Quantifying Dynamic Stability and Maneuverability in Legged Locomotion[1]

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SYNOPSIS.   Animals can swerve, dodge, dive, climb, turn and stop abruptly. Their stability and maneuverability are remarkable, but a challenge to quantify. Formal stability analysis can allow for quantitative comparisons within and among species. Stability analysis used in concert with a template (a simple, general model that serves as a guide for control) can lead to testable hypotheses of function. Neural control models postulated without knowledge of the animal's mechanical (musculo-skeletal) system can be counterproductive and even destabilizing. Perturbations actively corrected by reflex feedback in one direction can result in perturbations in other directions because the system is coupled dynamically. The passive rate of recovery from a perturbation in one direction differs from rates in other directions. We hypothesize that animals might exert less neural control in directions that rapidly recover via passive dynamics (*e.g.,* in body orientation and rotation). By contrast, animals are likely to exert more neural control in directions that recover slowly or not at all via passive dynamics (*e.g.,* forward velocity and heading). Neural control best enhances stability when it works with the natural, passive dynamics of the mechanical system. Measuring maneuverability is more challenging and new, general metrics are needed. Templates reveal that simple analyses of summed forces and quantification of the center of pressure can lead to valuable hypotheses, whereas kinematic descriptions may be inadequate. The study of stability and maneuverability has direct relevance to the behavior and ecology of animals, but is also critical if animal design is to be understood. Animals appear to be grossly over-built for steady-state, straight-ahead locomotion, as they appear to possess too many neurons, muscles, joints and even too many appendages. The next step in animal locomotion is to subject animals to perturbations and reveal the function of all their parts.

INTRODUCTION

Animals can negotiate the most complex terrain, turn in an instant and stop on a dime. We contend that the time has come to propose simple, testable, quantitative hypotheses explaining this remarkable ability. The mechanisms that allow extraordinary stability and maneuverability have remained largely unexplored for several reasons. First, the methodology and search for simple, general principles initially demanded the study of steady-state, straight-ahead locomotion. To characterize more complex responses to perturbations, one must first define the steady-state condition to which the animal will return. Just as the fields of exercise physiology, gas transport and energy utilization first advanced our understanding of the steady-state (*e.g.,* Taylor and Weibel, 1981; Taylor *et al.*, 1982) and are now taking the next logical step toward the study of intermittent locomotion (see Amer. Zool., 41:137–246, 2001), so should locomotor biomechanics and neural control move beyond the steady-state. Second, sufficient knowledge of individual systems in traditional disciplines is required before their interactions can be explored most productively. Useful hypotheses are available for individual neurons, muscles, feedforward pattern generators and feedback circuits functioning in moving animals. Due to the focused efforts, shared

techniques and the common language required in these sub-disciplines, these communities have been somewhat isolated from one another. The time has come for an integrative view of locomotion (Dickinson *et al.*, 2000). Third, the study of stability and maneuverability requires a truly interdisciplinary effort. Relevant, general control models have been developed in fields as diverse as comparative biology (Cruse, 1990; Duysens *et al.*, 2000; Pearson, 1993; McIntyre and Bizzi, 1993), the human biomechanics of arm movements (Hogan, 1990), walking and maintaining posture (Bauby and Kuo, 2000; Mackinnon and Winter, 1993; Zehr and Stein, 1999), and in the motor control branch of psychology focusing on hand movements (Hanken *et al.*, 1985). As is shown by the recent approaches in these diverse areas, we argue that a principled understanding will not only draw together fields within biology broadly construed, but must integrate biology with engineering and mathematics.

In the present publication we define stability, briefly introduce an established method to quantify stability, show how quantifying the stability of a dynamic model can lead to novel hypotheses of control and animal design, and discuss simple measurements of maneuverability. Although we analyze legged locomotion in particular, the approach can be used for all modes of locomotion and behavior in general. We hope to encourage investigators, particularly those who collect kinematic data, to consider the value of dynamical stability and maneuverability analyses. Our primary goal is to further articulate a paradigm for understanding

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the mechanisms of locomotion by using these analyses to formulate and test hypotheses generated from dynamic models (Full and Koditschek, 1999). We contend that at least two interconnected classes of dynamic models are required to integrate function across the various levels of organization. One model that we term a "template," incorporates the fewest possible degrees of freedom and serves as a control target (Full and Koditschek, 1999). The second model, the "anchor," is a more complex physically realistic model within which the template behavior is embedded. We argue that efforts to build templates and to anchor them in realistic animal data represent a productive avenue toward an integrated view of neuromechanical control.

