in revealing which control architecture best represents periodic locomotor behaviors like running. It is important to impress upon the reader that nonlinear hybrid systems, such as those governing animal locomotion, are unlike linear systems used in

engineering in that their behavior cannot be fully characterized by their reactions to a standard set of stimuli. While linear time-invariant systems can be fully described by their response to impulses, chirps, and other textbook stimuli, our choices here are not governed by any such hope.

Instead, we chose perturbations that modify some aspects of the dynamical system while keeping other aspects fixed. We have tried to select perturbations that are “biological” in that one may expect such deviations from steady state horizontal running in a natural environment. We have also tried to pick perturbations that are tractable experimentally. These choices should not be seen by the reader as an exact recipe for experiments in all studies of running. Rather, these are exemplars from different classes of perturbations, applied to the study of running to provide the reader with concrete instances. The exact choice of perturbation should be made in light of a specific locomotor behavior, the animal system and its experimental feasibility – but we are confident that these broad classes of perturbations are generally useful.

Types of Outcomes

Many outcomes are possible as a result of a perturbation. The outcome may depend on both the magnitude of the perturbation and that phase in which it was applied. In the remainder of this section, we describe types of outcomes that can readily be observed and quantified in kinematic phase measurements using an insect as our animal runner. In the next section we go on to relate these outcomes to perturbation type and control architecture class.

First, an insect may recover back to its original phase and frequency (Fig. 6A). Second, the perturbation may cause all the legs of a tripod to change phase from the original phase to settle back down to a phase different from the original phase (control compared to phase shifted; Fig. 6B). Third, the perturbation may cause all the legs of an animal to change frequency (shown by a slope change in the phase plot; Fig. 6C). Finally, the perturbation may cause an orbit shift changing both phase and frequency from the original the shape of the trajectories in time and making phase comparisons more challenging to interpret (Fig. 6D).

Phase Changes

By definition, the phase of undisturbed locomotion is a linear function of time, with a constant frequency as its slope. Phase change outcomes (**P** and **D** in Table 1) are changes in which the animal remains near the same periodic orbit, and thus moving with the same frequency, but at a constant offset relative to the phase’s expected value at that time according to the motion prior to perturbation.

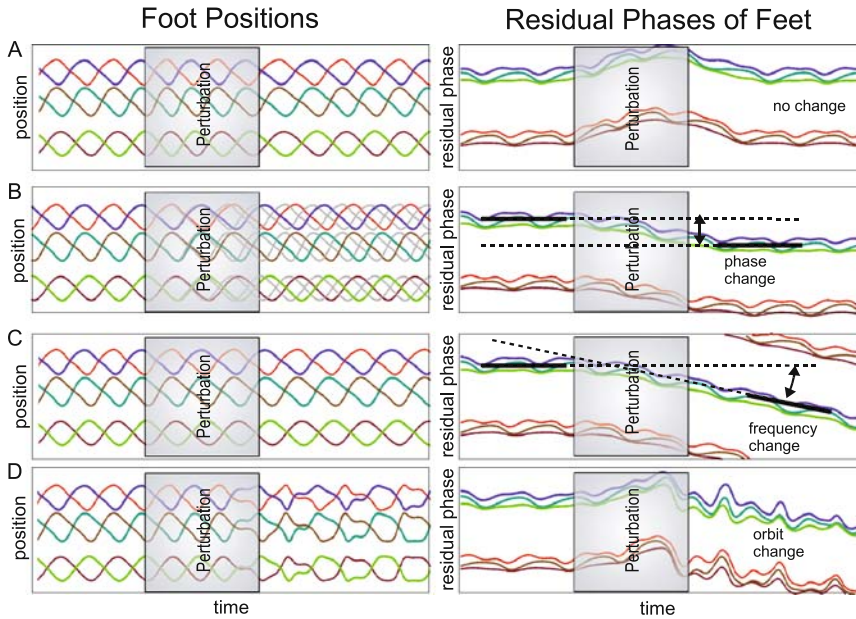








Fig. 6 Types of outcomes from a transient perturbation, such as a bump, expressed in terms of fore-aft foot position and residual phases as a function of time. The left column shows the fore-aft position of each foot as in Fig. 4, and the right column shows the residual kinematic phase based on an extrapolation of the phase before perturbation. Each cycle in the left column represents a single stride. **A** phase and frequency recovery (no change). **B** a phase change outcome, where frequency is recovered but phase is not. The gray lines extrapolate foot motions prior to perturbation to illustrate how phase shifted movements differ from unshifted movements. **C** a frequency change outcome. **D** a gradual breakdown of the periodic orbit’s shape

Table 1 The table summarizes the changes we would expect to see in phase, frequency and orbit shape if running animals using a controller architecture from a given class (*column*) are perturbed with the given perturbation (*row*). By performing multiple experimental perturbations we can obtain independent lines of evidence about the controller’s architectural class

