The role of the mechanical system in control: a hypothesis of self-stabilization in hexapodal runners

T. M. Kubow and R. J. Full

Department of Integrative Biology, University of California at Berkeley, Berkeley, CA 94720, USA

To explore the role of the mechanical system in control, we designed a two-dimensional, feed-forward, dynamic model of a hexapodal runner (death-head cockroach, Blaberus discoidalis). We chose to model many-legged, sprawled posture animals because of their remarkable stability. Since sprawled posture animals operate more in the horizontal plane than animals with upright postures, we decoupled the vertical and horizontal plane and only modelled the horizontal plane. The model was feed-forward with no equivalent of neural feedback among any of the components. The model was stable and its forward, lateral and rotational velocities were similar to that measured in the animal at its preferred velocity. It also self-stabilized to velocity perturbations. The rate of recovery depended on the type of perturbation. Recovery from rotational velocity perturbations occurred within one step, whereas recovery from lateral perturbations took multiple strides. Recovery from fore-aft velocity perturbations was the slowest. Perturbations were dynamically coupled—alterations in one velocity component necessarily perturbed the others. Perturbations altered the translation and/or rotation of the body which consequently provided ‘mechanical feedback’ by altering leg moment arms. Self-stabilization by the mechanical system can assist in making the neural contribution of control simpler.

Keywords: locomotion; biomechanics; insects; arthropods

1. INTRODUCTION

‘Many researchers in neural motor control think of the nervous system as a source of commands that are issued to the body as direct orders. We believe that the mechanical system has a mind of its own, governed by the physical structure and laws of physics. Rather than issuing commands, the nervous system can only make suggestions which are reconciled with the physics of the system and task [at hand]’ (Raibert & Hodgins 1993, p. 350).

Despite Raibert & Hodgins (1993) recognition that the nervous-control system, the mechanical system, and the environment all interact to determine behaviour, appeals (Chiel & Beer 1997) urging true integration are still required. In the present manuscript, we propose a simple control hypothesis for sprawled posture locomotion. We determined the extent of control offered by a feed-forward system without the benefit of feedback from the equivalent of neural reflexes. We contend that an understanding of the control algorithms potentially embedded in the mechanical system is required to define the variables controlled by the nervous system. Once control tasks are identified, then we can lay on the appropriate types of neural feedback over the control provided by the mechanical system. In the future, this approach could lead to a general control model resulting from the synthesis of feed-forward and feedback models that take advantage of the mechanical system (Schmitz et al. 1995; Cruse et al. 1996).

We chose to model sprawled posture arthropods because of their remarkable stability, simple nervous system and an increased probability that their mechanical system contributes to control. Sprawled posture animals are stable, in the vertical plane, because the height of their centre of mass is low relative to the width of their support base. As a result, sprawled posture animals can resist over-turning torques better than animals with upright postures (Alexander 1971). Sprawled posture animals with at least three legs on the ground can be statically stable during locomotion if their centre of mass falls within the tripod of support (Gray 1944; Ting et al. 1994).

We chose to make the model dynamic. Blickhan & Full (1987) demonstrated that rapid-running, legged arthropods must be treated as dynamic systems. Six- and eight-legged, sprawled posture animals accelerate and decelerate their bodies with each step in the same way as two- and four-legged animals do (Cavagna et al. 1977; Full 1989; Blickhan & Full 1993). Legged animals with both sprawled and upright postures can be modelled in the vertical plane as bouncing, spring-mass systems (Blickhan 1989; Alexander 1990; McMahon & Cheng 1990; Blickhan & Full 1993; Farley et al. 1993). Moreover, ghost crabs, cockroaches and ants exhibit aerial phases at fast speeds (Burrows & Hoyle 1973; Blickhan & Full 1987; Full & Tu 1991; Zollikofer 1994). The American cockroach runs on only two legs when sprinting at 50 body lengths per second (Full & Tu 1991). Most importantly, rapid-running...
insects can be statically unstable even when they have three legs on the ground at once (Ting et al. 1994). A cockroaches' centre of mass can fall outside its tripod base of support at fast speeds, yet the animal remains dynamically stable.

We chose a two-dimensional (2D), horizontal plane model for several reasons. We decoupled the model from the vertical plane because sprawled posture animals may operate primarily in the horizontal plane (Binnard 1995; Full 1997). The negative consequences of falling so close to the substrate in sprawled posture animals may be minor compared to the disruption of movement in the horizontal plane. Moreover, a whole suite of legged morphologies permit bouncing in the vertical plane. Perhaps the advantages and disadvantages of the sprawled posture morphology become more evident in the horizontal plane. Evidence for this contention comes from data on the individual-leg ground-reaction forces in cockroaches (Full et al. 1991). Legs generate opposing forces throughout the step period (figure 1). The zero horizontal foot force interaction criteria used in the design of some legged robots (Waldron 1986) to reduce energy expenditure is violated. The front (prothoracic) pair of legs only decelerate the insect during the stance phase, while at the same time the hind (metathoracic) pair of legs only accelerate the animal forward. The middle (mesothoracic) pair of legs first decelerate and then accelerate the body during a step. Large lateral forces have been measured (Full et al. 1991). Ground reaction forces tend to align along the axis of each leg, minimizing joint torque (Full et al. 1991; Full 1993).