Defining stability is a challenge

Static stability. Traditionally, stability in legged locomotion is taken to refer to static stability. The necessity for static stability in arthropods has been used as one of, if not the most important, reason, why insects have at least six legs and use two sets of alternating tripods of support during locomotion (Hughes, 1952). Numerous investigators (Alexander, 1982; Delcomyn, 1985; Graham, 1985; Hughes, 1952) have discussed the stepping patterns that insects require to maintain static stability during locomotion. Yet, few have attempted to quantify static stability as a function of gait or variation in body form (Cruse, 1976; Hughes, 1957). Research on legged walking machines provided an approach to quantify static stability (McGhee, 1976; Song, 1984; Sun, 1974). The minimum requirement to attain static stability is a tripod of support, as in a stool. If an animal's center of mass falls outside the triangle of support formed by its three feet on the ground, it is statically unstable and will fall. In the quasi-static gait of a robot or animal, the center of mass moves with respect to the legs, and the likelihood of falling increases the closer the center of mass comes to the edge of the triangle of support.

Dynamic stability analysis is required for all but the slowest movements. Ting *et al.* (1994) discovered that the degree of static stability decreased as insects ran faster, until at the highest speeds they became statically unstable during certain parts of each stride, even when a support tripod was present. In the sagittal plane, six and eight legged animals are best modeled as dynamic, spring-load, inverted pendula (Blickhan and Full, 1987; Full and Tu, 1990) in the same way as two- and four-legged runners (Blickhan and Full, 1993; Cavagna *et al.*, 1977). At the highest speeds, ghost crabs, cockroaches and ants exhibit aerial phases (Blickhan and Full, 1987; Full and Tu, 1991; Zollikofer, 1994). In the horizontal plane, insects and other legged runners are best modeled by a dynamic, lateral leg spring, bouncing the animal from side to side (Schmitt and Holmes, 2000a, b).

These models, and force and velocity measurements on animals, suggest that running at a constant average speed, while clearly a dynamical process, is essentially periodic in time. We define locomotor stability as the ability of characteristic measurements (*i.e.,* state variables such as velocities, angles and positions) to return to a steady-state, periodic gait after a perturbation.

Quantifying dynamic stability—dynamical systems theory

The field of dynamical systems provides an established methodology to quantify stability. Our aim in the present publication is not to explain the details of dynamical systems theory (see Guckenheimer and Holmes, 1983; Strogatz, 1994), but to give sufficient background so that those studying locomotion can see its potential in description and hypothesis formation. It is important to note that dynamical systems theory involves the formal analysis of how systems at any level of organization (neuron, networks or behaviors) change over time. In this context, the term dynamical system is not restricted to a system generating forces (kinetics) and moving (kinematics), as is the common usage in biomechanics. The description of stability resulting from dynamical systems theory, which addresses mathematical models, differential equations and iterated mappings, does not necessarily provide us with a direct correspondence to a particular biomechanical structure (Beck *et al.*, 1995). Instead, the resulting stability analysis acts to guide our attention in productive directions to search for just such a link between coordination hypotheses from dynamical systems and mechanisms based in biomechanics and motor control (*e.g.,* Taga, 1995a, b; Taga *et al.*, 1991; Dingwell and Cusumano, 2000).

Define and measure variables that specify the state of the system. The first task in the quantification of stability is to decide on what is best to measure. The goal is to specify a set of variables such as positions and velocities that completely define the state of the system. State variables are distinct from parameters such as mass, inertia and leg length that are more or less fixed for a given animal. State variables change over time as determined by the dynamics of the system. Ideally, their values at any instant in time should allow the determination of all future values. Put another way, if two different trials of a running animal converge to the same values, their locomotion patterns should be very similar from that time forward.

Periodic trajectories called limit cycles characterize locomotion. During stable, steady-state locomotion the value of state variables oscillates rhythmically over time (*e.g.,* lateral velocity in Fig. 1A). In addition to representing the behavior of the state variables with respect to time, we can examine their behavior relative to one another. Figure 1B shows a plot of the state variables (*e.g.,* lateral, rotational and fore-aft velocity) in state space. Time is no longer an axis, but changes as one moves along the loop in this three dimensional space. The closed loop trajectory tells us that the system is periodic in time. Such a trajectory in state space is known as a limit cycle. If any other path converges to this cycle, it has stabilized to the same trajectory.
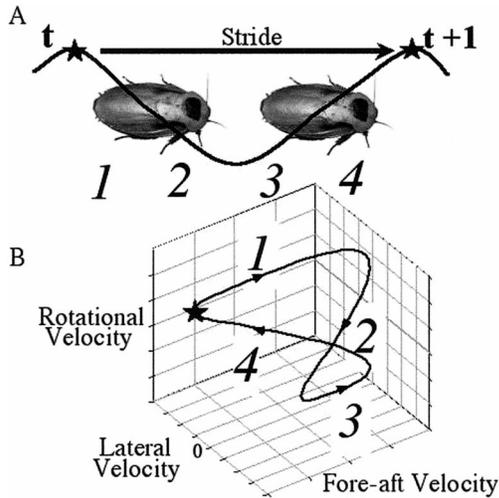
FIG. 1. Periodic orbit or limit cycle. A. Variation in a single state variable, lateral velocity over one stride. A cycle is present within which lateral velocity repeats from t to t +1. B. Periodic orbit showing a limit cycle in state space. Lateral, rotation and fore-aft velocity oscillate following a regular trajectory over a stride. Any point in the cycle can be considered an equilibrium point (star) of the associated return map.

