



How well can spring-mass-like telescoping leg models fit multi-pedal sagittal-plane locomotion data?

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ABSTRACT

Idealized mathematical models of animals, with point-mass bodies and spring-like legs, have been used by researchers to study various aspects of terrestrial legged locomotion. Here, we fit a bipedal spring-mass model to the ground reaction forces of human running, a horse trotting, and a cockroach running. We find that, in all three cases, while the model captures center-of-mass motions and vertical force variations well, horizontal forces are less well reproduced, primarily due to variations in net force vector directions that the model cannot accommodate. The fits result in different apparent leg stiffnesses in the three animals. Assuming a simple fixed leg-angle touch-down strategy, we find that the gaits of these models are stable in different speed-step length regimes that overlap with those used by humans and horses, but not with that used by cockroaches.

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1. Introduction

In the study of legged locomotion, simple models consisting of point-mass bodies and massless legs with telescoping actuators have been found variously insightful. Several variants have been used, including the telescoping leg as a general force-actuator (Alexander, 1980; Srinivasan and Ruina, 2006), a simple passive linear or non-linear spring (McGeer, 1990; McMahan and Cheng, 1990; Blickhan and Full, 1993; Farley and Gonzalez, 1996; Seyfarth et al., 2002; Ghigliazza et al., 2003; Geyer et al., 2005), and a spring in series with a general force-actuator (Alexander, 1992). These models serve as analogs that simplify the problem of understanding the mechanics of legged locomotion of real animals. They have been used both to describe what is observed, and to predict what might happen in nature. Most significantly for the purposes of this paper, it has been found that center-of-mass (CoM) motions of the spring-mass model (Fig. 1) are qualitatively similar to those of running animals over a wide range of body mass, and with differing numbers of legs (Blickhan and Full, 1993; Farley and Gonzalez, 1996).

Here we examine in greater depth the approximation of bipedal, quadrupedal, and hexapedal animal gaits by the spring-mass model, and discuss the sagittal-plane stability of the most

common instantiation of this model over the parameter regimes appropriate for three representative animals. The spring-mass model is typically restricted to the sagittal plane, a practice that we follow in the present paper. See, for instance, Seipel and Holmes (2005, 2006) for studies of three-dimensional point-mass dynamics of similar models.

This paper is organized as follows. Section 2 reviews the spring-mass model and describes its space of solutions, focussing on periodic single and double stance gaits in which the left and right legs follow similar paths. In Section 3, we describe how the model is fitted to data by estimating apparent leg stiffness, we introduce a simple test of a key assumption, and we compare CoM motions and ground reaction forces (GRFs) predicted by the model with data from running humans and cockroaches, and a trotting horse. Stability of these three families of gaits, corresponding to the three different apparent leg stiffnesses derived from data, is considered in Section 4, and we conclude in Section 5.

2. The bipedal spring-mass model

The spring-mass model or spring-loaded inverted pendulum (SLIP, Fig. 1) is generally used to describe bipedal running, although it has been applied to animals as diverse as cockroaches, centipedes and oxen, over a wide range of speed and body mass (Blickhan and Full, 1993). Single leg stance is typically assumed, but here we allow double stance phases, as in Geyer et al. (2006).

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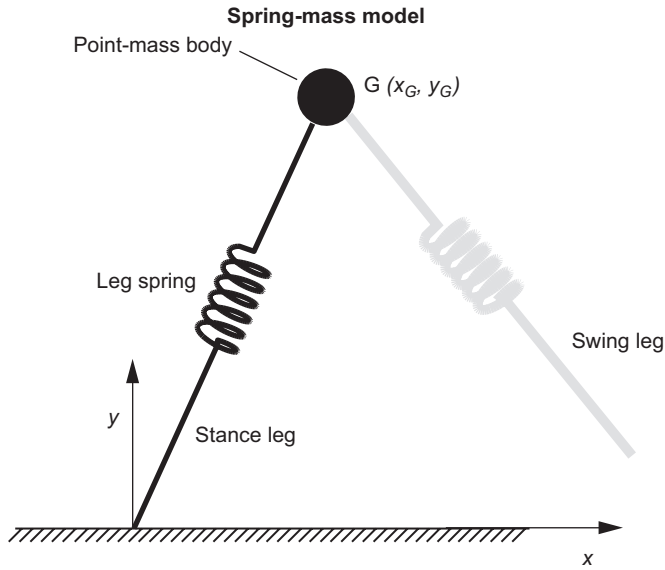


Fig. 1. The bipedal spring–mass model has a point-mass upper body and two massless legs that behave like passive linear springs. Leg forces act along the line joining foot contact point and center of mass.

We describe the model in Section 2.1, and characterize its solutions in Section 2.2.

