Biomechanics of quadrupedal walking: how do four-legged animals achieve inverted pendulum-like movements?

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Summary

Walking involves a cyclic exchange of gravitational potential energy and kinetic energy of the center of mass. Our goal was to understand how the limbs of walking quadrupeds coordinate the vertical movements of the fore and hind quarters to produce these inverted pendulum-like movements. We collected kinematic and ground reaction force data from dogs walking over a range of speeds. We found that the fore and hind quarters of dogs behaved like two independent bipeds, each vaulting up and over its respective support limb. The center of mass moved up and down twice per stride, like a single walking biped, and up to 70% of the mechanical energy required to lift and accelerate the center of mass was recovered *via* the inverted pendulum mechanism. To understand how the limbs produce these center of mass movements, we created a simple model of two independent pendulums representing the movements of the fore and hind quarters. The model predicted that the fore and hind quarter movements would completely offset each other if the fore limb lagged the hind limb by 25% of the stride time and body mass was distributed equally between the fore and hind quarters. The primary reason that dogs did not walk with a flat trajectory of the center of mass was that each fore limb lagged its ipsilateral hind limb by only 15% of the stride time and thereby produced time periods when the fore and hind quarters moved up or down simultaneously. The secondary reason was that the fore limbs supported 63% of body mass. Consistent with these experimental results, the two-pendulum model predicts that the center of mass will undergo two fluctuations per stride cycle if limb phase is less than 25% and/or if the total mass is not distributed evenly between the fore or hind quarters.

Key words: locomotion, physiology, mechanical energy, work, ground force, gait, *Canis familiaris*.

Introduction

Legged animals generally get from place to place using a walking gait. Gaits are traditionally defined by footfall patterns, with walking animals having at least one leg in contact with the ground at all times (Howell, 1944). However, phylogenetically and morphologically diverse walking animals share much more in common than just maintaining at least one foot in contact with the ground throughout a stride. Studies of walking crabs, frogs, lizards, alligators, birds and bipedal and quadrupedal mammals revealed that, during a stride, the center of mass attains its highest position when it is moving slowest (Ahn et al., 2004; Blickhan and Full, 1987; Cavagna et al., 1976, 1977; Farley and Ko, 1997; Griffin and Kram, 2000; Heglund et al., 1982; Minetti et al., 1999; Willey et al., 2004). This out-of-phase fluctuation in vertical position and forward speed of the center of mass appears to be a fundamental characteristic of walking gaits and is often modeled with an inverted pendulum.

The inverted pendulum model of walking is characterized by a cyclic exchange between gravitational potential energy and kinetic energy (Cavagna et al., 1976). This exchange process is best understood for bipedal animals. At the beginning of a step, as the body's center of mass slows and gains height, kinetic energy (E_k) is converted into gravitational potential energy (E_p). During the second half of the step, as the body falls forward and downward, E_p is converted back into E_k. Energy recovery *via* this exchange is never perfect (i.e. 100%) because the transition from one leg to the next inevitably results in energy loss (Alexander, 1991; Donelan et al., 2002b). However, due to effective energy exchange when the body is supported by one limb, bipedal animals can substantially reduce the muscular work of walking (Cavagna et al., 1976, 1977).

The maximum values of mechanical energy recovery are lower for quadrupeds (30–65%) than for bipeds (70–80%), suggesting that the inverted pendulum mechanism for exchange of center of mass energy may be less effective in

quadrupedal animals (Cavagna et al., 1977; Farley and Ko, 1997; Griffin and Kram, 2000; Heglund et al., 1982; Minetti et al., 1999). Differences in limb number make it more difficult to understand how the limbs produce inverted pendulum-like dynamics in quadrupeds than in bipeds. Bipeds behave like a single inverted pendulum, so the actions of that inverted pendulum determine the vertical displacements and velocity fluctuations of the center of mass. Walking quadrupeds, however, appear to behave more like two inverted pendulums, with a 'fore quarters pendulum' located at the pectoral girdle and a 'hind quarters pendulum' located at the pelvic girdle (Fig. 1) (Alexander and Jayes, 1978a,b).