Two types of stability exist—asymptotic and neutral. Characterizing stability requires perturbations to state variables (Fig. 2). Most generally, stability can be defined as the ability of a system to return to a stable limit cycle or equilibrium point after a perturbation. There are at least two types of stable systems. In an asymptotically stable system, the return after the perturbation is to the original equilibrium or limit cycle. In a neutrally stable system, the return to stability after perturbation is to a new, nearby, equilibrium or limit cycle. In an unstable system perturbations tend to grow.

Quantifying the rate of recovery from a perturbation. Return of a perturbed state variable to a limit cycle can be mapped discretely from cycle to cycle at the same phase (Fig. 3A, B). Mapping all possible perturbations from one cycle to the next produces a return map. A linearized version of the mapping function (an n × n matrix, if there are n state variables) can yield quantitative measures of stability for a local region (Guckenheimer and Holmes, 1983; Strogatz, 1994). The percentage of the perturbation remaining after each cycle is given by the eigenvalue. Eigenvalues closer to zero indicate a more rapid rate of recovery, whereas values closer to one indicate a slower rate of recovery. A stability value (eigenvalue) of 0.37 means that only 37% of the perturbation remains after a single cycle (Fig. 3B). In the next cycle, the remaining perturbation is reduced again by 37%, so that only 13.7% is left. Reducing the perturbation by a constant percentage after each cycle results in asymptotic recovery.

Quantifying the direction of recovery from a perturbation. The local direction of recovery is given by the eigenvectors of the linearized mapping function (Fig. 3C). If a state variable is perturbed, and no other
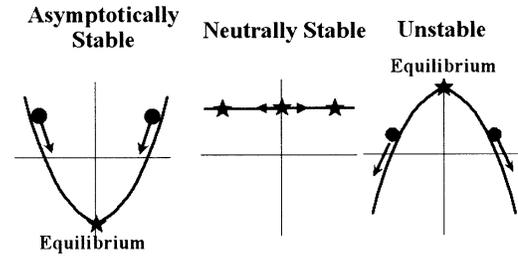

FIG. 2. Types of stability. Schematic representations of asymptotic stability with an equilibrium point (star), neutral stability with a continuum of equilibrium points, and an example of instability. The axes represent any two state variables.

state variable is affected as recovery begins, then the system is said to be uncoupled. In this case, the eigenvectors lie along the axes of the state variables. More often, perturbations delivered in one direction necessarily result in perturbations in other directions because the system is coupled dynamically (Fig. 3D). In a coupled system, the eigenvectors do not coincide with the state variables axes. The return path depends on the relative rates of recovery along the eigenvectors. The rate of recovery from a perturbation in one direction can differ from rates in other directions. For example, a perturbation increasing lateral velocity alone could result in a rapid increase in rotational velocity as lateral velocity begins to recover (Fig. 3F). After several cycles, both rotational and lateral velocity may recover back to equilibrium together slowly. The coupled dynamics could be explained by two independent, orthogonal eigenvectors that differ in rates of recovery. The eigenvector showing rapid recovery (eigenvalue = 0.37) pulls the system toward a decrease in lateral velocity, while increasing rotational velocity (Fig. 3I). The eigenvector showing slow recovery (eigenvalue = 0.72) pulls the system toward a decrease in both lateral and rotational velocity (Fig. 3L). Initially, the fast eigenvector dominates, producing partial recovery from the lateral velocity perturbation, but creating a natural perturbation in rotational velocity. Later, the slower eigenvector dominates, producing recovery in both state variables.

Quantifying neutral stability and instability. Stability values (eigenvalues) that approach or equal one imply that state variables recover slowly to the original equilibrium or not at all. A value of one indicates recovery to a new equilibrium and neutral stability (Fig. 3M–O). If the stability value (eigenvalue) is greater than one, then perturbations along that eigenvector grow and the system is unstable (Fig. 3P–R).

Forming hypotheses of control—the importance of working with the natural dynamics