2.1. Model description

The spring-mass model (Fig. 1) has a point-mass upper body G with mass m . The position of G in the sagittal plane at time t is $(x_G(t), y_G(t))$ with respect to the inertial frame as shown. Locomotion proceeds in the positive x direction. The two massless legs with point-feet are denoted leg-1 and leg-2 when convenient, with foot positions x_{c1} and x_{c2} , respectively, when in ground contact. The ground is assumed level and horizontal, so that $y_{c1} = y_{c2} = 0$, and legs exert forces $F_1(t)$ and $F_2(t)$ on the body only when in ground contact. Leg forces act along lines joining the foot points to the CoM. It is assumed that feet never slip on the ground whatever the required frictional forces, and when the legs are not in ground contact, they may be swung around arbitrarily as required.

One complete cycle of a periodic gait is usually called a *stride*. When not considering exactly periodic gaits, we will use the term stride to refer to any segment of the gait from one touch-down of a leg to the next touch-down of the same leg. During a stride, one or both or neither leg may be on the ground at any given moment. In the following, we will consider gaits in which the two legs act similarly but 180° out of phase. A *step* is then defined as half a stride: from the touch-down of one leg to the next touch-down of the other leg. A *flight phase* occurs when neither leg is in ground contact; a *single stance phase* when exactly one leg is in ground contact, and a *double stance phase* when both legs are in ground contact. Since we restrict attention to at most one single stride of any gait and each leg has only one fixed foot–ground contact point during a single stride, we may set leg-1’s foot position $x_{c1} = 0$ without loss of generality. We further assume that $t = 0$ at touch-down when the foot of leg-1 begins ground contact.

The equations governing CoM motion during a double stance phase are

$$m\ddot{x}_G = F_1 x_G / l_1 + F_2 (x_G - x_{c2}) / l_2, \quad (1)$$

$$m\ddot{y}_G = F_1 y_G / l_1 + F_2 y_G / l_2 - mg, \quad (2)$$

where $l_1 = \sqrt{x_G^2 + y_G^2}$ and $l_2 = \sqrt{(x_G - x_{c2})^2 + y_G^2}$ are the respective leg lengths when in stance.

Equations describing single stance and flight phases are obtained by setting F_1 or F_2 or both to zero, as appropriate, in Eqs. (1) and (2). For instance, the single stance equations with leg-1 on the ground are

$$m\ddot{x}_G = F_1 x_G / l_1, \quad (3)$$

$$m\ddot{y}_G = F_1 y_G / l_1 - mg. \quad (4)$$

In flight, CoM motions are ballistic: $\dot{x}_G(t) = v_{x,LO}(t_0)$ and $\dot{y}_G(t) = v_{y,LO}(t_0) - g(t - t_0)$, where $v_{x,LO}(t_0)$ and $v_{y,LO}(t_0)$ are the horizontal and vertical velocity components at lift-off, which occurs at time t_0 .

Most versions of the model employ a linear leg spring with a force-free rest length l_0 and spring constant k . When the leg length l_i is less than l_0 and the foot is in ground contact, the leg force F_i obeys the simple linear relation $F_i = k_{spring}(l_0 - l_i)$, and the foot is assumed to lose ground contact when the compressive (positive) leg force falls to zero. When the leg is not in ground contact, its length is assumed to remain equal to l_0 until touch-down and it is assumed that the leg angle at touch-down can be chosen arbitrarily, but that the touch-down angle is the same on every step for a given gait.

2.2. The space of periodic solutions

Any periodic gait of the spring-mass model is completely characterized by initial conditions and information about when each leg is in ground contact. The model is capable of both running-like motions (with a flight phase and no double stance phase; Blickhan, 1989; Blickhan and Full, 1993) and walking-like motions (with no flight phase and a double stance phase; Geyer et al., 2006; Holmes et al., 2006b; O’Connor and Kuo, 2006).

2.2.1. One-step periodic gaits without double-stance

We first consider gaits in which each step is identical (in the sagittal plane): leg-1’s behavior during stance is identical to that of leg-2, and restrict to gaits that have one stance phase and one flight phase in every step. Given the mass m , leg length l_0 , and leg stiffness k , such periodic gaits, which include the classic running gaits of the spring-mass model (Blickhan, 1989), form a two-parameter family.

To see this, note that the stance phase is completely characterized by four initial conditions at touch-down $(x_G(0), \dot{x}_G(0), y_G(0), \dot{y}_G(0))$, which are constrained by two conditions. The first requires that the leg-length at touch-down be l_0 ; the second requires that the velocity *direction* at the next step’s touch-down be identical to the current step’s. Periodicity in velocity *magnitude* is not an extra condition; because it automatically follows from conservation of total energy and the fact that the potential energy is the same at every touch-down by the selection of the touchdown angle and the touch-down leg length.