	NCA0 <i>Spring Mass No Clock</i>	NCA1 <i>Clocked Spring-Mass</i>	NCA2 <i>Leg Tracker</i>	NCA3 <i>Clock Feedback</i>
 Bump	P	D	=	P
 Step	P	D	=	P
 Incline	O(F)→N	D,P→N	P→N	P,F
 Mass	P	P	P	P,F
 Substrate	O(F)	O	=	P,F
 Impulse	P	D	=	P

= no asymptotic changes F frequency change
 P continuous phase resetting O change of orbit
 D discrete phase resetting N no stable solutions

We separate two classes of phase change outcomes: discrete phase changes (**D**) and continuous phase changes (**P**). Discrete phase changes have characteristic values that depend only weakly on the magnitude of the applied perturbation such as the height of a bump or the grade of an incline. Typically, the discrete phase change (**D**) appears when the perturbation magnitude exceeds a threshold, and remains constant beyond that threshold. Continuous phase changes (**P**) depend in a continuous way on the magnitude of the perturbation and appear gradually as the perturbation magnitude grows.

Frequency Changes

Frequency change outcomes (**F** in Table 1) are experimental outcomes where the period of the motion changes. Frequency expresses itself as the slope of the trend-line of phase as a function of time, and therefore frequency change outcomes correspond to significant changes in this slope. In practice, it is convenient to examine the residual phase, and statistically reject a slope of zero.

Mathematically speaking, a frequency change always requires a change of orbit – but changes in orbit shape may be too small to detect directly even when the associated frequency is different. Whenever frequency changes, the phases before and after the perturbation are no longer directly comparable because the linear equations predicting them have different slopes, causing the phase difference to be a function of time.

Orbit Changes

Orbit change outcomes (**O** in Table 1) are outcomes where the limit cycle (the closed curve in the high dimensional state space along which the oscillations repeat) is sufficiently deformed that significant changes may be readily observable in the animal's kinematics. In such cases the coordinate transformation defining the phase of the original orbit must break down, and phases can no longer be compared in a simple way before and after the perturbation. The breakdown of the old phase coordinate implies a large increase in magnitude of the fitting error when fitting a linear model to phase estimates applied to post-perturbation kinematic data. The large errors signify that the old phase estimate is no longer as useful because it assumes different orbit kinematics than those observed. A statistical hypothesis test of what constitutes a breakdown of the phase estimate, and thus an **O** outcome, is the converse of establishing that a phase estimate is useful: finding that the goodness of fit of a linear regression of the phase estimate is below what the investigator considers to be the minimal acceptable quality.

While relating phases across orbit changes is challenging, frequencies remain comparable in as much as they tell us whether the period of the new pattern of

motions is different from the period of the old pattern. For some architecture and perturbation combinations the new orbit is almost certainly expected to have a different frequency (**O(F)** in Table 1).

Destabilization Failures

Sometimes a given controller cannot handle a certain class of perturbation, leading to a situation where no steady state periodic solution is possible (**N** in Table 1). In such a case the kinematic patterns either do not approach any specific orbit and undergo continuous changes, or the motions lead to some failure like crashing into the ground.

Perturbation Types and Their Expected Outcomes

Table 1 illustrates several perturbation types that are sufficient when considered collectively for identifying the controller architecture class. Here we describe the perturbation types, the reasoning behind their selection, and the expected outcomes they generate.

In repeated experiments with a given perturbation type, it is important to note that outcome may well depend on both the magnitude and the phase at which the perturbation was applied. Given the large variability in most biological data, proper experimental design and a large number of replicates are paramount. A more detailed treatment of these important topics is outside the scope of this chapter.

Bump Perturbation

The simplest perturbation we consider is running over a bump. The bump provides a transient change in terrain followed by an environment that is in all ways identical to that preceding perturbation. We imagine that for each of the NCAs, a bump would be manifest as a change in ground height restricted to a single stance period.

The NCA0 controllers are governed entirely by their mechanical state. A bump modifies this state to a degree that depends continuously on the size of the bump. The NCA0 system has no memory of its prior phase and frequency, but the similarity between terrain before and after perturbation suggests that a return to the old limit cycle would provide a stable solution – incurring a phase lag or lead related to the size of the bump. Hence the expected outcome is **P**.

NCA1 controllers are governed by the inexorable nature of their driving clock. If the clock is oblivious to the mechanical state, a well defined phase relationship between the internal driving signal and the physical response can only occur if the mechanical interactions with the environment bring the body into phase with the clock. In turn, this implies that the mechanical orbit is

partitioned into basins converging to different phase offset relative to the driving clock. Bump perturbations are thus likely to generate discrete phase changes (**D**) when crossing basin boundaries and no changes if these boundaries are not crossed.

Systems with effective tracking will tend to function the same way regardless of external perturbation. Such is the case for the NCA2 class whose controller brings the tracking error to zero for all transient perturbations in the mechanical state. This implies that the mechanical phase before and after a bump must follow the same linear schedule (=), exactly as dictated by the CPG.