Surprisingly, we discovered that the present 2D, feed-forward, dynamic, hexapod model self-stabilized to perturbations.

2. THEORETICAL MODEL

(a) Model description and assumptions

Our 2D, dynamic, hexaped model was anchored in the wealth of biomechanical data collected on running deathhead cockroaches, Blaberus discoidalis (Full & Ti 1990; Full et al. 1991, 1993; Blickhan & Full 1993; Ting et al. 1994; Kram et al. 1997). We assumed the model to be a hexaped with a rigid body and massless legs (figure 1). Movement was constrained to the horizontal plane. This choice of plane completely removed gravity from the model. Only three degrees of freedom were permitted, two translational and one rotational. We defined the two translational degrees of freedom in two coordinate systems. In the global reference frame, we defined forward movement as positive $y$, whereas sideways movement was defined as movement along the $x$-axis (figure 2). In the reference frame of the body, fore–aft movement was in the head-to-tail direction and lateral motion was to the left or right (figure 2).

We did not include segmented legs in the model. Force inputs were single-leg ground-reaction forces acting on the body at a given foot position which stayed fixed relative to the ground for the duration of a step. The model would be underconstrained in determining joint torques and angles if we included leg segments without additional data.

The model's control system was purely feed-forward. Explicit feedback control algorithms were not included. Leg forces were generated relative to the body using the same pattern during every step. Perturbations will undoubtedly alter leg force patterns in the animal. We contend that the response to a perturbation could consist of at least three components: (i) an active component resulting from reflexes; (ii) a passive, rapid...
component resulting from intrinsic musculoskeletal properties; and (iii) a passive component dependent on posture. We chose not to model all three of these components first given the lack of experimental data. To model the complete system, we argue that it is preferable to model first the stabilizing effect of posture on whole body dynamics and only then add rapid, passive and reflexive components. Given this approach, the assumption of a constant force pattern certainly demands future testing. There were no input kinematics other than the initial foot positions relative to the body at the beginning of each step, stride period, and duty factor (table 1). Stride length and the movement of the centre of mass (e.g. the three resultant velocities) were the model’s outputs.

All forces were approximated as sine-wave functions. The force produced during each step by a single leg was a half sine or 180°, except for the fore–aft force of the middle leg which was a full sine-wave function. The peak of each wave used were the average maximal values recorded from the animals (table 1).

(b) Modelling environment

We created the model using a dynamic modelling program (Working Model 4.0, Knowledge Revolution, CA).

![Figure 2. Coordinate system of 2D dynamic hexapod model.](image)

(a) $x, y$ represent the global coordinate system where $y$ is in the forward direction and $x$ represents movement to the side. (b) $j$ represents the coordinate system relative to the body axis where 1 is the fore–aft and 2 is the lateral axis. Positive fore–aft is towards the anterior of the animal. Positive lateral is towards the animal’s right side when viewed dorsally. (c) For a body rotation of zero, body (fore–aft, lateral) and global ($x, y$) coordinate systems are the same. Legs are numbered from $i = 1–6$ (front left, middle right, back left, front right, middle left, back right, respectively).

The simulation used a Kutta–Merson integrator with a variable time-step and an error of $1 \times 10^{-3}$. Time constants of stabilization were estimated by fitting velocity versus time to an exponential curve (Kaleidagraph, Synergy Software, PA). To generate plots illustrating the mechanisms behind the self-stabilization, we also implemented the model in a mathematics package (Matlab 5.1, The Mathworks, Inc., MA) for the special case of a duty factor of 0.5. We integrated with Matlab function ode23 and its default parameters (relative error of $1 \times 10^{-3}$ and absolute error of $1 \times 10^{-6}$).

(c) Model equations and symbols

We defined the dynamic model’s movement in global coordinates ($x, y$; figure 2). We refer to parameters relative to the body as fore–aft (head–tail; $j = 1$) and lateral (side-to-side; $j = 2$).

Leg force production ($F$) for the middle legs in the fore–aft direction was defined as

$$F_y = A_j \sin(\frac{2\pi s}{k})$$

for $k \gg s \gg 0$ and $i = 2, 5$ and $j = 1$ where $i$ represents a particular leg (1–6, see figure 2), $j$ designates direction relative to the body axis (1, fore–aft and 2, lateral), $A$ is force amplitude (N), $s$ is the remainder of $(t + \tau - \phi_j)/\tau$, $t$ is time (s), $\phi$ is phase shift relative to the left front leg, $\tau$ is stride period (s), $k$ is the stance period (s) equal to $\tau \delta$ and $\delta$ is duty factor (see Appendix A).