For the running gaits of interest, the CoM trajectory within a stance phase is mirror-symmetric about mid-stance (a vertical line through the foot contact point) and the CoM velocity vector is horizontal at mid-stance. The two parameters characterizing the space of such one-step periodic solutions can then be taken as the spring compression or CoM height at mid-stance and the horizontal velocity at mid-stance.

2.2.2. One-step periodic gaits with double stance

The spring-mass model is also capable of gaits with a double stance phase but no flight phase, as discovered by Holmes et al. (2006b) and Geyer et al. (2006). Two qualitatively different

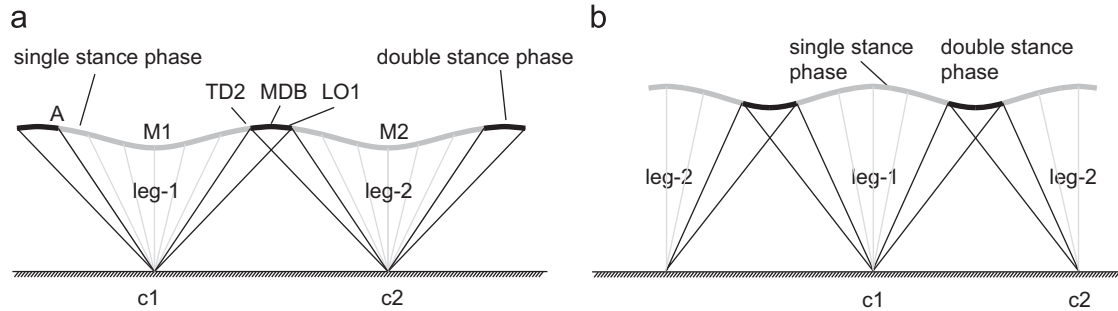


Fig. 2. Two spring-mass gaits with a double stance and no flight phase, one qualitatively similar to a cockroach run (a), the other similar to a human walk (b). In a running cockroach, the CoM reaches maximum height when all six legs are on the ground (Full and Tu, 1990, 1991). In human walking, the CoM height is maximal at the middle of each single stance phase (Geyer et al., 2006).

examples are shown in Fig. 2, one resembling running gaits of cockroaches (Fig. 2a; Holmes et al., 2006b) and another resembling the walking gaits of humans (Fig. 2b; Geyer et al., 2006). Here M1 denotes mid-stance of leg-1, which continues in ground contact until lift-off at LO1. Leg-2 begins ground contact at TD2, before leg-1 loses contact, leading to a double stance phase. The lengths of leg-1 at LO1 and leg-2 at TD2 are both equal to l_0 . MDB denotes the middle of a symmetric double stance phase. Note the difference in where double stance occurs relative to CoM height in the two gaits.

The following counting arguments show that the set of such one-step periodic gaits is also characterized by two parameters (again given mass m , leg length l_0 , and stiffness k).

Assuming symmetry about mid-stance as above, each single-stance phase now requires specification of three parameters: horizontal velocity and vertical compression at mid-stance, and additionally, the duration of the single stance phase (because this phase does not end when one leg leaves the ground). Since the length of leg-2 at touch-down is l_0 , the touch-down angle follows from the state at TD2, and therefore is not an free parameter. The equations of motion for the double stance phase can be integrated forward in time until the vertical velocity of the CoM falls to zero (e.g., at the point MDB in Fig. 2). All that is required for a symmetric periodic gait is that the horizontal distance from the foot C1 to MDB be exactly half the distance between the stance feet C1 and C2 (the step length). This ensures that integrating Eqs. (1) and (2) forward in time from MDB will be identical to integrating the same equations backward in time, with a mirror-reflection about the vertical line through MDB. This one constraint on the three parameters implies that the space of such periodic solutions is a two-parameter family.

As we shall see, for both single- and double-stance gaits, the two parameters can be taken as the average speed and the step length. A slightly more cumbersome argument shows, without appeal to symmetry, that the space of *all* one-step periodic gaits is also characterized by two-parameter families.

3. Fitting spring-mass model to data

Several researchers have pointed out that periodic gaits of the spring-mass model exhibit GRF profiles similar to those of real animals, including running humans, trotting horses, and running cockroaches (e.g., Blickhan, 1989; McMahon and Cheng, 1990; Blickhan and Full, 1993; Farley et al., 1993). However, they essentially all compare either mechanical energy fluctuations, or vertical GRFs of the spring-mass model, with the corresponding quantities in the animal. Simultaneous comparison of horizontal and vertical GRFs appears not been carried out in detail, although Blickhan (1989) compares the ratio of peak vertical and horizontal

forces. In Section 3.1, we describe a simple way of fitting the spring-mass model to real animal data, requiring only the speed, step length and duty factor (the fraction of a full stride for which either leg is in ground contact). In Section 3.2, we present a graphical device that enables verification or falsification of some key assumptions underlying the spring-mass model.