The NCA3 controllers allow feedback to affect the clock by changing its frequency. The effect of these countervailing influences on clock rate by transient perturbations, such as bumps, is to generate a phase change (**P**) – the integral of the induced frequency change during the recovery period. The phase change is continuously dependent on perturbation magnitude because the recovery time and frequency change also depend on perturbation magnitude.

The reader may now already observe in Table 1 a general difficulty in distinguishing regulatory outcomes affected by algorithmic “internal” controllers from those due to comparably tuned mechanical feedback systems. For example, the Table 1 summarizes our prediction of identical outcomes (no change) for NCA0 and NCA3 architectures (continuous phase shift) when perturbed by bumps. The difficulty separating NCA0 and NCA3 is due in no small part to the fact that purely mechanical nonlinear systems can exhibit very complicated behaviors – as complicated as those exhibited by systems with sophisticated feedback mechanisms. Nevertheless, some general properties can separate NCA0 and NCA3 architectures with bump perturbations. First, NCA0s have no hidden state variables so their mechanically observable state should completely predict their behavior whereas one may imagine that different “internal” conditions will yield different kinematically observable dynamics for the NCA3 class. Second, because mechanical feedback can operate very quickly compared to algorithmic or neuromuscular feedback, it is reasonable to assume that very fast responses are purely mechanical as in NCA0. For responses to span times on the order of a stride period with no obvious mechanical conservation law maintaining them, a neural representation that persists over time is required, and thus implicates a NCA3 controller.

Step Perturbation

Idealized mechanical models are often posited as manifesting conserved quantities, such as total energy and components of linear and angular momenta. While true physical systems cannot be entirely lossless, it is frequently the case that strongly under-damped mechanical components can yield behavior manifesting a reasonable facsimile of the idealized conservation properties. For these types of systems, a slightly more obtrusive terrain perturbation for running would be a step – a sudden and enduring change in ground height. The kinematic and dynamic changes are still localized in space and time, but the

regime after the perturbation differs in one of the key integrals of motion – the potential energy. In such a case the controller is required to compensate for the energy imbalance, which is never necessary in level running.

Because it is encountered by the legs as a transient, a step perturbation has similar outcomes to those of a bump perturbation for controllers of the NCA1, NCA2 and NCA3 classes. All these classes of controllers can and do stabilize the total energy of the system. Several purely mechanical NCA0 controller models have been proposed whose elements are tuned to closely approximate an energy conserving system – for example, the “passively stabilized” SLIP models in (Ghigliazza et al., 2005). A step forces such a simple system to shift orbits, thereby likely changing the frequency. A sufficiently large step would cause the runner to halt by not being able to transition into flight, or to crash into the ground by having too much kinetic energy for the leg spring to absorb and return. Accordingly, for this kind of NCA0 variant the step recovery would be summarized by the symbol F or N.

However, some systems in the NCA0 class may regulate energy without neural feedback, for example by having positive force feedback (Geyer et al., 2003). In such cases the hybrid system’s limit cycle is regulated with respect to energy. Since the floor remains level after its initial shift, any initial excess or deficit of energy will be bled out after a number of strides. The same limit cycle will reappear on a new isochron, so there will be a permanent change in the recovered phase relative to the old one. Magnitude of the phase changes is expected to be continuous in the magnitude and direction of perturbation. We have entered this outcome in the summary Table 1 as P, rather than the F or N consequences of the simpler “passively” stabilized mechanical variants described in the previous paragraph.

As the step perturbation to these architectures illustrates, roughly conserved mechanical quantities can readily reveal architectural differences, because they preclude full asymptotic stability in the absence of concerted neuromuscular feedback. They offer apt targets of the experiments we propose, because results reveal a specific non-mechanical regulatory mechanism. For example, the outcomes plotted along the corresponding row of Table 1 show the difference between NCA1, NCA2 and NCA3 controllers when encountering a step. The first would typically have kinematic phase lagging the clock, whereas in the second the tracking controller would correct the kinematic phase offset back to zero. In contrast, in the third, the transient errors would have temporarily altered the internal clock frequency to allow the kinematics time to “catch up” with the result of an overall phase resetting.

Finally, the reader should observe that the same difficulties as in the case of the bump perturbation are encountered here in distinguishing purely mechanical from neurally generated implementations of the same style of control. Similar outcomes of NCA0 with NCA3 suggest the desirability of adding some internal perturbations, such as disrupting neural feedback, to the complement of purely mechanical perturbations we consider in this chapter.

Incline Perturbation

In both bumps and steps the post-perturbation regime is geometrically similar to the pre-perturbation regime, with respect to the animal's body. The same body kinematics could, in principle, work equally well before and after the perturbation event. However, if an animal were to use the exact same kinematics (relative to gravity) running up an incline as it does running horizontally, it would introduce a systematic error in all foot placements and center of mass forces. Thus, an incline would challenge the controller to adjust to a new, slightly modified kinematic regime. For our posited physical models, an "incline" should be construed as a regular, linear change in ground height as a function of distance traveled.