Unless a quadruped's fore and hind inverted pendulums move in-synch, such as in a walking pace or a walking trot, the center of mass displacements and velocity fluctuations will differ from those of either inverted pendulum. For example, if weight is distributed equally between the fore and hind quarters and the footfalls are evenly spaced in time, the fore and hind quarter dynamics would completely offset each other (Fig. 1). Thus, even when the fore and hind quarters each behave individually as an inverted pendulum with perfect energy exchange, the combined center of mass can undergo no

energy fluctuations and no inverted pendulum-like exchange. Although prior observations indicate that the center of mass of quadrupedal animals does not move in a perfectly smooth flat line (Cavagna et al., 1977; Farley and Ko, 1997; Minetti et al., 1999), it is not known how the movements of the fore and hind quarters are coordinated to produce the observed inverted pendulum-like behavior.

Unlike the example in Fig. 1, animals use a wide range of footfall patterns (Hildebrand, 1968, 1976), and some quadrupeds support substantially more than half their body mass on either their fore limbs or hind limbs (Demes et al., 1994; Schmitt and Lemelin, 2002). These two factors, footfall pattern and body mass distribution, may allow for much larger oscillations of the center of mass than predicted from Fig. 1 by, respectively: (1) synchronizing the movements of the fore and hind quarters, even if only for brief time periods during the stride, and (2) allowing the center of mass to track the movements of the heavier half of the body. Although quadrupeds are likely to differ from the hypothetical example in Fig. 1 in at least one of these ways, the example provides a framework for investigating the determinants of the center of mass motion in quadrupeds.

We hypothesized that quadrupeds achieve sufficient fluctuations in both E_p and E_k to produce inverted pendulum-like dynamics *via* two mechanisms: (1) by having footfalls that are unevenly spaced in time (i.e. not 25% limb phase) and (2) by having an unequal mass distribution between the fore and hind quarters. This hypothesis was based on our hypothetical example in Fig. 1 as well as previous observations of limb phase relationships other than 25% and unequal fore–hind limb loading in quadrupeds (Budsburg et al., 1987; Roush and McLaughlin, 1994).

To test our hypothesis, we collected ground reaction force and high-speed video data from six dogs (*Canis familiaris*) walking over a range of speeds, and we calculated the mechanical energy fluctuations of the center of mass. Next, we compared the vertical displacements of the fore and hind quarters with those predicted if the legs functioned as incompressible struts during stance. Based on that comparison, we created a two-pendulum model to characterize the movements of the fore and hind quarters. This model provided insight into how limb phase and mass distribution collaborate to determine the center of mass movements in walking quadrupedal animals.
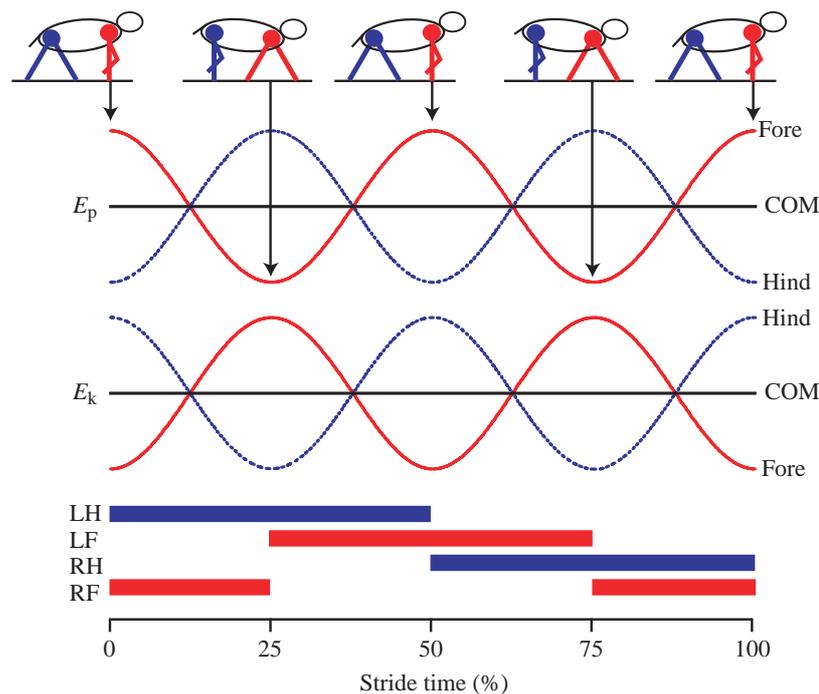