Leg force production for the lateral forces of the middle legs and for the front and hind legs in both directions was defined as

$$F_y = A_j \sin(\frac{\pi s}{k})$$

during the swing period

$$k < s < \tau, F_y = 0.$$

Table 1. Inputs in the 2D dynamic model of the cockroach, Blaberus discoidalis

<table>
<thead>
<tr>
<th>variable</th>
<th>reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>body mass (kg)</td>
<td>0.0025</td>
</tr>
<tr>
<td>body inertia: yaw (kg m⁻²)</td>
<td>2.04 × 10⁻²</td>
</tr>
<tr>
<td>stride frequency (Hz)</td>
<td>10</td>
</tr>
<tr>
<td>duty factor</td>
<td>0.6</td>
</tr>
<tr>
<td>leg position $x, y$ (m)</td>
<td>Kram et al. 1997</td>
</tr>
<tr>
<td>front</td>
<td>± 0.011, 0.02</td>
</tr>
<tr>
<td>middle</td>
<td>± 0.013, 0.007</td>
</tr>
<tr>
<td>hind</td>
<td>± 0.013, 0.01</td>
</tr>
<tr>
<td>fore–aft leg force magnitude (N)</td>
<td>Full et al. 1991</td>
</tr>
<tr>
<td>front</td>
<td>-0.0049</td>
</tr>
<tr>
<td>middle</td>
<td>± 0.004</td>
</tr>
<tr>
<td>hind</td>
<td>0.0049</td>
</tr>
<tr>
<td>lateral leg force magnitude (N)</td>
<td>Full et al. 1991</td>
</tr>
<tr>
<td>front</td>
<td>± 0.0051</td>
</tr>
<tr>
<td>middle</td>
<td>± 0.0051</td>
</tr>
<tr>
<td>hind</td>
<td>± 0.01, 0.0032</td>
</tr>
</tbody>
</table>

* Colour plots used to illustrate the mechanism of stabilization used a duty factor of 0.5 to simplify the calculations.
The total force \( (TF) \) produced by all legs was

\[
TF_j = \sum_{i=1}^{6} F_{ij}. \tag{4}
\]

We capitalized on the many symmetries in the motion. For example, by using an alternating tripod

\[
\phi_1 = \phi_2 = \phi_3 \Rightarrow s_1 = s_2 = s_3, \tag{5}
\]

\[
\phi_4 = \phi_5 = \phi_6 \Rightarrow s_4 = s_5 = s_6. \tag{6}
\]

Force opposition in the fore–aft force of the front and hind legs allows

\[
A_{11} = -A_{31}, \tag{7}
\]

\[
A_{41} = -A_{61}, \tag{8}
\]

and lateral force opposition in the front and middle legs gives

\[
A_{12} = -A_{22}, \tag{9}
\]

\[
A_{42} = -A_{52}. \tag{10}
\]

Using these symmetries to cancel terms, we can expand the summation of equation (4)

\[
F_{11} = -F_{31}, \tag{11}
\]

\[
F_{41} = -F_{61}, \tag{12}
\]

\[
TF_1 = F_{21} + F_{41} \text{(middle legs)}, \tag{13}
\]

\[
TF_2 = F_{32} + F_{62} \text{(hind legs)}. \tag{16}
\]

Rotating to global coordinates (global positive \( y \) points anteriorly when the model has zero body rotation; global positive \( x \) points to the model’s right when viewed dorsally; figure 2), the translational acceleration of the centre of mass in the \( y \) and \( x \) direction become

\[
\ddot{y} = (TF_1 \cos(\theta) + TF_2 \sin(\theta))/m, \tag{17}
\]

\[
\ddot{x} = (TF_2 \cos(\theta) - TF_1 \sin(\theta))/m, \tag{18}
\]

where \( \theta \) is body rotation relative to the \( y \)-axis (positive being anticlockwise when model viewed dorsally; figure 2) and \( m \) represents body mass.

Expanding, we find that force in the \( y \)-direction is primarily due to the fore–aft force of the middle legs, but for larger rotations is influenced by the lateral force of the hind legs.

\[
\ddot{y} = [A_{32} \sin(\pi s_2/k) + A_{42} \sin(\pi s_2/k)] \cos(\theta)
+ [A_{33} \sin(\pi s_3/k) + A_{43} \sin(\pi s_3/k)] \sin(\theta)]/m, \tag{19}
\]

\[
\ddot{x} = [(A_{32} \sin(\pi s_2/k) + A_{42} \sin(\pi s_2/k)) \times \cos(\theta)
- (A_{33} \sin(\pi s_3/k) + A_{43} \sin(\pi s_3/k)) \times \sin(\theta)]/m. \tag{20}
\]

Torque can be calculated from the moment arms \( (l) \) and forces in the fore–aft \( (j = 1) \) and lateral \( (j = 2) \) directions:

\[
l_{il} = (p_{l2} \times \cos(\theta(t - s_l)) - p_{l1} \times \sin(\theta(t - s_l))
- x(t) + x(t - s_l)) \times \cos(\theta(t))
+ (p_{l3} \times \cos(\theta(t - s_l)) + p_{l2} \times \sin(\theta(t - s_l))
- y(t) + y(t - s_l)) \times \sin(\theta(t)), \tag{21}
\]

\[
l_{il} = (p_{l2} \times \cos(\theta(t - s_l)) + p_{l3} \times \sin(\theta(t - s_l))
- y(t) + y(t - s_l)) \times \cos(\theta(t))
+ (p_{l2} \times \cos(\theta(t - s_l)) - p_{l3} \times \sin(\theta(t - s_l))
- x(t) + x(t - s_l)) \times \sin(\theta(t)), \tag{22}
\]

where \( p \) is position at leg touchdown relative to body position along fore–aft, lateral axis and \( x(t), y(t) \) specify the global location of the centre of mass.