Our NCA0 system will alter its frequency (**F**) or fail entirely when confronted by inclines. If feedback only at the transitions allows energy to be injected in this predominately mechanical architecture, then touchdown events will repeatedly occur "too early". Each time the controller will compensate for a wrong "neutral point." For small slopes there will be a net change in steady state cycle period resulting in a permanent frequency shift relative to the original. As the slope increases, the qualitative kinematic features of the steady state behavior will begin to depart significantly from the level ground periodic orbit. The combination of orbit and frequency change we denote symbolically by **O(F)**. For larger slopes, no stabilization may be possible and critical failure may result. Thus in the end, the NCA0 system manifests disrupted orbits and gait instability that we mark with the symbol **N** in Table 1. This is illustrated in Fig. 6D by showing a phase plot of a system whose orbit is losing its similarity to the initial steady state orbit.

The oblivious clock of NCA1 systems would also encounter difficulties with inclines, although the approach to instability with increasing incline would likely take a different course. An incline perturbation would change the frequency of steady state solutions. For small inclines, this may well be within the basin of convergence for correctable phase differences and would express itself as a consistent phase error proportional to the incline. Namely, these intermediate inclines (significant but prior to failure) might induce significant enough postural changes in the body (in consequence of the passive compliant response to shifted gravitational loading) as to be dynamically viable and measureable as phase changes (**P**, **D**). At inclines sufficient to exceed the phase convergence basin of zero phase change, no steady state solutions are likely to exist (**N**).

NCA2 controllers deal with persistent kinematic challenges such as inclines by applying a constant correction each cycle. This leads initially to a phase change that is continuously dependent on the incline magnitude (**P**), and the existence of steady state solutions over a small range of incline gradients. The persistently corrective controller effort could be viewed a "penalty" for the mismatch between the CPG driving frequency tuned to flat ground and the changed frequency necessary for "optimal" incline running. Eventually, the

frequency mismatch and inappropriate kinematic posture would disrupt the attracting cycle entirely (**N**).

Both NCA1 and NCA2 architectures have a driving clock that runs oblivious to the environment. With sufficiently large slopes, we might expect such a mismatch between stride frequency and ground contact mechanics to incur sub-harmonic oscillations. If these occur, systematic differences will appear between the kinematics of even and odd steps, causing the phase estimation function to degrade. The gradual deterioration of the orbit (**O**) will have a systematic structure, where the linear phase model residuals in even cycles have one characteristic form and the residuals in odd cycles have another form. In both NCA1 and NCA2 the clock frequency cannot change, almost entirely precluding the possibility of frequency change outcomes.

The NCA3 controllers have the capability to avoid the frequency mismatch penalty by changing their CPG frequency to accommodate the incline. The nominal gait will be retuned for the slope just as in the case of NCA2. However, now there is a chance if the feedback to the clock has sufficient influence at time constants well within the stride period, then the “early” (or “late”) touchdowns may be corrected by advancing (retarding) the clock phase and then retarding (advancing) it to correct for wrongly anticipated stance phase duration. In this case, we would expect a distorted version of the original limit cycle. The cycle may have the same frequency albeit shifted phase, since the system would settle down on a new isochron (**P**). The system also may operate at a different frequency, since the internal clock advance and retard effects might not necessarily balance. The change in frequency means that the phase evolution controller governing the system before the incline is no longer meaningful. In the new limit cycle’s phase coordinate, corresponding orbit events such as touchdown will be phase shifted relative to their positions in the previous orbit by a magnitude that is continuously dependent on the grade of the incline. Figure 6C illustrates a NCA3 system compensating for an incline by changing frequency (**F**).

Dynamical Perturbation

The last three rows in Table 1 address perturbations that have already appeared in the empirical animal motor literature and we include their consideration in this chapter for the sake of continuity. Adding mass and changing the moment of inertia of human runners has been studied for its own sake and as a model for dinosaurs (Carrier et al., 2001; Lee et al., 2001). Humans (Ferris et al., 1998) have been run on substrates of variable compliance. Jindrich and Full have reported the response of intact cockroach runners to sudden impulse perturbations (Jindrich and Full, 2002). In none of these previous studies has the relative kinematic phase explicitly been measured. We now briefly review what the expected phase responses would be to each of these distinct dynamical perturbations and include the outcomes in Table 1.