A formal dynamical analysis can be a powerful mathematical tool when used for hypothesis generation, rather than simply as one of many curve-fitting techniques. Hypotheses of neural control at the level of the whole animal can be generated from the stability analysis of dynamic models. One such template is the
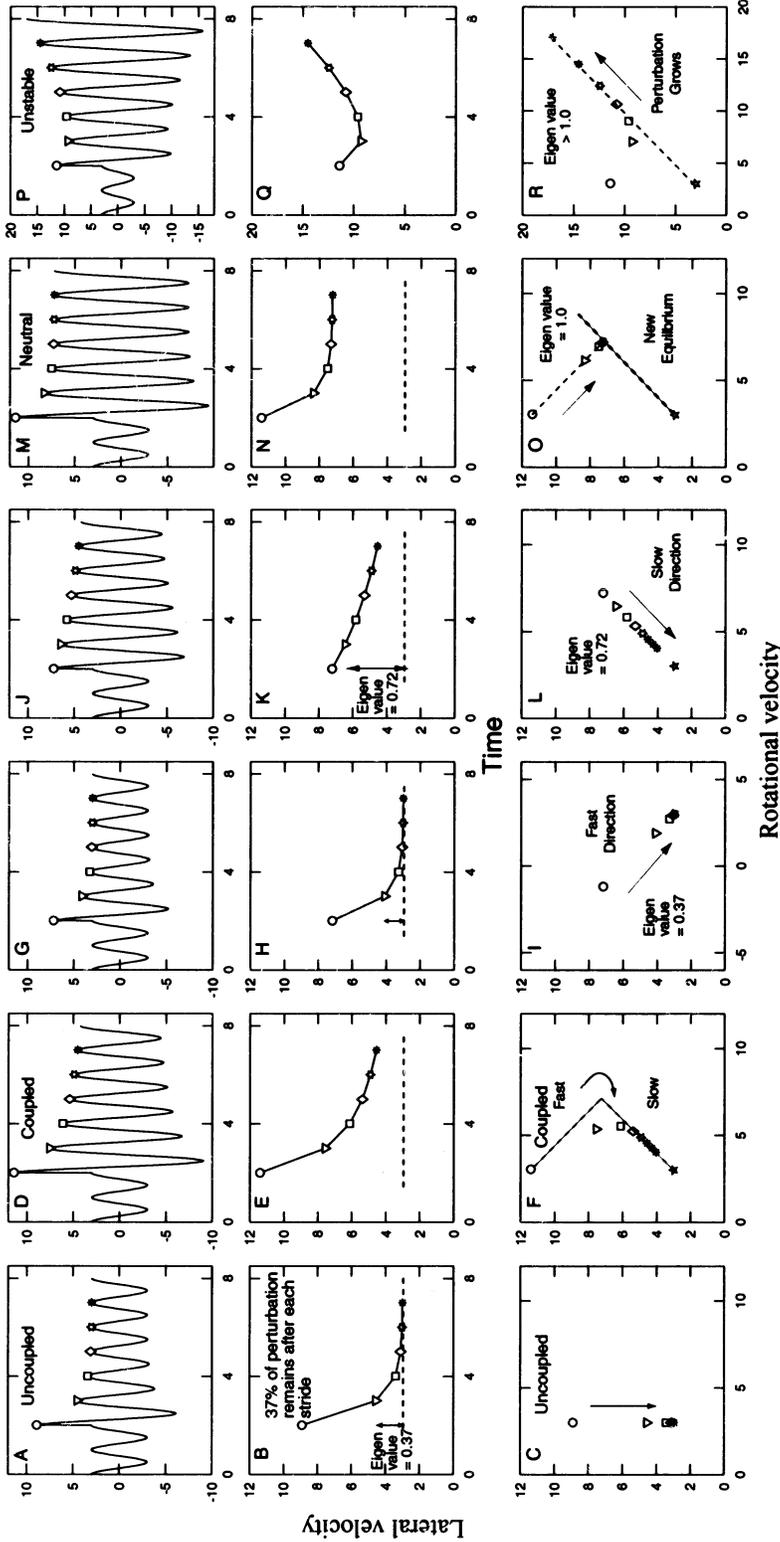
FIG. 3.   Quantifying dynamic stability. First row simulates the change in lateral velocity of the body over time. Second row shows the rate of recovery (eigenvalue) in lateral velocity of the body over time. The dashed horizontal line in the second row represents the equilibrium value. Third row shows the direction of recovery (eigenvector) in lateral and rotational velocity of the body. Arrows show the direction of recovery, except in the case of instability. Stars represent equilibrium points. The initial perturbations are represented by open circles. A–C. Asymptotic recovery in an uncoupled system—lateral velocity perturbation. In this model, the perturbation in lateral velocity only affects lateral velocity. The eigenvalue corresponds to the percent of the perturbation remaining after each stride. D–F. Asymptotic recovery in a coupled system—lateral velocity perturbation. In this model, the perturbation in lateral velocity affects both lateral and rotational velocity. Fast and slow components of recovery are apparent. G–I. Asymptotic recovery in a coupled system—direction of slow recovery. Perturbation in lateral and rotational velocity. J–L. Asymptotic recovery in a coupled system—direction of fast recovery. Perturbation in lateral and rotational velocity. M–O. Neutral stability in a coupled system. Perturbation in lateral velocity with recovery along the fast direction to a new equilibrium. P–R. Instability in a coupled system.
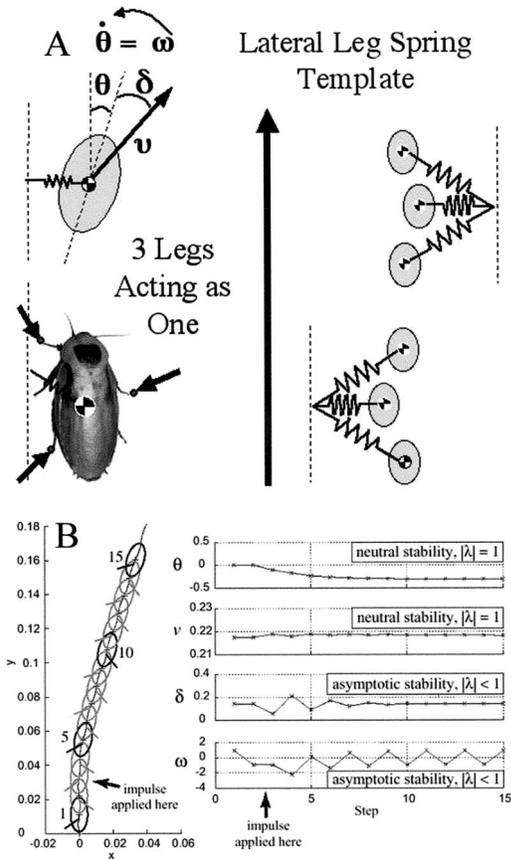
FIG. 4. Model of a passive, dynamic self-stabilizing system. A. Lateral Leg Spring model (Schmitt and Holmes, 2000a, b). Three legs of an insect's stance support tripod are collapsed to a single virtual leg spring. The template bounces from side to side as it moves forward. B. Response to perturbation. The diagram shows the model recovering from a perturbation to a stable gait ($v = 0.2175$, $\delta = 0.14$, $\theta = 0$, $\omega = -0.9295$ with parameters k = 2.25, m = 0.0025, I = 2.04×10^{-7}, d = -0.0025, $\beta = 1$), applied at the beginning of the third step. The graphs show the state variables at the beginning of each step. The model is neutrally stable in θ and v (corresponding eigenvalues = 1), but asymptotically stable in ω and δ; the corresponding eigenvalues are less than one in magnitude. Note that ω changes sign with each step and so is not expected to decay to a straight line as the other state variables do. (From Schmitt et al., 2002.)