The torque for each leg is

\[
T_i = (F_{i1} l_{i1} - F_{i2} l_{i2}). \tag{23}
\]

The total torque \( (TT) \) is the sum for all legs

\[
TT = \sum_{i=1}^{6} T_i. \tag{24}
\]

Because of the symmetries in the force equations and the fact the body position terms are equal for the three legs of a tripod some differences in moment arm lengths become only a function of body angle change during a stride. See equations (25)–(28) in Appendix B. Most noteworthy about these equations is that the moment arm differences are unchanged by motion of the centre of mass. Equal, but opposing leg forces which cancel, allow further simplification of the torque equations

\[
T_1 = -F_{31} l_{31} + F_{22} l_{22}, \tag{29}
\]

\[
T_2 = F_{21} l_{21} - F_{22} l_{22}, \tag{30}
\]

\[
T_3 = F_{31} l_{31} - F_{32} l_{32}, \tag{31}
\]

\[
T_4 = -F_{61} l_{41} + F_{52} l_{42}, \tag{33}
\]

\[
T_5 = F_{51} l_{51} - F_{52} l_{52}, \tag{34}
\]

\[
T_6 = F_{61} l_{61} - F_{62} l_{62}, \tag{35}
\]

\[
T_4 + T_5 + T_6 = F_{61} (l_{41} - l_{41}) + F_{52} (l_{42} - l_{52})
+ F_{51} l_{51} - F_{62} l_{62}. \tag{36}
\]
Substituting the moment arms from equations (25)–(28), total torque ($T_{\text{total}}$) becomes the sum of torque from four sources

$$T_{\text{front+hind}}(\theta) + T_{\text{front+middle}}(\theta) + T_{\text{hind}}(\theta, x) + T_{\text{middle}}(\theta, x),$$

where all sources are a function of $\theta$. $T_{\text{hind}}$ is the torque most affected by changes in $y$, and $T_{\text{middle}}$ is the torque most affected by changes in $x$. The forces listed in parentheses below the torques are those responsible for producing the torques. The explicit formulation of these torques are equations (B5)–(B8) in Appendix B. Fortunately, the primary components of these equations can be identified. First, $T_{\text{front+hind}}(\theta)$ (equation (B5)) is primarily the magnitude of the fore–aft forces of the front or hind legs multiplied by the lateral distance between their foot placements. Second, $T_{\text{front+middle}}(\theta)$ (equation (B6)) is primarily the magnitude of the lateral force of the front or middle legs multiplied by the fore–aft distance between their foot placements. Third, $T_{\text{hind}}(\theta, y)$ (equation (B7)) is the torque due to the lateral force of the hind legs, and is the torque primarily affected by changes in movement along the fore–aft axis. Finally, $T_{\text{middle}}(\theta, x)$ (equation (B8)) is the torque due to fore–aft force of the middle legs, and is the torque primarily affected by changes in movement along the lateral axis.

The four identifiable sources of torque are all affected by the amount of body rotation during a step. If we assume that the body rotates a small amount, so $\cos(\theta) >> \sin(\theta)$, then changes in initial fore–aft velocity primarily affect the torque created by the lateral force of the hind leg (equation (B7)) as the sine terms drop out of equation (B8) removing $y/\theta$. Similarly, changes in initial lateral velocity primarily affect the torque created by the fore–aft force of the middle leg (equation (B8)) as the sine terms drop out of equation (B7) removing $x/\theta$. Notice equations (B5) and (B6) have no centre of mass position terms.

3. MODEL INPUT PARAMETERS

The body mass and inertia used in the model were taken from direct measurements on the death–head cockroach, B. discoidalis (Kram et al. 1997; table 1). The stride period ($\tau$) and duty factor ($\delta$) were set to 100 ms and 0.6, respectively based on the data at a preferred velocity ($ca. 25\text{ cm}\text{s}^{-1}$ from Full et al. (1991)).

Leg position at touchdown relative to body coordinates with the centre of mass as the origin was estimated from three-dimensional kinematic data available from Kram et al. (1997) (table 1). The assumption of massless legs appears reasonable because when totalled they only represent 6% of the body mass in cockroaches compared to 20–50% in mammals and birds (Kram et al. 1997). Phase shift was made relative to the left front leg. We imposed a perfect alternating tripod, such that left front, right middle, and left hind legs all had the same phase of zero. Right front, left middle, and right hind legs all had the same phase of $\tau/2$, or 180° out of phase with the other three legs forming the tripod. The magnitude of the leg ground-reaction forces were taken from direct measurements using a force platform (Full et al. 1991; table 1).