For NCA0 systems, a center of mass shift (either magnitude or position) or change in moments will again change the steady state posture, incurring a small but likely measurable offset (in proportion to leg compliance) in phase (**P**) that varies continuously with the shift. A small change in substrate mechanics (e.g. damping or compliance) may likely incur changes in individual leg transients at touchdown and liftoff and thus alter the kinematic phase (**P**) by shifting the ground-contact-feedback-triggered schedule for application of energy during leg stance. More dramatic substrate changes might lead to a severe deformation in the steady state kinematics, causing the original phase estimation function to have little power (**O**). A transient impulse applied to the center of mass carries kinetic energy and momentum that need to be bled off, entailing a change in phase that depends continuously on the magnitude of the impulse (**P**).

For the NCA1 system, a center of mass shift or change in moments will once again change the steady state posture, incurring a small but likely measurable offset in phase (**P**) that varies continuously with the shift. A change in substrate mechanics may once again incur changes in individual leg transients at touchdown and liftoff, but should not have a measurable effect on steady state phase (=) until the ground becomes so much more compliant that the kinematic shape of the limit cycle is altered (**O**). A transient impulse applied to the center of mass should yield no change for small impulses, but may switch the system to a new stable CPG-body phase relationship when larger. The phase change is thus a discrete function of impulse magnitude (**D**).

For the leg tracking controller of NCA2, a COM shift (either magnitude or position) or change in moments will once again change the steady state posture, incurring a small but likely measurable offset (in proportion to leg compliance) in phase that varies continuously with the shift. A change in substrate mechanics (e.g. damping or compliance) may once again incur changes in individual leg transients at touchdown and liftoff but should not have a measurable effect on steady state phase. A transient impulse applied to the mass center should yield no change in phase.

Finally, for the NCA3 systems, center of mass shifts, changes in moments and changes in substrate compliance may all be compensated for by the controller in two ways. One form of feedback stabilization would be for forces to change so as to maintain a close semblance of the original kinematics, by way of the tracking controller. This type of stabilization would tend to induce a continuous phase change (**P**). The other form of stabilization would change the frequency of the motion, also leaving the kinematics essentially the same, and adapting the rate of motion to the change in environment. Due to the dependency of this interplay on the specific feedback gains, it is difficult to predict a general outcome. One may reasonably assume that NCA3 controllers are exceptionally good at maintaining the shape of kinematic trajectories, suggesting that changes in orbit shape (**O**) are very unlikely.

A transient impulse applied to the mass center might well introduce a lagging change in frequency (transient) and thus a likely phase shift (**P**) in rough proportion to the magnitude of perturbation.

Conclusions

In an effort to create testable hypotheses for the control of running, we introduce a progression of neuromechanical control architectures. Within a dynamical systems framework, we explore the coupling of an internal “neural” pattern generator with an “external” mechanical body and legs. We progress from strongly feedforward controllers dominated by the mechanical system viewed as a hybrid oscillator to a controller with feedback signals driven by mechanical perturbations that influence the feedforward command signal emanating from the neural pattern generator (Figs. 2 and 3).

To begin to define these architectures, we use a series of legged physical models (robots) that offer the most direct exposition of our central argument that “external” body-limb kinematics can offer a window into “internal” architecture. Specifically, we propose that kinematically derived measurements of mechanical phase manifest the internal neural clock phase and hence can be used to capture aspects of the coupled motor system’s phase response curve during rhythmic behavior.

By reasoning about the likely properties of the phase response curve for each architecture in the progression, we conclude that an appropriately diverse battery of distinct mechanical perturbations must elicit an observable pattern of phase and frequency changes that distinguish each individual architecture. Thus, we hypothesize that applying such a battery of perturbations to an intact runner – robot or animal – may shed significant light on the nature of its seemingly inaccessible feedforward/feedback internal architecture. Mathematically succinct exemplars of this architectural plane are straightforward to design and their analysis should be of considerable interest.

In particular, it is interesting to speculate on the extent to which our informal reasoning about the likely empirical phase response of complicated mechanisms to perturbations might be shown to be mathematically necessary. Because we take advantage of the ubiquity of isochrons (Guckenheimer and Holmes, 1983; Winfree, 1980) in coupled oscillators (Cohen et al., 1982), such mathematical prescriptions might likely extend to the far more elaborate kinematics of runners. If so, such perturbation batteries attain the character of an empirical assay with the power to characterize important aspects of an intact runner’s motor control operating point.

Experiments now in progress with laboratory animals will soon reveal the true empirical power of these hypotheses.

References

- Bailey, S A, Cham, J G, Cutkosky, M R, and Full, R J. *Experimental Robotics VII*, volume 271 of *Lecture Notes in Control and Information Sciences*, chapter Comparing the Locomotion Dynamics of the Cockroach and a Shape Deposition Manufactured Biomimetic Hexapod, pages 239–248. Springer Berlin/Heidelberg, Jan 2001. ISSN: 0170-8643.