recently proposed Lateral Leg Spring Model for terrestrial locomotion in the horizontal plane (Fig. 4A; Schmitt and Holmes, 2000a, b), inspired by the more anchored model (Kubow and Full, 1999).

Self-stabilization without neural reflexes—the lateral leg spring template. Animals appear to bounce from side to side as they run, just as they bounce up and down. A single virtual passive leg spring projecting laterally in the horizontal plane represents a group of legs in each stance phase (Schmitt and Holmes, 2000a). The dynamic model has three degrees of freedom, as the body is free to rotate and translate in the fore-aft and lateral direction. Relevant state variables describing its behavior include heading ($\theta + \delta$; the compass direction), forward velocity (v), body orientation (δ; difference between the long axis of the body

and direction of travel) and rotational velocity (ω; in yaw). Surprisingly, the template passively self-stabilizes when perturbed (*e.g.,* pushed to the side) during running without the equivalent of neural reflexes (Fig. 4B). A formal dynamical analysis shows that heading and forward velocity are neutrally stable (eigenvalues = 1), whereas body orientation and rotational velocity are asymptotically stable (eigenvalues < 1).

Exert more control in directions that are neutrally stable or recover slowly via passive dynamics. The Lateral Leg Spring Template adopts a stable heading and velocity after a perturbation, but these differ from those observed before the perturbation (Schmitt *et al.,* 2002). Stability analysis of the template predicts that if the animal is to maintain its compass direction (heading) and forward velocity after a perturbation, then it must exert neural feedback to do so. In general, variables that are near neutral stability or are unstable will likely require more control by active feedback with the equivalent of neural reflexes. By more control, we mean a greater amount of computation, and a greater degree of timely, sensory information stimulating muscles that demand different phase relationships to produce stability.

Exert less control in directions that rapidly recover via passive dynamics. By contrast, the naive use of feedback to control a single state variable that recovers rapidly by way of natural dynamics can actually result in a less stable system with a slower recovery to a perturbation. For example, if rotational velocity and body orientation are perturbed in one direction, then the natural dynamics will first increase the perturbation by overshooting the equilibrium and then spiral towards it in a few strides (Fig. 5A; *e.g.,* start lower left). Likewise, if rotational velocity and body orientation are perturbed in the other direction, then the natural dynamics will first increase the perturbation by overshooting the equilibrium and then spiral towards it in a few strides (Fig. 5A; *e.g.,* start upper right). Consider a perturbation that increases rotational velocity to the right, but body orientation to the left (Fig. 5B; *e.g.,* start upper left). One simple control strategy would be to urgently realign the body position in the next stride using negative feedback. Unfortunately, the natural dynamics would begin to recover body rotational velocity, but would misalign the body orientation nearly back to the original perturbed value. If negative feedback were applied repeatedly (Fig. 5B; dashed lines), the next stride would consistently result in a re-perturbation of body orientation. A more effective control strategy would be to simply do nothing and let the natural dynamics correct the perturbation over several strides. Alternatively, negative feedback could be applied along the eigenvector adjusting rotational velocity in concert with body orientation.