There are three different types of initial state perturbations corresponding to the three degrees of freedom. We perturbed the velocity of the body independently along the fore–aft (figure 3b), lateral (figure 3c), and rotational

---

*Phil. Trans. R. Soc. Lond. B* (1999)
4. RESULTS AND DISCUSSION

(a) Model dynamics similar to an animal in stable state

The mean forward velocity of the model's centre of mass was 0.21 m s\(^{-1}\) with an amplitude of oscillation of ca. 0.013 m s\(^{-1}\) (figure 4a). The mean forward velocity was similar to that measured as the preferred speed of B. discoidalis (Full et al. 1991). The variation in forward velocity was comparable to that derived from force platform measurements (Full & Tu 1990). The period of oscillation of the model's centre of mass equalled half of the stride period. A deceleration during the first half of a step was followed by an acceleration. These are the same phase relationships observed by the cockroach during running (Full & Tu 1990).

The sideways (\(x\)-axis) velocity of the model's centre of mass fluctuated with a period equal to the stride period (figure 4b). The mean sideways (\(x\)-axis) velocity was zero with an amplitude of oscillation equal to 0.026 m s\(^{-1}\). These values were comparable to those derived from force platform measurements (Full & Tu 1990).

Body rotation fluctuated with the same period as lateral velocity with an amplitude of 12° (figure 4c). The pattern and magnitude of the body rotation were comparable to that measured in running animals (Kram et al. 1997).

(b) Slow rate of recovery from fore–aft velocity perturbations

We introduced a series of large, instantaneous velocity perturbations (initial fore–aft velocity = 0.00, 0.11, 0.22, 0.33, 0.44 m s\(^{-1}\)) to the model's centre of mass. The model recovered from each perturbation as a decaying exponential with nearly the same time constant (5 s; figure 5). Recovery to 63% of the stable fore–aft velocity took nearly 50 strides.

(c) Mechanism of recovery from fore–aft velocity perturbations

The model recovered from perturbations of fore–aft velocity because

(i) perturbing fore–aft velocity changed the distance the centre of mass travels during a step;
(ii) changes in the distance moved by the centre of mass altered the moment arm of the lateral forces produced by each leg (equation (22)). Alterations in...
the moment arms of the lateral forces change torques (equation (B7));
(iii) changes in torque shifted the phase of the body angle so as to align the lateral forces with the velocity vector. The lateral force component will produce a rearward \((y\text{-axis})\) deceleration at faster than stable velocities and a forward \((y\text{-axis})\) acceleration at slower than stable velocities (equation (17)).

Consider the example in which the model’s centre of mass was perturbed faster than the stable velocity (e.g. \(>0.3\,\text{m}\,\text{s}^{-1}\) for the 0.5 duty factor case, 0.21 normally). Single-headed arrows represent lateral forces perpendicular to the body. Double-headed arrows represent moment arms of the lateral forces. (b) End of the first step \(t_2\). The model’s centre of mass moved further forward than it would at its stable velocity. The more forward position of the centre of mass increased the lateral force moment arm of the left hind leg. The increased moment arm of the hind leg decreased the initial clockwise torque and subsequently increased the anticlockwise torque. Changes in torque reduced clockwise rotation relative to the stable velocity condition. The induced phase shift resulted in a body angle of near zero at the end of the first step. (c) Second step \(t_3\). The body axis was tilted to the left during the period of the second step. This body orientation generated a deceleration of the centre of mass in the reward \((y\text{-axis})\) direction tending to stabilize the forward velocity. Large arrow represents the net lateral force relative to the body.

The increased moment arm of the hind leg decreased the initial clockwise torque and subsequently increased the anticlockwise torque. Changes in torque reduced clockwise rotation relative to the stable velocity condition. The induced phase shift resulted in a body angle of near zero at the end of the first step. (c) Second step \(t_3\). The body axis was tilted to the left during the period of the second step. This body orientation generated a deceleration of the centre of mass in the reward \((y\text{-axis})\) direction tending to stabilize the forward velocity. Large arrow represents the net lateral force relative to the body.

Figure 6. A spatial model representing the mechanisms of recovery from a fore-aft velocity perturbation. (a) Beginning of the first step \(t_1\). The model’s centre of mass was perturbed faster than the stable velocity (i.e. \(>0.3\,\text{m}\,\text{s}^{-1}\) for the 0.5 duty factor case, 0.21 normally). Single-headed arrows represent lateral forces perpendicular to the body. Double-headed arrows represent moment arms of the lateral forces. (b) End of the first step \(t_2\). The model’s centre of mass moved further forward than it would at its stable velocity. The more forward position of the centre of mass increased the lateral force moment arm of the left hind leg. The increased moment arm of the hind leg decreased the initial clockwise torque and subsequently increased the anticlockwise torque. Changes in torque reduced clockwise rotation relative to the stable velocity condition. The induced phase shift resulted in a body angle of near zero at the end of the first step. (c) Second step \(t_3\). The body axis was tilted to the left during the period of the second step. This body orientation generated a deceleration of the centre of mass in the reward \((y\text{-axis})\) direction tending to stabilize the forward velocity. Large arrow represents the net lateral force relative to the body.