3.1. Back-calculating leg stiffness

In Section 2.2 we noted that for a given model specified by m , l_0 and k , there exists a two-parameter family of one-step periodic running gaits. However, while we can directly measure body mass m and estimate leg length l_0 for a given animal, its apparent leg stiffness must be inferred from measurements on the running animal, as it appears to be largely a behavioral choice (adjustable, e.g., by coactivation of muscle groups, or by using a running gait with higher forces and a smaller duty factor). It is therefore more convenient to regard the model with only m and l_0 specified as having a *three-parameter* family of one-step periodic running gaits. Fitting the model to a specific gait is equivalent to estimating appropriate values for these three parameters.

One strategy for fitting to running data is to determine those parameters that minimize squared error between the measured and model GRFs. This will perhaps give the overall best fit, but here we employ a simpler procedure based on the intuition that solving for the three unknowns typically requires at least three equations. We can obtain three such meaningful equations by requiring that, given m and l_0 , the model's gait match three different aspects of the animal gait. Here, we require that the average speed, step length, and duty factor of the model equal those of a running animal. Note that for gaits with flight phases the duty factor is less than 0.5, and for gaits with double-stance phases, it is greater than 0.5.

It is not clear that these three equations will always have a solution, or when they do, that it is unique. Indeed, we have found multiple, qualitatively different, one-step periodic gaits of the model that have the same forward speed, step period, and duty factor. However, when solutions exist, they are at least generically locally unique (there are no neighboring parameter sets that are also solutions), since we have three equations in three unknowns. We will seek fits with a simple root-finding procedure (`fsolve` in MATLAB), in which we solve for initial conditions and stiffness that result in periodic gaits satisfying a given speed, step period and duty factor. Using this technique, we now ask how well model gaits match certain aspects of real animal data.

Note that we refer to the stiffness thus computed as the *apparent* leg stiffness as it is based on steady state running data as opposed to data on the animal's response to perturbations.