- Balasubramaniam, R and Turvey, M T. Coordination modes in the multisegmental dynamics of hula hooping. *Biological Cybernetics*, 90:176–190, 2004.
- Bernstein, N. *The Co-ordination and Regulation of Movements*. Pergamon Press, Oxford, 1967.
- Biess, A, Nagurka, M, and Flash, T. Simulating discrete and rhythmic multi-joint human arm movements by optimization of nonlinear performance indices. *Biological Cybernetics*, 95(1):31–53, 2006.
- Bizzi, E, Tresch, M C, Saltiel, P, and d’Avella, A. New perspectives on spinal motor systems. *Nature Reviews Neuroscience*, 1:101–108, 2000.
- Blickhan, R. The spring mass model for running and hopping. *Journal of Biomechanics*, 22(11–12):1217–1227, 1989.
- Blickhan, R, and Full, R J. Similarity in multilegged locomotion: Bounding like a monopode. *Journal of Comparative Physiology A Sensory Neural and Behavioral Physiology*, 173(5):509–517, 1993.
- Burke, R E. Revisiting the notion of ‘motor unit types’. *Progress in Brain Research*, 123:167–175, 1999.
- Burke, R E. Some unresolved issues in motor unit research. *Advances in Experimental Medicine and Biology*, 508:171–178, 2002. PMID: 12171107.
- Büschges, A, and El-Manira, A. Sensory pathways and their modulation in the control of locomotion. *Current Opinion in Neurobiology*, 8:733–739, 1998.
- Calvitti, A, and Beer, R D. Analysis of a distributed model of leg coordination, i. individual coordination mechanisms. *Biological Cybernetics*, 82(3):197–206, February 2000.
- Carrier, D R, Walter, R M, and Lee, D V. Influence of rotational inertia on turning performance of theropod dinosaurs: clues from humans with increased rotational inertia. *Journal Of Experimental Biology*, 204(22):3917–3926, November 2001.
- Chiel, H J, Beer, R D, Quinn, R D, and Espenschied, K S. Robustness of a distributed neural network controller for locomotion in a hexapod robot. *IEEE Transactions on Robotics and Automation*, 8(3):293–303, 1992.
- Cohen, A, Holmes, P J, and Rand, R H. The nature of coupling between segmental oscillators of the lamprey spinal generator for locomotion: a model. *Journal of Mathematical Biology*, 13:345–369, 1982.
- Cruse, H. Coactivating influences between neighbouring legs in walking insects. *Journal of Experimental Biology*, 114:513519–519, 1985a.
- Cruse, H. Which parameters control the leg movement of a walking insect? ii. the start of the swing phase. *Journal of Experimental Biology*, 116:357–362, 1985b.
- Cruse, H. What mechanisms coordinate leg movement in walking arthropods? *Trends in Neuroscience*, 13:15–21, 1990.
- Cruse, H, and Epstein, S. Peripheral influences on the movement of the legs in a walking insect *carausius morosus*. *Journal of Experimental Biology*, 101:161–170, 1982.
- Daley, M A, and Biewener, A A. Running over rough terrain reveals limb control for intrinsic stability. *PNAS*, 103(42):15681–15686, October 2006.
- Domen, K, Latash, M L, and Zatsiorsky, V M. Reconstruction of equilibrium trajectories during whole-body movements. *Biological Cybernetics*, 80(3):195–204, 1999.
- Ekeberg, O, Blümel, M, and Büschges, A. Dynamic simulation of insect walking. *Arthropod Structure and Development*, 33:287–300, 2004.
- Ferris, D P, and Louieand, M, Farley, C T. Running in the real world: adjusting leg stiffness for different surfaces. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 265(1400):989–994, June 1998.
- Fitzhugh, R. Impulses and physiological states in theoretical models of nerve membrane. *Biophysical Journal*, 1:445–466, 1961.
- Full, R J, and Farley, C T. Musculoskeletal dynamics in rhythmic systems – a comparative approach to legged locomotion. In J M Winters and P E Crago, editors, *Biomechanics and Neural Control of Movement*, pages 192–202. Springer-Verlag, New York, 2000. ISBN-10: 0-387-94974-7, ISBN-13: 978-0-387-94974-1.