Fig. 1. A hypothetical diagram of quadrupedal walking. The fore quarters and hind quarters are represented as independent inverted pendulums. If the mass distribution is equal between the fore and hind quarters and the limbs cycle at evenly spaced time intervals, the pendular movements of the fore quarters and hind quarters offset each other. When the fore quarters are highest (i.e. gravitational potential energy is maximum), the hind quarters are lowest. Similarly, when the fore quarters are moving fastest (i.e. maximum kinetic energy), the hind quarters are moving slowest. As a result, the gravitational potential energy (E_p) and kinetic energy (E_k) are constant throughout the stride. Bars indicate foot–ground contact times, and the footfall order is left hind (LH), left fore (LF), right hind (RH) and right fore (RF) limb. COM, center of mass.

Materials and methods
Animals

Data were obtained from six healthy pet dogs (*Canis familiaris* L.): two Labrador retrievers,

one Labrador–Great Dane cross and three Rhodesian Ridgebacks. The UC Berkeley Animal Care and Use Committee approved the experiments, and owners gave written consent for their dogs to participate in the study. The dogs ranged in body mass from 27.3 kg to 48.5 kg (mean 37.8 kg), fore limb length ranged from 0.54 m to 0.74 m (mean 0.66 m), and hind limb length ranged from 0.45 m to 0.61 m (mean 0.56 m). Fore and hind limb lengths were measured during standing as the distance from the paw–ground contact point to the highest part of the scapula and the hip, respectively.

Measurements

Owners led their dogs along a runway that had two AMTI force platforms (AMTI model LG6-4-1; Newton, MA, USA) built flush into it. We instructed the owners to lead their dogs with a slack leash and to target four speeds (0.55, 0.80, 1.05 and 1.30 m s^{-1}). Owners and dogs were allowed as many practice trials as needed to acclimate to this procedure. We measured the speed of the owners walking past two infrared photocells placed 3 m apart on either side of the force platforms. We later selected a random sample of trials to compare these photocell speeds to the mean speed of the dog walking through the 3 m section using our video data. The two speed measurements produced nearly the same values (within 0.01 m s^{-1} of each other), so we used the photocell speeds in our analyses.

We collected the vertical (F_z), fore–aft (F_y) and lateral (F_x) components of the ground reaction force at 1 kHz using Labview Software and a computer A/D board (National Instruments, Austin, TX, USA). Data were then filtered at 100 Hz with a fourth-order zero-lag Butterworth low-pass filter. We collected ground reaction forces when all the limbs were on the ground for a complete stride (i.e. whole-body forces) and then just for individual limbs. For whole-body forces, we summed the signals from the two force platforms and analyzed data when all the feet were on the force platforms for a complete stride. We used these data to calculate the mechanical energy fluctuations of the center of mass. Individual limb ground reaction force data were collected from separate left and right limb contacts with the force platforms. We then used these data to calculate the vertical displacements of the fore and hind quarters separately.

We recorded video data in the sagittal plane at 200 fields s^{-1} and in the frontal plane at 60 fields s^{-1} (JC Labs, Mountain View, CA, USA). Video and force platform data were synchronized using a circuit that illuminated a light-emitting diode in the video field and simultaneously sent a voltage signal to the A/D board. The video data were used to determine foot–ground contact time, stride time and limb phase.

Kinematics, whole-body ground reaction forces and mechanical energies

For each dog, we analyzed two trials in which the mean speed was closest to the target speed and the net change in speed was lowest. The mean speeds of the analyzed strides were very close to the target speeds (0.57±0.01, 0.79±0.02,

1.06±0.03 and 1.31±0.02 m s^{-1}; mean ± S.D.). The mean net speed change of the analyzed strides was –2.1±1.6% (±S.D.) of the mean trial speed.