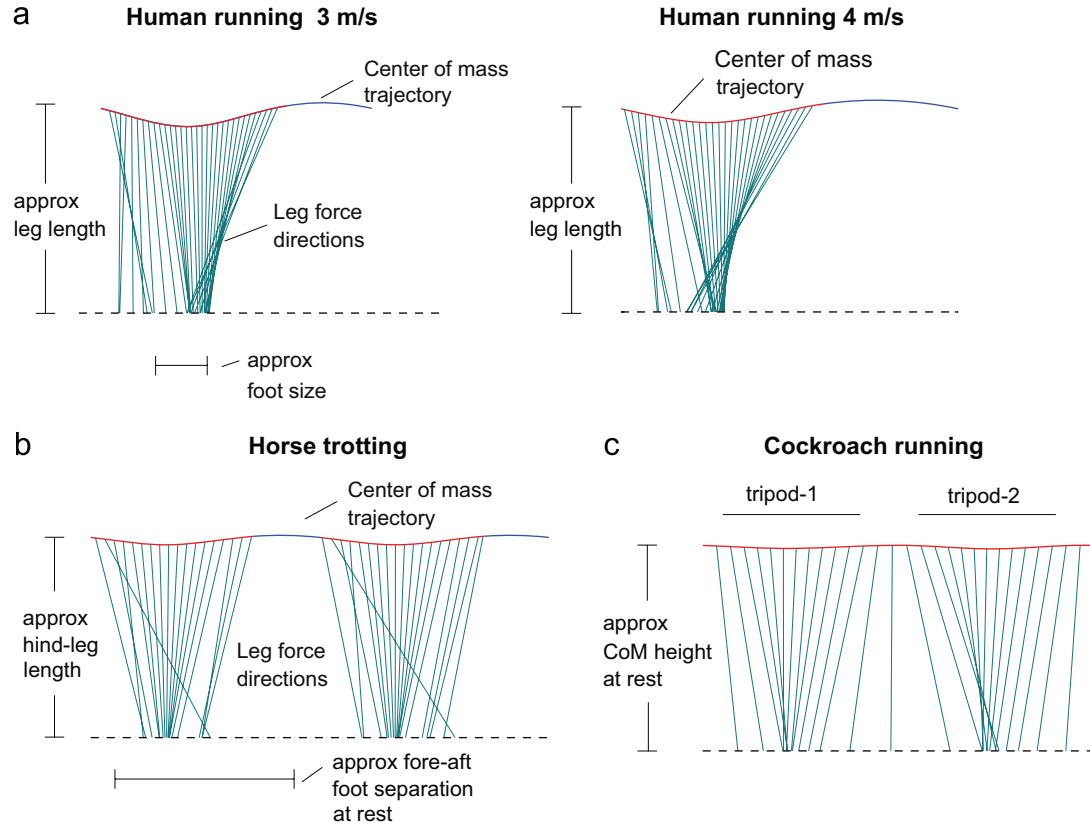


Fig. 3. CoM trajectories for a running human at two different speeds (a), for a trotting horse (b), and for a running cockroach (c). Thin lines extending from the trajectory to the ground indicate the direction of total leg force(s) (GRFs) at successive instants. These lines may not pass through the real animal's CoM, but are plotted as if attached to it for convenience. The amount of "spread" in intersections of force directions with the ground during each stance phase indicates how well the gait data satisfy some of the assumptions implicit in the telescoping leg model of Fig. 1. Trajectory segments in (a) and (b) without leg force vectors are flight phases. Data from Kram et al. (1998) (a) 3 m s^{-1} ; Hamill et al. (1983) (a) 4 m s^{-1} ; Dutto et al. (2004); Hoyt et al. (2000) (b), and Full and Tu (1990) (c). See text for further details.

3.2. A quick test of assumptions: an effective footprint

Before comparing the detailed fits of the spring-mass model with animal GRF data, we present a graphical device that assesses how well key assumptions underlying the spring-mass model are satisfied by the animal data.

Given the fore-aft and vertical GRFs F_x and F_y and the initial position of the CoM ($x_G(0), y_G(0)$), the CoM trajectory $x_G(t)$ and $y_G(t)$ of a locomoting animal can be obtained by integrating the balance of linear momentum

$$m\ddot{x}_G = F_x, \quad (5)$$

$$m\ddot{y}_G = F_y - mg. \quad (6)$$

Assuming that the leg force vector always passes through the CoM and given its direction (F_x, F_y), we can then compute the point ($x_p, y_p = 0$) on the ground from which the force must originate

$$\frac{x_p - x_G}{y_p - y_G} = \frac{F_x}{F_y} \quad \text{or} \\ x_p(t) = x_G(t) - \frac{y_G(t)F_x(t)}{F_y(t)}. \quad (7)$$

If the motion were exactly that of a point-mass animal with massless legs and point feet, x_p would remain fixed in place during a single-stance phase. Deviations from this can be due to the animal's extended foot rolling on the ground, to its legs exerting non-zero moments about the CoM, to having an extended upper body and a massive leg, or to the presence of multiple stance feet. Because these effects are independent, they could in

principle cancel, giving the illusion of a leg force originating from a fixed ground point. Thus a small locus of x_p during single stance is a necessary, but not sufficient, condition for the animal to satisfy the assumptions underlying the spring-mass model.

Eqs. (5)–(7) show that the calculation of $x_p(t)$ requires only GRF measurements. Three specific examples are shown in Fig. 3, in which leg force directions emanating from the CoM at successive instants during stance intersect the ground plane in "effective footprints." We discuss these plots in the next section, in the context of how well the spring-mass model compares with animal data via GRF measures.

Bullimore and Burn (2006) introduced a spring-mass model in which the "point foot" moves forward at constant speed during the stance phase to represent the effect of a moving center of pressure under an extended foot. Our data-derived locus of x_p need not lie within the confines of a foot because it may be affected by more factors (as described in the previous paragraph) than an extended foot.

3.3. Comparisons with animal data

3.3.1. Human running

Fig. 4a shows vertical and horizontal GRFs for a human running at about 3 m s^{-1} from Kram et al. (1998), and for the spring mass model with the same mass, leg length, speed, step length and duty factor,¹ computed as described in Section 3.1. We correct the GRF

¹ To the extent that these quantities are known precisely; e.g., the leg length is greater at the end of stance due to the length of the foot, but we neglect this here.

data of Kram et al. (1998) slightly so that initial and final velocities match as they would for a perfectly periodic motion, and we pick initial velocity conditions so that the CoM path is periodic and its horizontal position moves forward by a distance consistent with the average speed during a step. (These are standard techniques used to reduce drifts in position and velocity due to integration of noisy force data. Also note that the dashed “ground lines” in Fig. 3 are not necessarily the true ground positions relative to the CoM trajectories: the actual ground probably lies slightly above this line, which is set one leg length below the CoM at touch-down.)