Forming hypotheses on the dynamic stability of animal design

A formal stability analysis used in conjunction with a dynamic model can yield testable hypotheses of an-
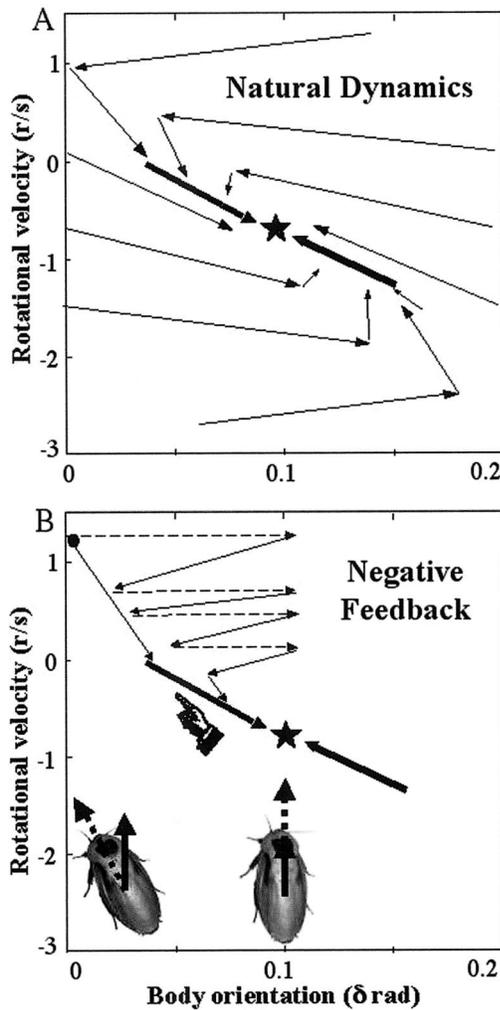
FIG. 5. Control strategies working with and against the natural dynamics. A. Return map of the Lateral Leg Spring Template to perturbations in rotational velocity and body orientation. The star represents the equilibrium values. Arrows show the path of recovery dictated by the natural dynamics with no feedback imposed. Thin arrows represent one stride and thick arrows three or more strides. B. Negative feedback working against the natural dynamic. The closed circle represents a perturbation away from equilibrium (star) in the direction of the pointing hand. Dashed arrows show an instantaneous correction in body orientation to the equilibrium value provided by negative feedback. Thin arrows represent changes in one stride due to the natural dynamics. Recovery takes fewer strides without feedback when the natural dynamics is rapid.

imal design when the model's parameters are varied. Small variations in parameters may reflect individual differences, whereas larger changes could make predictions about species differences. Varying individual parameters is likely to reveal just how tuned or dependent parameters are on one another.

The Lateral Leg Spring Template predicts that insects may be a rather highly tuned system. Average forward velocity (υ), body mass (m), virtual leg spring stiffness (k), body inertia (I), landing angle (β), and virtual leg length (l) are parameters of the model that can profoundly affect its behavior in general and its

stability in particular. When parameter values approximating those of an insect (*Blaberus discoidalis*) are input into the model, the model self-stabilizes after a perturbation without need for negative feedback. The extent of this stability (eigenvalue or percentage of the perturbation remaining after each cycle) varies as a function of the parameter values.

Stability varies as forward velocity is increased (Fig. 6A). At subcritical forward velocities, here less than 0.16 m/sec, the template predicts that no stable gaits exist. At forward velocities greater than 0.16 m/sec, the template predicts a periodic gait with heading and forward velocity after a perturbation being neutrally stable (eigenvalue = 1), whereas body orientation and rotational velocity are asymptotically stable (eigenvalue < 1). The effectiveness of recovery of the template can be shown best by quantifying the recovery rate of the slowest variable (maximum eigenvalue less than 1) at each forward velocity. As a parameter is varied, the template is most stable when its slowest recovering variable recovers more rapidly than any other parameter value. With respect to forward velocity, the template predicts the insect to be most stable at a velocity of 0.22 m/sec (Schmitt *et al.*, 2002). Slower or faster velocities are less stable. Remarkably, the preferred speed of the animal is very near 0.22 m/sec (maximum speed approximately 0.7 m/sec; Kram *et al.*, 1997; Ting *et al.*, 1994; Full and Tu, 1990). A similar pattern is observed for the other parameters. The most stable virtual leg stiffness value is found near the estimate for the actual insect (Fig. 6B). Relatively small variations in inertia away from the animal's value decreases stability (Fig. 6C). Varying virtual leg length and landing angle (sprawl) away from the animal's values also reduce stability (Fig. 6D, E). Hence, the template predicts that the insect is operating at or near optimal conditions for passive, dynamic self-stabilization.

Testing hypotheses of passive, dynamic self-stabilization in running animals is challenging. Preliminary experiments on cockroaches lend support to this hypothesis for brief (10 msec), lateral perturbations (Jindrich and Full, 2001). Cockroaches were able to initiate recovery in less than 15 msec within the step during which an impulsive perturbation occurred. Preflexes (musculo-skeletal, spring and damper-like behavior) appear to dominate rapid stabilization, rather than neural reflexes.