Video recordings were used to calculate the stride time from the time between successive footfalls of the same limb. Duty factor was calculated as the foot–ground contact time divided by stride time. Finally, we determined limb phase from the percentage of stride time that each limb first contacted the ground relative to the left hind limb; therefore, the left hind limb phase was always 0%. Because walking is a symmetrical gait (i.e. limb phase between each pair of left and right limbs is approximately 50%), the footfall pattern can be characterized as the average limb phase of the fore limbs relative to their ipsilateral hind limbs.

We calculated the velocity and displacement fluctuations of the center of mass from the force platform measurements as described in detail elsewhere (Blickhan and Full, 1993; Cavagna, 1975). The E_k and E_p were calculated from the velocity and vertical displacement of the center of mass, respectively (Blickhan and Full, 1993; Cavagna, 1975; Willems et al., 1995). The instantaneous total mechanical energy of the center of mass (E_{com}) was calculated from the sum of the E_k and the E_p at each instant. Percent recovery, defined as the percent reduction in mechanical work required to lift and accelerate the center of mass due to the inverted pendulum mechanism, was calculated as follows (Blickhan and Full, 1987; Cavagna et al., 1976, 1977; Farley and Ko, 1997; Heglund et al., 1982; Minetti et al., 1999; Willems et al., 1995):

$$\% \text{ Recovery} = [(\Sigma\Delta E_k + \Sigma\Delta E_p - \Sigma\Delta E_{com})/(\Sigma\Delta E_k + \Sigma\Delta E_p)]\times 100 . \quad (1)$$

A key parameter in determining the magnitude of percent recovery is the phase of the E_k and E_p fluctuations. We calculated the mechanical energy phase by determining the fraction of the stride time between the minimum E_k and the maximum E_p, multiplying it by 360° and adding 180°. The phase would be 180° if E_k and E_p fluctuated exactly out of phase. A phase value of >180° indicates that E_k reached its minimum after E_p reached its maximum.

Fore and hind quarter vertical displacements

To understand the link between fore and hind quarter vertical displacements and center of mass dynamics, we collected individual limb ground reaction forces for each dog at each target speed. We generally obtained three acceptable force traces for each fore and hind limb per speed per dog. For each component of the ground reaction force, we calculated an average fore and hind limb force trace for each dog and then calculated an average force trace for all the dogs. To do so, we normalized forces to body weight (W_b) and expressed time as a percentage of contact time before averaging.

We calculated the vertical displacements of the fore and hind quarters by double integration of their vertical accelerations. These accelerations were determined from the vertical ground reaction forces under the fore and hind limbs and the effective

mass of the fore and hind quarters, which was estimated as the mass supported by either the fore or hind limbs during standing (Jayes and Alexander, 1978). This approach was validated after data collection because the distribution was independent of speed. The assumption of this approach, that the vertical displacements of the fore quarters depend mainly on the fore limb forces and that the hind quarter vertical displacements depend mainly on the hind limb forces, is reasonable for two reasons (Jayes and Alexander, 1978). First, the fore and hind quarters are connected by a flexible trunk. Second, the trunk is long compared with the small vertical displacements of the fore and hind quarters, so the trunk remains primarily horizontal. Thus, an axial force transmitted through the trunk would have a negligible vertical component. A similar approach, however, would not accurately determine the individual fore–aft movements of the fore and hind quarters because the trunk is likely to transmit fore–aft forces between them (Alexander and Jayes, 1978b). This was confirmed after data collection: we found that the fore and hind limbs generated net braking and propulsive forces, respectively. These net forces must be offset by forces transmitted *via* the trunk to prevent the hind quarters from overtaking the fore quarters.

To determine if the vertical center of mass displacements were more influenced by the fore or hind limbs, we compared the times between the peak center of mass displacement ($t_{peak,com}$) and the peak fore ($t_{peak,fore}$) and hind ($t_{peak,hind}$) quarters displacements. This temporal relationship (ϕ) was calculated as a percentage of the time interval between the peak fore and hind quarter displacements:

$$\phi = [(t_{peak,com} - t_{peak,hind})/(t_{peak,fore} - t_{peak,hind})]\times100 . \quad (2)$$

If ϕ=0%, the center of mass and the hind quarters reached their peak vertical positions simultaneously, whereas if ϕ=100%, the center of mass and the fore quarters reached their peak vertical positions simultaneously.