The vertical GRF of the model is close to that of the human in shape and magnitude, although the model cannot reproduce the oscillations during the first half of stance. However, the maximum horizontal force for the model exceeds that of the data by ≈ 1.75 , in general agreement with the findings of Bullimore and Burn (2006).

The source of this discrepancy is revealed by the effective footprint plot of Fig. 3a, in which the leg force directions do not pass through a common point. Indeed, their spread during the first half of the stance phase seems substantially larger than can be explained by the foot’s actual length (shown in the figure; also pointed out by Alexander and Jayes, 1980). Thus, human leg forces were more vertical than is consistent with passage through a single ground point: hence the discrepancy in horizontal forces. Nonetheless, both vertical and horizontal CoM position fluctuations are well captured by the model (not shown here; cf. Geyer et al., 2006): the former due to the similarity of vertical forces, and the latter because the horizontal position as a function of time is dominated by the average forward speed rather than fluctuations about it.

We also examined the results of a footprint calculation at another speed, 4 m s^{-1} , derived from data obtained by Hamill et al. (1983) using a stationary force-plate, which is sometimes considered more reliable for horizontal GRFs than the force-treadmill employed by Kram et al. (1998). We find that the force vector directions of both data sets are remarkably similar throughout the stance phase: see Fig. 3a. The discrepancy between the spring-mass model and the horizontal GRFs is also seen for the 4 m s^{-1} data (not shown in Fig. 4a).

3.3.2. Horse trotting

When a horse trots, two contralateral (diagonally opposite) legs are approximately in ground contact simultaneously in each stance phase. These pairs alternate, creating a gait qualitatively similar to human running.

Fig. 4b compares GRFs of the model with data from a horse trotting at 4.5 m s^{-1} (data taken from Dutto et al., 2004; Hoyt et al., 2000). In this case the qualitative shapes and magnitudes of both horizontal and vertical forces are similar for model and data.

Fig. 3b shows leg force direction data for the same animal, which accounts for the close match in Fig. 4b. The stance leg pairs produce net forces that act through a relatively small region, especially during the middle 60% of each stance phase. Here, the effective footprint is shorter than the distance between the hooves.

3.3.3. Cockroach running

Insects frequently run in an alternating tripod gait, with three legs (front and hind on one side and middle on the other) in simultaneous ground contact in the center of each stance phase, but with more legs in ground contact during tripod transitions. Fig. 3c shows an example of a cockroach running at $\approx 25 \text{ cm s}^{-1}$ from Full and Tu (1990). This gait has previously been described by a bipedal model by identifying the tripod support phase with a single stance phase of a biped, and the bipedal double stance phase with the tripod transition in which all six legs may be simultaneously in ground contact (Schmitt and Holmes, 2000). The spread in the apparent contact point of the “equivalent” biped is relatively small during the tripod phase. This fact may have motivated earlier researchers to seek an analogy between insect and bipedal gaits (Blickhan and Full, 1993), although it was not stated in these terms.

Fig. 4c compares GRFs of a spring-mass model with speed, step period, duty factor, mass, and average body height approximately matched to those of a running cockroach, *Blaberus discoidalis* (Full and Tu, 1990; Ting et al., 1994). As noted above, single stance corresponds to support by one tripod of the insect’s double tripod gait, and double stance to both tripods (all six legs) being on the ground. While there is good qualitative agreement in shape and the net force directions are similar (compare Fig. 4c with 3c), quantitative comparisons of force magnitudes (dotted and solid curves in panel (b)) are less encouraging.

As noted in Section 2.2 and Fig. 2b, human walking also has double-stance phases, but they are qualitatively different from those of cockroach running. In human walking, the midpoint of single stance is when the CoM is at its highest point. This is almost exactly out of phase with the cockroach gait, in which the highest CoM position occurs during the double-stance phase. Geyer et al. (2006) first showed that the qualitative aspects of human walking can be achieved by a spring-mass model with bipedal support.