Consider the example in which the model’s centre of mass was perturbed faster than the stable velocity (e.g. \(>0.3\,\text{m}\,\text{s}^{-1}\) for the 0.5 duty factor case, 0.22 for the 0.6 duty factor case; figure 6a). During the first step, the model’s centre of mass moved further forward than it would at its stable velocity. The more forward position of the centre of mass increased the lateral force moment arm of the left hind leg (equation (22); figure 6b). The increased moment arm of the hind leg decreased the initial clockwise torque and subsequently increased the anticlockwise torque (equation (B7); lighter blue followed by darker red in figure 7). These changes in torque reduced clockwise rotation relative to the stable velocity condition. The induced phase shift resulted in a body angle of near zero at the end of the first step (time = 0.05 s; figure 8). As a result, the body axis was tilted to the left during the period of the second step (figure 6c; positive angles in figure 8). This body orientation generated a deceleration of the centre of mass in the rearward \((y\text{-axis})\) direction (equation (17); blue in figure 8) tending to stabilize the forward velocity.

(d) No recovery in heading from lateral velocity perturbations
Perturbations to lateral velocity \((-0.20, -0.10, 0, 0.10, 0.20\,\text{m}\,\text{s}^{-1})\) deflected the model’s centre of mass and produced a change in heading. The body rotation at the beginning of each stride eventually stabilized to a new angle equal to the arctan (lateral velocity perturbation/initial fore-aft velocity) (figure 9). The time constant for aligning the body axis with the new heading was approximately 0.8 s.

(e) Intermediate rate of recovery in lateral velocity from lateral velocity perturbations
The model recovered from each lateral velocity perturbation as a decaying exponential with nearly the same time constant \((0.8\,\text{s};\) figure 10). Recovery to 63% of the stable lateral velocity took approximately eight strides. Recovery from lateral velocity perturbations was more than six times faster than the recovery to a perturbation in fore-aft velocity.

(f) Perturbations are coupled
Single-component velocity perturbations (fore-aft, lateral or rotational) introduced at the model’s centre of mass affected all of the components of velocity. The coupling was obvious when we perturbed velocity in one direction and examined the components in the other two directions. For example, when we introduced a lateral velocity perturbation, fore-aft velocity was altered (figure 11a). Fore-aft velocity began with no perturbation, but over the first few strides became perturbed from the steady-state velocity on the same time-course as the recovery in lateral velocity. Subsequently, fore-aft velocity recovered slowly from the lateral velocity perturbation. The time-scale for recovery was similar to that of an induced fore-aft velocity perturbation.

Coupling is best illustrated when two velocity components are plotted on a single graph. Figure 11b shows that a lateral velocity perturbation to the model’s centre of
mass becomes coupled into a fore–aft velocity perturbation. The large lateral velocity perturbation (negative to the left) induced a small increase in fore–aft velocity as lateral velocity recovered. Lateral velocity recovered rapidly, whereas a fore–aft velocity recovered more slowly from its coupling-induced perturbation.

**Mechanism of recovery from lateral velocity perturbations**

The model recovered from lateral velocity perturbations in two phases:

(i) the body rotated to align with the velocity vector. The velocity vector’s new heading was determined by the magnitude of the lateral velocity perturbation;

(ii) after the body rotation, the lateral velocity perturbation was equivalent to a fore–aft velocity perturbation in the new heading which recovered, as described previously, for a fore–aft velocity perturbation.

Consider a lateral velocity perturbation from the left side to the model’s centre of mass (positive lateral
This lateral velocity perturbation deflected the centre of mass velocity vector to the right, resulting in a new heading. During the first quarter of the step, the right middle leg generated a torque (negative, clockwise) favouring alignment of the body axis with the new heading (figure 12b). However, because the centre of mass had moved to the right, the moment arm of the middle leg was reduced (equation (21)). This reduction resulted in a decreased clockwise torque unfavourable to alignment with the new heading (equation (B1)); however, the moment arm of the middle leg was greatly reduced (equation (B1)). The reduced moment arm of the middle leg resulted in a greatly decreased anticlockwise torque thereby favouring alignment to the new heading (equation (B1); yellow area in figure 13). During the third quarter of the step, the right middle leg generated a torque (positive, anticlockwise) opposing the alignment of the body axis with the new heading (figure 12c). However, because the centre of mass had moved even further to the right, the moment arm of the middle leg was greatly reduced (equation (21)). The reduced moment arm of the middle leg resulted in a greatly decreased anticlockwise torque thereby favouring alignment to the new heading (equation (B1); yellow area in figure 13).