- Full, R J, and Koditschek, D E. Templates and anchors: Neuromechanical hypotheses of legged locomotion on land. *Journal of Experimental Biology*, 202(23):3325–3332, 1999.
- Full, R J, Kubow, T, Schmitt, J, Holmes, P, and Koditschek, D E. Quantifying dynamic stability and maneuverability in legged locomotion. *Journal of Integrative and Comparative Biology*, 20:149–157, 2002.
- Geyer, H, Seyfarth, A, and Blickhan, R. Positive force feedback in bouncing gaits? *Proceedings of the Royal Society of London Series B-Biological Sciences*, 270(1529):2173–2183, October 2003.
- Ghigliazza, R M, Altendorfer, R, Holmes, P, and Koditschek, D E. A simply stabilized running model. *SIAM Review*, 47(3):519–549, September 2005.
- Ghigliazza, R M, and Holmes, P. A minimal model of a central pattern generator and motoneurons for insect locomotion. *SIAM Journal of Applied Dynamical Systems*, 3(4):671–700, 2004.
- Ghigliazza, R M, and Holmes, P. Minimal models of bursting neurons: How multiple currents, conductances, and timescales affect bifurcation diagrams. *SIAM Journal of Applied Dynamical Systems*, 3(4):636–670, 2004b.
- Goldman, D I, Chen, T S, Dudek, D M, and Full, R J. Dynamics of rapid vertical climbing in cockroaches reveals a template. *Journal of Experimental Biology*, 209:2990–3000, 2006.
- Golubitsky, M, Stewart, I, Buono, P L, and Collins, J J. Symmetry in locomotor central pattern generators and animal gaits. *Nature*, 401(6754):693–695, 1999.
- Grasso, R, Zago, M, and Lacquaniti, F. Interactions between posture and locomotion: motor patterns in humans walking with bent posture versus erect posture. *Journal of Neurophysiology*, 83(1):288–300, 2000. PMID: 10634872.
- Grillner, S. Neurobiological bases of rhythmic motor acts in vertebrates. *Science*, 228:143–149, 1985.
- Guan, L, Kiemel, T, and Cohen, A H. Impact of movement and movement-related feedback on the lamprey central pattern generator for locomotion. *Journal of Experimental Biology*, 204(Pt 13):2361–2370, 2001.
- Guckenheimer, J. Isochrons and phaseless sets. *Journal of Mathematical Biology*, 1:259–273, 1975.
- Guckenheimer, J, and Holmes, P. *Nonlinear Oscillations, Dynamical Systems, and Bifurcations of Vector Fields*. Springer-Verlag, 1983.
- Haken, H, Kelso, J A, and Bunz, H. A theoretical model of phase transitions in human hand movements. *Biological Cybernetics*, 51(5):347–356, 1985.
- Hinder, M R, and Milner, T E. The case for an internal dynamics model versus equilibrium point control in human movement. *Journal of Physiology (London)*, 549(3):953–963, 2003.
- Hodgkin, A L, and Huxley, A F. A quantitative description of membrane current and its application to conduction and excitation in nerves. *Journal of Physiology*, 117:500–544, 1952.
- Holmes, P, Full, R J, Koditschek, D E, and Guckenheimer, J. The dynamics of legged locomotion: Models, analyses, and challenges. *SIAM Reviews*, 48(2):207–304, 2006.
- Ivanenko, Y P, Grasso, R, Macellari, V, and Lacquaniti, F. Control of foot trajectory in human locomotion: Role of ground contact forces in simulated reduced gravity. *Journal of Neurophysiology*, 87(6):3070–3089, 2002.
- Jaric, S, and Latash, M L. The equilibrium-point hypothesis is still doing fine. *Human Movement Science*, 19(6):933–938, 2000.
- Jindrich, D L, and Full, R J. Dynamic stabilization of rapid hexapedal locomotion. *Journal of Experimental Biology*, 205(18):2803–2823, 2002.
- Kawato, M. Internal models for motor control and trajectory planning. *Current Opinion in Neurobiology*, 9:718–727, 1999.
- Kelso, J A, Fink, P W, DeLaplaine, C R, and Carson, R G. Haptic information stabilizes and destabilizes coordination dynamics. *Proceedings of the Royal Society B - Biological Science*, 268(1472):1207–1213, 2001.