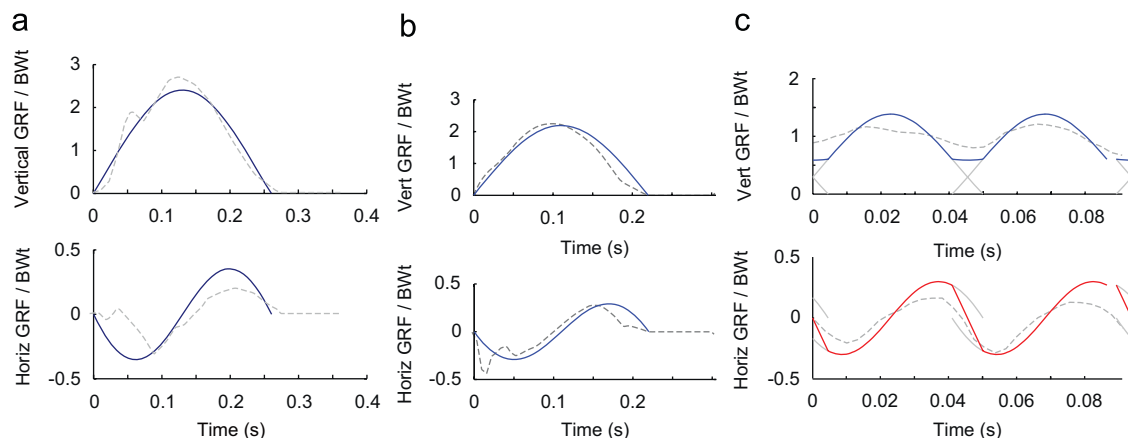


Fig. 4. Vertical and horizontal ground reaction force data for animal locomotion: comparison with the best-fit spring-mass model. (a) Human running. (b) Horse trotting. (c) Cockroach running without a flight phase. The solid line is the spring-mass model fit and the lighter dashed line is the animal data. For all three animals, the vertical GRFs are better fit by the spring-mass model than the horizontal GRFs.

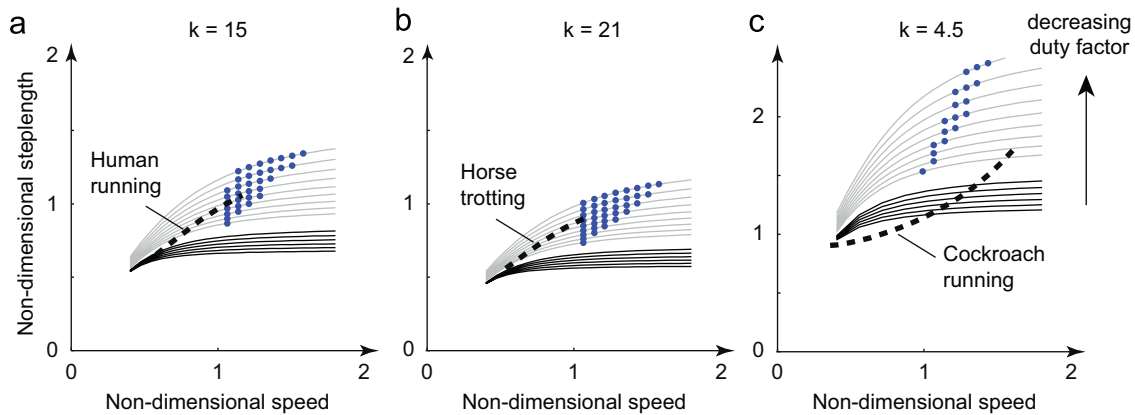


Fig. 5. Branches of one-step periodic gaits of the spring-mass model with mass, leg length and stiffness parameters matched to the (a) human, (b) horse, and (c) cockroach data of Figs. 4a–c. Dark solid lines correspond to gaits with duty factors greater than 0.5, starting from a duty factor of 0.52 in increments of 0.015; light solid lines are gaits with equally spaced duty factors between 0.35 and 0.47. Thick dashed lines denote speed-step length combinations used by running humans, trotting horses and running cockroaches respectively. Filled circles denote regions of partial asymptotic stability under the constant touch-down angle protocol.

Here, we have shown that cockroach gaits are also qualitatively captured by the spring-mass model with appropriate parameters. We note that for *B. discoidalis* the duty factor falls from 0.65 at low speeds towards 0.5 at high speeds (Ting et al., 1994, Fig. 4) and that it is possible for gaits of this type to change continually to duty factors below 0.5 as the double-stance phase shrinks and a flight phase emerges around CoM apex (see Fig. 5c). In contrast, the human-like double-stance gaits appear to lie on distinct solution branches from those that support running gaits with flight phases (Geyer et al., 2006, Fig 4a).

4. Stability of periodic gaits

Here we comment on the stability and stabilizability of gaits of the spring-mass model, as customized to parameter regimes appropriate to the examples of Section 3. For simplicity, we consider only running-like gaits, both with and without double stance.

The spring-mass model was originally motivated by observation of (approximately) periodic gaits in running animals. However, gait stability is assessed by assuming that the leg continues to behave as a passive linear spring even when perturbed from a periodic gait. Since the model is completely conservative (total kinetic+potential+elastic energy is constant), no periodic orbit can be asymptotically stable: *energy-changing* perturbations to the state cannot decay. In contrast, whether or not *energy-preserving* perturbations decay depends on the rule determining touch-down leg angle when the state is off the periodic trajectory.