Quantifying maneuverability with simple measures

Maneuverable animals can veer, climb, dive, turn, stop and negotiate obstacles with ease. Descriptions of maneuverability for all modes of locomotion are growing in number (see this volume). Unfortunately, maneuverability can be far more difficult to quantify fully than stability. A common theory and general maneuverability metrics need to be developed. Here we describe two indices for terrestrial turning as an example of simple measures that might allow valuable comparisons (Jindrich and Full, 1999).
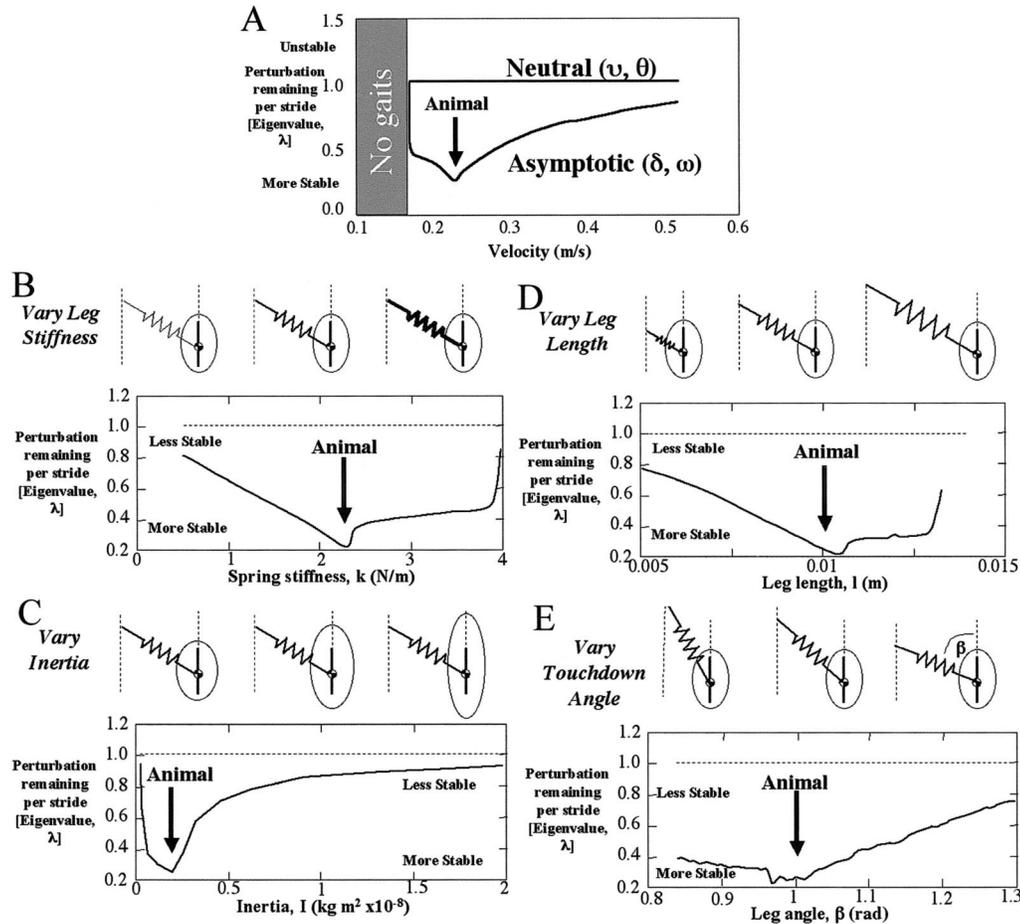
FIG. 6. Stability of the Lateral Leg Spring Template as a function of speed, body mass and animal design. The stability measure is the amount of perturbation remaining after each stride (eigenvalue). Eigenvalues less than one reveal asymptotic stability, whereas as values greater than one represent instability. Eigenvalues equal to one signify neutral stability. Forward velocity (υ) and heading (θ) are neutrally stable. Asymptotically stable eigenvalues plotted correspond to the slowest recovering variable (maximum among eigenvalues less than 1) at each parameter value. Arrows represent the parameter value estimate for an insect (cockroach, *Blaberus discoidalis*). A. Forward velocity (υ). Grey area represents the range of velocities where no stable, periodic gaits are found. B. Virtual leg spring stiffness (k). C. Body inertia (I). D. Virtual leg length (l). E. Landing angle (β).

Simple maneuverability measures for turning. Executing a successful turn involves at least two requirements. The animal's average heading (the direction of the average velocity vector of the center of mass) must be deflected, and the animal's body must rotate to keep the body axis aligned with its heading (Fig. 7). In mechanical terms, the change in linear momentum must be accompanied by a transient pulse in angular momentum. Animals must generate coordinated linear and angular impulses.