Compass gait displacements

We compared the empirical vertical displacements of the dogs with those predicted if the fore and hind quarters vault up and over rigid limbs to assess whether it was reasonable to compare a walking dog with two linked bipeds with strut-like legs. In the theoretical rigid-leg gait, often referred to as a 'compass gait' (Rose and Gamble, 1994), each stance limb remained at a constant length and rotated symmetrically over the point of contact during the first and second halves of the stance phase as described by Lee and Farley (1998). To predict the vertical displacement for the compass gait and compare it with our empirical data, we incorporated experimentally derived values for limb phase, ground contact time and standing leg length. The values for the vertical displacement of the fore (z_{fore}) and hind (z_{hind}) quarters were used to calculate the vertical displacement of the center of mass (z_{com}) assuming a compass gait:

$$z_{com}(t) = z_{fore}(t)M_f + z_{hind}(t)M_h , \quad (3)$$

where M_f and M_h are the dimensionless fraction of body mass

supported by either the fore or hind limbs, respectively, and t is time.

Based on human walking data, in which the vertical position of the center of mass is lowest at approximately mid-double support, we assumed that the transition from left to right limb support occurred instantaneously at the middle of the double support phase. Although this assumption could have a significant effect on the absolute magnitude of the theoretical displacements (~2-fold range), the magnitude of the center of mass displacement relative to the fore and hind quarters varied by <20% across the full range of possible limb transition times within the left–right double support phases. The relative timing of the center of mass displacement (ϕ) was unaffected by the limb transition assumption.

Two-pendulum model of quadrupedal walking

This model focuses on the link between the motions of two independent pendulums and the motion of the system center of mass to address the question of how the motions of quadrupeds' fore and hind quarters are coordinated to produce inverted pendulum-like movement of the center of mass (see Appendix 1 for details). In the model, the vertical displacements of the two pendulums were equal and the vertical displacement of the center of mass of the combined two-pendulum system was expressed relative to that of a single pendulum. We investigated the sensitivity of the center of mass vertical displacement to the mass distribution and phase of the two pendulums. Although each individual pendulum's motion does not depend on mass, the motion of the center of mass of the whole two-pendulum system is affected by the mass distribution between the pendulums. With this model, we hoped to gain insight into how body mass distribution and limb phase affect center of mass movements in walking quadrupedal animals. We did not examine the velocity and kinetic energy fluctuations of the two-pendulum system center of mass due to the likely fore–hind quarter interactions in the fore–aft direction as discussed earlier.

We calculated the magnitude (Δz_{com}) and timing (ϕ) of the center of mass vertical displacement for a full range of pendulum phase relationships (θ) and mass distributions (M_f). We varied θ from 0% (pendulums in-phase) to 25% (pendulums out-of-phase) and M_f from 0.5 (half of total mass in fore pendulum) to 1.0 (total mass in the fore pendulum). Note that M_f is dimensionless because it represents the fraction of the total mass in the fore pendulum. The full range of possible limb phase relationships for this model is 0 to 25% because the maximum possible phase shift between successive peaks in the vertical displacements of the fore and hind pendulums is 25%. This is because the model does not distinguish between left and right limb movements. For example, in terms of the two-pendulum model, a 50% limb phase (i.e. diagonal limb pairs move synchronously) is the same as a 0% limb phase (i.e. ipsilateral limb pairs move synchronously).

Results

Mechanical energy fluctuations

Unlike the hypothetical example in Fig. 1, the dogs exchanged ΔE_p with ΔE_k of the center of mass, and *vice versa*, twice during a stride (Fig. 2). The magnitude of ΔE_k was determined primarily by the fore–aft velocity component. At $0.8~\mathrm{m~s^{-1}}$, the vertical and lateral velocity components comprised less than 6 and 8%, respectively, of ΔE_k. The ΔE_p and ΔE_k were similar in magnitude and nearly out of phase, thereby reducing the magnitude of the total mechanical energy fluctuations of the center of mass. This pattern indicates that the dogs utilized an inverted pendulum-like exchange of E_p and E_k, as found in a previous study (Cavagna et al., 1977).