Perhaps the simplest touch-down rule is to maintain the leg at a constant angle with respect to a reference frame fixed to the ground during flight, so that the touch-down angle remains identical, independent of perturbations. Ghigliazza et al. (2003) and Seyfarth et al. (2002) show that under this rule, the spring-mass model is asymptotically stable with respect to energy-preserving perturbations, over a small but non-infinitesimal subset of the family of all periodic trajectories. Perturbations that change energy lead to attraction to a neighboring trajectory, a phenomenon called partial asymptotic stability in Holmes et al. (2006a), although domains of attraction are typically small.

We illustrate by computing branches of gaits over representative speed ranges for the three animals considered in Section 3.3. Fig. 5 shows graphs of non-dimensional step length versus non-dimensional speed for a range of duty factors encompassing flight and double stance phases. The non-dimensional quantities are

defined as follows:

$$\text{non-dimensional speed} = \frac{u}{\sqrt{gl_0}}, \quad (8)$$

$$\text{non-dimensional step length} = \frac{L_s}{l_0}, \quad (9)$$

where u denotes the average forward speed and L_s the physical step length. We only show branches with double-stance gaits (dark solid curves) qualitatively similar to that in Fig. 2a. The running gaits with flight phases (light solid curves) are all qualitatively similar to Fig. 4a, and there is a smooth continuation of these types of gaits from duty factors less than 0.5 to duty factors greater than 0.5.

We investigated the stability of these gaits under the constant touch-down angle protocol by finding eigenvalues of the Jacobian obtained by computing how perturbations of mid-stance conditions change the state at the next mid-stance. The regions of stability are qualitatively similar in all three cases: in particular, *none of the double stance gaits we considered were stable*. Notably, there is some overlap between the stability regions and the speed-step length combinations (thick dashed curves) used by humans and horses, but not those of cockroaches: no stable cockroach-like double-stance gaits were found. Somewhat interestingly, the speed-step length combinations used by humans and horses seem to be located at roughly the same positions relative to the rest of those figures.

Touch-down at constant leg angle is just one special control strategy. Alternatively, the leg can be retracted at a constant speed from a pre-set angle, at, say, apex of the flight phase. The retraction speed provides a parameter with which to modify the stability eigenvalues, and thus affect stability. It is therefore not surprising that improved stability can be obtained by picking an appropriate retraction rate (Seyfarth et al., 2003; Altendorfer et al., 2004).

If touch-down angles are chosen based on the perturbed system state as in feedback control, it can be shown that sufficiently small (in practice, relatively large) energy-preserving perturbations can be completely eliminated in finitely many steps and consequently, in finite time (see Carver, 2003; Seyfarth et al., 2003 for details). That this is possible can be argued as in Section 2.2 by counting the number of parameters required to describe the set of periodic orbits. Any one-step periodic running gait can be associated with two numbers: for the present purpose, most simply, the desired state at apex of free flight (horizontal velocity component and height). When slightly perturbed from the

periodic orbit, these numbers will change. If the apex state at step n differs from that desired but has the same energy, it will lie on a curve passing through the desired state. By simply choosing an appropriate leg touch-down angle for the next step, one can negate the sufficiently small energy-preserving perturbation and so achieve the desired state at the next apex (cf. [Altendorfer et al., 2004](#)).

5. Conclusions

We used a simple technique to find one-step periodic spring-mass model gaits that match the speed, step length and duty factor of a given animal gait. Comparisons of the model with human data show that, while capturing the vertical motions well, it does a poorer quantitative job of describing horizontal motions. The quantitative comparison with a trotting horse is better. Center-of-mass (COM) trajectories of running cockroaches can also be accommodated qualitatively by the spring-mass model, while quantitative comparison of ground reaction forces (GRFs) is again imperfect. These examples show that the simple spring-mass model can encompass a wide range of animals in both size and leg number, at the expense of quantitative accuracy, and our results complement the theoretical study of [Bullimore and Burn \(2006\)](#) by providing estimates of horizontal force discrepancies and effective footprints with which their “point of force translation” could be fitted.

We then considered stability of spring-mass model gaits and again illustrated using the examples of human, horse and cockroach. We found that the spring-mass model with constant touch-down angle protocol is stable for a range of speeds and step lengths overlapping with those used by running humans and trotting horses, but not by cockroaches, perhaps suggesting qualitative differences in the way these animals might manage stable locomotion, e.g., by use of multiple leg supports in stance ([Ting et al., 1994](#); [Seipel and Holmes, 2006](#)). Computation of maximal stability regions with more realistic models that involve neuromechanical feedback control with sensory noise and delays are likely to shed more definitive light on this question. For instance, while the dynamical timescales are much shorter in cockroaches, so are sensory delays ([Höltje and Hustert, 2003](#)).

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