(h) Rapid rate of recovery from rotational velocity perturbations

Rotational velocity exhibited the most remarkable recovery from perturbations. Rotational velocity perturbations (30,
15, 0, −15, −30 rad s⁻¹) converged to the stable pattern within one step period (Figure 14a).

Interestingly, the delay in recovery of rotational velocity from a rotational velocity perturbation resulted in a misalignment of the body axis with the velocity vector. No initial perturbation in body angle was found at the beginning of the rotational velocity perturbation, but the rotation velocity perturbation subsequently turned into a body rotation which recovered more slowly than rotational velocity (Figure 14b). The body angle perturbation recovered on the same time-scale as did a lateral velocity perturbation. The model revealed that a rotational velocity perturbation must be corrected rapidly. The greater the delay in correction, the more the body axis rotated.

(i) Mechanism of recovery from rotational velocity perturbations

Recovery from a rotational velocity perturbation had two phases:

(i) rotational velocity recovery—recovery from a rotational velocity perturbation resulted from individual leg force vectors changing direction so as to move out of alignment with the model’s centre of mass thereby producing a correcting torque (equations (B5)–(B8));

(ii) body axis rotation and misalignment with the velocity vector corrected—the mechanism is described for the recovery to a lateral velocity perturbation.

Consider an anticlockwise rotational velocity perturbation to the model. Prior to the rotational perturbation, the force vector from, for example, the left front leg tended to be aligned through the centre of mass (Figure 15a). After an anticlockwise rotational velocity perturbation, the rotation of the left front leg force vector resulted in a misalignment with the centre of mass thereby generating a clockwise rotational torque stabilizing the rotational velocity perturbation (Figure 15b). Rotational velocity was stabilized within one step (constant slope of far right path at the end of one step in Figure 16) due to the clockwise rotational torque (blue area in Figure 16).

5. CONCLUSION

The self-stabilizing behaviour of the dynamic, feedforward hexapod model suggests an important role in control for the mechanical system. Essentially, control algorithms can be embedded in the form of the model itself. Control results from information being transmitted through mechanical arrangements. Perturbations change the translation and/or rotation of the body that consequently provide ‘mechanical feedback’ by altering leg moment arms.
The degree of sprawl, magnitude and orientation of ground-reaction forces rotate with the body. Only small rotational torques are produced. An anticlockwise rotational perturbation results in a clockwise rotational moment because the direction of ground-reaction forces rotate with the body. Perhaps the most debatable assumption involved setting leg force production to be an unchanging pattern relative to the body. Certainly for extreme perturbations, it is unlikely that a leg could continue to generate the same magnitude of force in global coordinates. Moreover, it remains to be determined if the animal rotates its leg force vector with its body axis rotation. Preliminary animal experiments show that large-scale perturbations do not necessarily alter electromyographical signals of major leg muscles (Full et al. 1998).

However, only future animal perturbation experiments will reveal whether or not components which are stabilized rapidly in the model, such as rotational velocity (figure 14), are controlled by the behaviour of the mechanical system. Whereas slow components such as fore–aft velocity (figure 5) demand neural feedback. Finally, the compromise between a simplified control system having stability in the reference frame of the body versus its loss of effectiveness in maintaining heading remains to be explored. The present model has no information about global trajectories. The heading of an animal immediately following a rapid perturbation could be directly compared to the model.

The present feed-forward model requires further development. The particular aspects of morphology and leg force production that favour self-stabilization remain unknown. Degree of sprawl, magnitude and orientation of leg forces, the effect of frequency, velocity and scaling all deserve future consideration. These parameters could be best investigated if there were a faithful analytical solution to the equations of motion.

The surprising performance of the feed-forward model has broad implications. First, the results demonstrate once again that dynamics, or the way motion evolves over time, can be important even for small, sprawled posture animals. Second, the findings encourage us to look beyond the reference frame(s) we are most familiar with. Meaningful dynamics can occur in the horizontal plane and may play a major role in manoeuvrability. Third, the model’s behaviour cautions us against the assumption that continuous, proportional, negative neural feedback is sufficient. Self-stabilization by the mechanical system can assist in making the neural contribution of control simpler. The fact that the dynamics are coupled and components (fore–aft, lateral and rotation) differ in their rate of recovery from perturbations demands that we reconsider what is being controlled by the nervous system. Control strategies should work with the natural body dynamics, rather than attempting to cancel them out. Neural feedback during rapid, gross, rhythmic behaviour may play a more important role in large-scale disturbances, corrections over multiple cycles and state dependent changes.

Finally, the model reinforces the necessity to create a field of neuromechanics integrating both disciplines.
RESULTS FROM THE EFFECT OF POSITION ON THE MOMENT ARMS AND INERTIA (generate a torque \(\theta\), sideways (\(x\)) and forward (\(y\)) translation. Feedback in this feed-forward system results from the effect of position on the moment arms.