The recovery of mechanical energy by the dogs reached a maximum of 70% at moderate speeds, a value similar to the maximum recovery in humans and other bipeds (Fig. 3A) (Cavagna et al., 1977). At moderate speeds (~$0.8~\mathrm{m~s^{-1}}$), the muscular work required to lift and accelerate the center of mass per distance walked was least (Fig. 3B) and percent recovery was greatest. Recovery was maximized because the fluctuations in E_p and E_k were nearly equal and approximately out of phase at these speeds (Fig. 3C,D). At all speeds, the E_p reached its maximum value within 10% of the stride time of when the E_k reached its minimum value.

Vertical displacements

To understand the interaction between limb function and center of mass dynamics, we calculated the fore quarter, hind quarter and center of mass vertical displacements during a stride (Fig. 4A). We focused on $0.80~\mathrm{m~s^{-1}}$ since the exchange of E_p and E_k was greatest at this speed.

We found that the displacement patterns of the fore quarters, hind quarters and center of mass for the dogs (empirical; Fig. 4A) were remarkably similar to the patterns calculated assuming that the legs behaved as rigid struts (compass gait; Fig. 4B). For the empirical data and the compass gait, the center of mass displacement was 0.57 and 0.58, respectively, of the fore quarters displacement and 0.43 and 0.47, respectively, of the hind quarters displacement. Moreover, the center of mass also reached its highest position at a similar moment in the stride in the dogs (ϕ=66%) and the compass gait (ϕ=62%). This ϕ value indicates that the center of mass fluctuations followed the fore quarters more closely than the hind quarters.

In both the dogs and the compass gait, the center of mass generally underwent two fluctuations in the vertical position per stride despite two fluctuations of the fore quarters and two fluctuations of the hind quarters. These four combined fluctuations of the fore and hind quarters produced two fluctuations of the center of mass because the displacements of the fore and hind quarters partially offset each other. The overall similarities between the empirical and compass gait data led us to further model walking quadrupeds as two pendulums: a fore quarters pendulum and a hind quarters pendulum.

Two-pendulum model of quadrupedal walking

Changing the pendulum phase and mass distribution dramatically altered the magnitude of the z_{com}. When the pendulums fluctuated exactly out of phase (θ=25%) and the mass was equally distributed between them (M_f=0.5), the z_{com} was zero (Fig. 5D), a result that matches our hypothetical example in Fig. 1. Reducing the phase shift (Fig. 5B) and/or redistributing the mass (Fig. 5C) between the pendulums
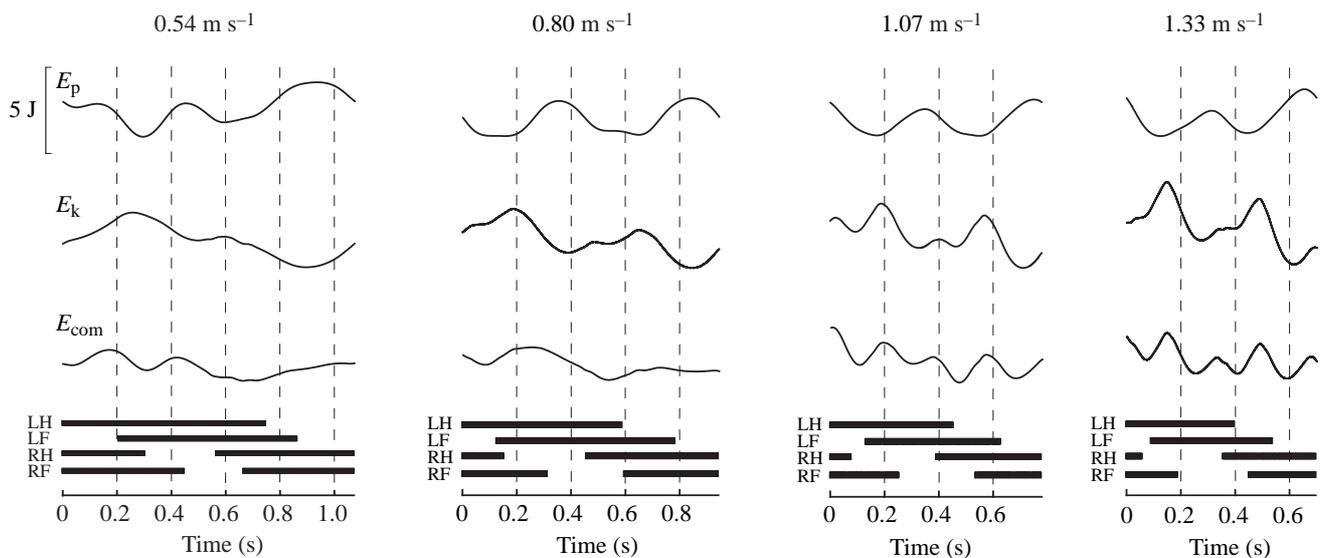