- Klavins, E, and Koditschek, D E. Phase regulation of decentralized cyclic robotic systems. *The International Journal of Robotics Research*, 21(3):257–275, 2002.
- Klavins, E, Komsuoglu, H, Full, R J, and Koditschek, D E. The role of reflexes versus central pattern generators in dynamical legged locomotion. In J Ayers, J Davis, and A Rudolph, editors, *Neurotechnology for Biomimetic Robots*, pages 351–382. MIT Press, Boston, MA, 2002.
- Koditschek, D E, and Bühler, M. Analysis of a simplified hopping robot. *International Journal of Robotics Research*, 10(6):587–605, 1991.
- Koditschek, D E, Full, R J, and Bühler, M. Mechanical aspects of legged locomotion control. *Arthropod Structure and Development*, 33(3):251–272, July 2004.
- Kohlsdorf, T, and Biewener, A A. Negotiating obstacles: running kinematics of the lizard *sceloporus malachiticus*. *Journal of Zoology*, 270(2):359–371, October 2006.
- Kording, K P, and Wolpert, D M. Bayesian decision theory in sensorimotor control. *Trends in Cognitive Sciences*, 10(7):319–326, 2006.
- Kuo, A D. The relative roles of feedforward and feedback in the control of rhythmic movements. *Motor Control*, 6(2):129–145, 2002.
- Lacquanti, F, Terzuolo, C, and Viviani, P. The law relating the kinematic and figural aspects of drawing movements. *Acta psychologica (Amst)*, 54(1–3):115–130, 1983. PMID: 6666647.
- Lee, D V, Walter, R M, Deban, S M, and Carrier, D R. Influence of increased rotational inertia on the turning performance of humans. *Journal of Experimental Biology*, 204(22):3927–3934, November 2001.
- Morris, C, and L’ecar, H. Voltage oscillations in the barnacle giant muscle. *Biophysics Journal*, 35:193–213, 1981.
- Mussa-Ivaldi, F A. Modular features of motor control and learning. *Current Opinion in Neurobiology*, 9:713–717, 1999.
- Nakano, E, Imamizu, H, Osu, R, Uno, Y, Gomi, H, Yoshioka, T, and Kawato, M. Quantitative examinations of internal representations for arm trajectory planning: minimum commanded torque change model. *Journal of Neurophysiology*, 81:2140–2155, 1999.
- Pearson, K G. The control of walking. *Scientific American*, 464:72–86, 1976.
- Pearson, K G. Common principles of motor control in vertebrates and invertebrates. *Annual Reviews - Neuroscience*, 16:265–297, 1993.
- Pearson, K G. Proprioceptive regulation of locomotion. *Current Opinion in Neurobiology*, 5:786–791, 1995.
- Peper, C, Liekeand, E, Ridderikhoff, A, Dafferthör, A, and Beek, P J. Explanatory limitations of the HKB model: Incentives for a two-tiered model of rhythmic interlimb coordination. *Human Movement Science*, 23:673–697, 2004.
- Raibert, M H. Legged robots. *Communications of the ACM*, 29(6):499–514, 1986.
- Richardson, M J E, and Flash, T. Comparing smooth arm movements with the two-thirds power law and the related segmented-control hypothesis. *Journal of Neuroscience*, 22(18):8201–8211, 2002.
- Riley, M A, and Turvey, M T. Variability and determinism in motor behavior. *Journal of Motor Behavior*, 34:99–125, 2002.
- Sadegh, N, and Witz, R. Stability analysis of an adaptive controller for robotic manipulators. In *Proceedings IEEE International Conference on Robotics and Automation*, Raleigh, NC, April 1987.
- Saltiel, P, Wyler-Duda, K, d’Avella, A, Tresch, M C, and Bizzi, E. Muscle synergies encoded within the spinal cord: evidence from focal intraspinal NMDA iontophoresis in the frog. *Journal of Neurophysiology*, 85(2):605–619, 2001.
- Saranli, U, Buehler, M, and Koditschek, D E. RHex: a simple and highly mobile hexapedal robot. *International Journal of Robotics Research*, 20(7):616–631, 2001.
- Schaal, S, and Schweighofer, N. computational motor control in humans and robots. *Current Opinions Neurobiology*, 6:675–682, 2005.

- Schaal, S. and Sternad, D. Origins and violations of the 2/3 power law in rhythmic three-dimensional arm movements. *Experimental Brain Research*, 136(1):60–72, 2001.
- Schaal, S, Sternad, D, Osu, R, and Kawato, M. Rhythmic arm movement is not discrete. *Nature Neuroscience*, 7(10):1136–1143, 2004.
- Schmitt, J, and Holmes, P. Mechanical models for insect locomotion: dynamics and stability in the horizontal plane – i. theory. *Biological Cybernetics*, 83(6):501–515, December 2000.
- Shadmehr, R, and Wise, S P. *Computational Neurobiology of Reaching and Pointing: A Foundation for Motor Learning*. MIT Press, 2005.
- Slotine, J J E, and Weiping, L. On the adaptive control of robot manipulators. In *Proceedings of the ASME Winter Annual Meeting*, Anaheim, CA, December 1986.
- Sternad, D, and Schaal, S. Segmentation of endpoint trajectories does not imply segmented control. *Experimental Brain Research*, 124(1):118–136, 1999.
- Sternad, D, Turvey, M T, and Schmidt, R C. Average phase difference theory and 1:1 phase entrainment in interlimb coordination. *Biological cybernetics*, 67(3):223–231, 1992.
- Todorov, E, and Jordan, M I. Smoothness maximization along a predefined path accurately predicts the speed profiles of complex arm movements. *Journal of Neurophysiology*, 80(2):696–714, 1998.
- Weingarten J D, Groff R E, and Koditschek D E. A framework for the Coordination of legged robot gaits. *2004 IEEE Conference on Robotics, Automation and Mechatronics*, 2: 679–686, 2004a.
- Weingarten, J D, Lopes, G A D, Buehler M, Groff R E, and Koditschek D E. Automated gait adaptation for legged robots. *Proceedings. ICRA '04. 2004 IEEE International Conference on Robotics and Automation*, 3:2153–2158 2004b.
- Whitcomb, L L, Rizzi, A A, and Koditschek, D E. Comparative experiments with a new adaptive controller for robot arms. *IEEE Transactions on Robotics and Automation*, 9(1):59–70, February 1993.
- Winfrey, A T. *The Geometry of Biological Time*. Springer-Verlag, New York, 1980.