Supported by an Office of Naval Research (ONR) Grant N00014-92-J-1250, and a Defense Advanced Research Projects Agency (DARPA) Grant N00014-98-1-0747. We thank Devin Jindrich, Phil Holmes and Johan van Leeuwen for their comments on the manuscript.

APPENDIX A

\[ l_{31} - l_{11} = (p_{32} \times \cos(\theta(t - s_i)) - p_{31} \times \sin(\theta(t - s_i)) + (p_{32} \times \cos(\theta(t - s_j)) - p_{31} \times \sin(\theta(t - s_j))) \times \cos(\theta(t)) + (p_{32} \times \sin(\theta(t - s_i)) + p_{31} \times \cos(\theta(t - s_i))) \times \sin(\theta(t)), \]

\[ l_{61} - l_{41} = (p_{62} \times \cos(\theta(t - s_i)) - p_{61} \times \sin(\theta(t - s_i)) + (p_{62} \times \cos(\theta(t - s_j)) - p_{61} \times \sin(\theta(t - s_j))) \times \cos(\theta(t)) + (p_{62} \times \sin(\theta(t - s_i)) + p_{61} \times \cos(\theta(t - s_i))) \times \sin(\theta(t)), \]

\[ l_{12} - l_{22} = (p_{12} \times \cos(\theta(t - s_i)) + p_{11} \times \sin(\theta(t - s_i)) + (p_{12} \times \cos(\theta(t - s_j)) - p_{11} \times \sin(\theta(t - s_j))) \times \cos(\theta(t)) + (p_{12} \times \sin(\theta(t - s_i)) - p_{11} \times \cos(\theta(t - s_i))) \times \sin(\theta(t)), \]

\[ l_{42} - l_{32} = (p_{42} \times \cos(\theta(t - s_i)) + p_{41} \times \sin(\theta(t - s_i)) + (p_{42} \times \cos(\theta(t - s_j)) - p_{41} \times \sin(\theta(t - s_j))) \times \cos(\theta(t)) + (p_{42} \times \sin(\theta(t - s_i)) - p_{41} \times \cos(\theta(t - s_i))) \times \sin(\theta(t)), \]

Resultant torques from opposing leg forces:

\[ T_{\text{front + hind}} = F_{31}[(p_{32} \times \cos(\theta(t - s_i)) - p_{31} \times \sin(\theta(t - s_i)) + (p_{32} \times \cos(\theta(t - s_j)) - p_{31} \times \sin(\theta(t - s_j))) \times \cos(\theta(t)) + (p_{32} \times \sin(\theta(t - s_i)) + p_{31} \times \cos(\theta(t - s_i))) \times \sin(\theta(t))], \]

\[ T_{\text{front + middle}} = F_{61}[(p_{62} \times \cos(\theta(t - s_i)) - p_{61} \times \sin(\theta(t - s_i)) + (p_{62} \times \cos(\theta(t - s_j)) - p_{61} \times \sin(\theta(t - s_j))) \times \cos(\theta(t)) + (p_{62} \times \sin(\theta(t - s_i)) + p_{61} \times \cos(\theta(t - s_i))) \times \sin(\theta(t))], \]

\[ T_{\text{hind}} = - F_{32}[(p_{31} \times \cos(\theta(t - s_i)) + p_{32} \times \sin(\theta(t - s_i)) + (p_{31} \times \cos(\theta(t - s_j)) + p_{32} \times \sin(\theta(t - s_j))) \times \cos(\theta(t)) + (p_{31} \times \sin(\theta(t - s_i)) - p_{32} \times \cos(\theta(t - s_i))) \times \sin(\theta(t))], \]

\[ T_{\text{middle}} = F_{62}[(p_{62} \times \cos(\theta(t - s_i)) - p_{61} \times \sin(\theta(t - s_i)) + (p_{62} \times \cos(\theta(t - s_j)) - p_{61} \times \sin(\theta(t - s_j))) \times \cos(\theta(t)) + (p_{62} \times \sin(\theta(t - s_i)) + p_{61} \times \cos(\theta(t - s_i))) \times \sin(\theta(t))], \]

Figure A1. Model force parameters. The first trace, \(F_{31}\), is the fore-aft (\(j = 1\)) force generated by the left hind leg (\(i = 3\)). The force lasts \(K\) seconds each step which equals the stride period \(T\) times the duty factor \(\hat{g}\). The second trace, \(F_{61}\), is the fore-aft force (\(j = 1\)) generated by the right hind leg (\(i = 3\)). The right hind leg has a phase shift (\(\phi_6\)) which is the time between its foot down and the foot down of the left front leg. The amplitude, \(A_{61}\), of the force curve is positive indicating a forward acceleration. To generate a force which has a frequency different to the stride frequency, we generated a within-stride time (\(S_3\)). This goes from zero at foot down to \(t\) for each leg. Since all legs in the first tripod (\(I = 1, 2, 3\)) have a phase shift of zero, they all have a within-stride time equal to \(S_3\). All legs in the second tripod (\(i = 4, 5, 6\)) have a phase shift equal to \(\tau\) so the within-stride time equals \(S_6\).
REFERENCES