The amount of deflection or change in heading will depend on the impulse perpendicular to the direction of movement relative to the animal's forward momentum (Linear Maneuverability Number, LMN; Jindrich and Full, 1999). A larger perpendicular force exerted over a longer period of time will increase the change in heading or turning angle (high LMN; Fig. 7A). Greater body mass or faster forward velocity for the same perpendicular impulse will decrease the change in heading and cause a smaller turn indicated by a low

LMN value. Running cockroaches are able to generate perpendicular force impulses comparable to 3/4 their linear momentum (LMN = 0.75) to produce 22–73 degree turns. The LMN has also been used by Drucker and Lauder (2001) to quantify turning in sunfish where values ranged from 0.12–0.74.

The second requirement for a successful turn involves rotating the body axis so that it aligns with the direction of the velocity vector (Fig. 7B). Minimizing the degree of misalignment between the angle of deflection (θ_d) and the angle of body rotation (θ_r) is important for resuming straight running following a turn (Jindrich and Full, 1999). The ratio of θ_r/θ_d can provide an index of how effective a propulsor or an appendage, such as a leg, can be in generating a torque to match the angle of deflection to the angle of rotation (Propulsor effectiveness number, PEN). The torque generated by a perpendicular force can under-rotate the body ($\theta_r < \theta_d$; PEN < 1) or over-rotate it ($\theta_r > \theta_d$; PEN > 1). Analysis of cockroach turning shows that
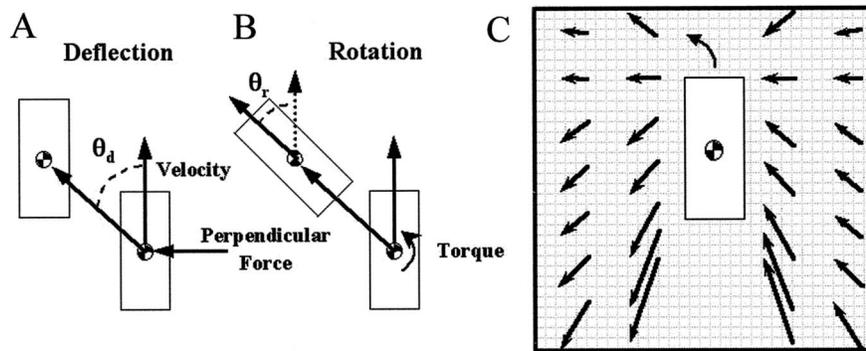
FIG. 7. Maneuverability measures. A. Change in heading. Perpendicular force generating a deflection of angle θ_d. B. Change in body orientation. Torque generating a body rotation of angle θ_r. C. Single leg forces required to produce a turn as a function of leg position. The grid shows position relative to the center of mass. Arrows represent force vectors necessary to turn model so that the angle of deflection equals the angle of rotation. (After Jindrich and Full, 1999.)

legs on the outside of the turn placed well in front of the center of mass are most effective in producing turns, whereas hind legs are the least effective and require the largest forces (Fig. 7C).

Turning the Lateral Leg Spring Template—altering the center of pressure is most effective. Turning in many-legged, sprawled-posture animals is most often viewed as resulting from an increase in step length, leg length or stride frequency of the outside legs (Franklin *et al.*, 1981; Frantsevich and Mokrushov, 1980; Graham, 1972; Jander, 1985; Strauss and Heisenberg, 1990; Zollikofer, 1994). Small turns by the Lateral Leg Spring Template can be elicited in 2–6 steps by lengthening and/or stiffening the outside virtual leg spring or increasing its step length (*i.e.,* decreasing its touchdown angle, β; Schmitt and Holmes, 2000*b*). But such turns are fragile. Parameters must be selected carefully to avoid unstable behavior and/or unnatural body orientations and headings. Propulsor effectiveness is poor, as the body orientation does not match the changes in heading. Although these mechanisms can produce a turn in actual animals, the small changes in the kinematics of cockroach turning are inconsistent with observed behavior (Jindrich and Full, 1999).

Large turns of 20–70 degrees are more easily elicited in the Lateral Leg Spring Template by a forward shift of the center of pressure (attachment point of the outside leg). The same appears to be true in the animal (Jindrich and Full, 1999). The individual foot forces of cockroaches sum to act as a single leg generating a force at a particular point on the body equivalent to the center of pressure. As in the Lateral Leg Spring Template, cockroaches appear to alter their center of pressure to produce a turn by using legs on the outside of the turn to generate the majority of force and torque impulse. Thus transient center of pressure positions may provide a third useful turning index.

The next steps in animal locomotion—stability and maneuverability

The study of stability and maneuverability not only has obvious behavioral and ecological relevance, but is also critical if animal design is to be determined. Animals appear to be grossly over-built for steady-state, straight-ahead locomotion. They appear to possess too many neurons, muscles, joints and even too many appendages. Bernstein (1935) realized that for any particular task neuromotor synergies must exist. Groups of neurons, muscles, joints and legs work together as if they were one (see, for example, Full, 1993; Raasch *et al.*, 1997). We argue that to ultimately reveal function, an animal performing steady-state locomotion must be subjected to perturbations (Full and Koditschek, 1999). Neuromotor synergies must be discovered, probed and broken if we desire a more complete understanding of an organism and all its parts.

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