Fig. 2. Gravitational potential energy (E_p), kinetic energy (E_k) and total mechanical energy (E_{com}) of the center of mass *versus* time for a dog walking at four different speeds. E_p and E_k generally fluctuated out of phase so the fluctuations in E_{com} were smaller than either one. Bars indicate foot–ground contact times. Data are for typical trials for one stride beginning with the left hind limb ground contact for a 30 kg dog. LH, left hind limb; LF, left fore limb; RH, right hind limb; RF, right fore limb.
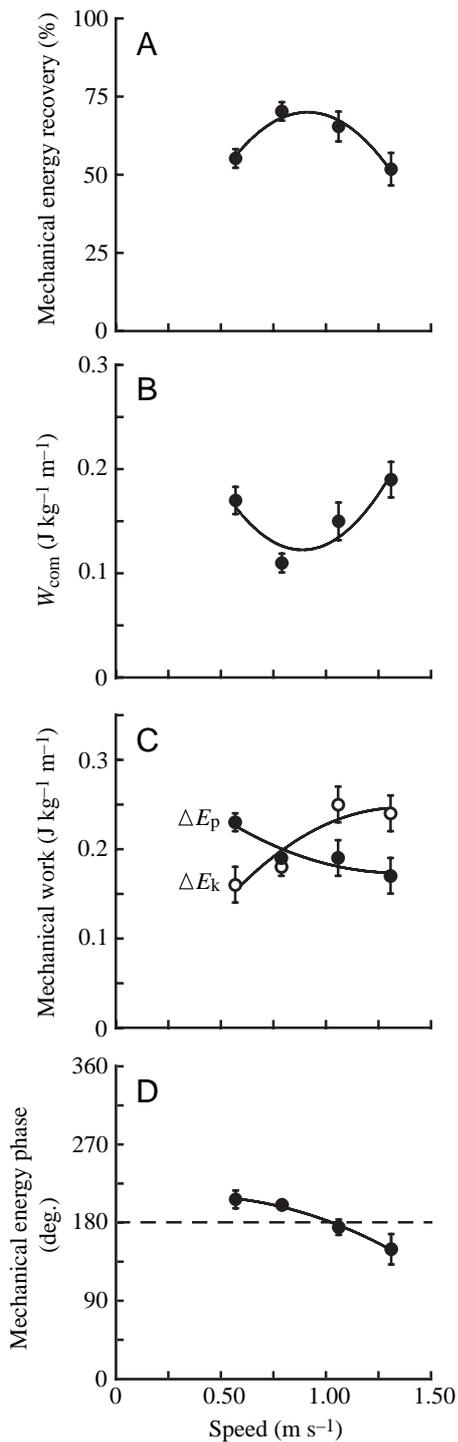
Fig. 3. Inverted pendulum mechanics of the center of mass for dogs walking at a range of speeds. (A) Recovery of mechanical energy *via* the inverted pendulum mechanism (recovery=$-117.5u^2+213.6u-27.1$, where u is speed; r^2=0.38). (B) Mass-specific work performed on the center of mass per distance traveled (W_{com}=$0.407u^2-0.718u+0.440$; r^2=0.39). (C) Mass-specific mechanical work per unit distance to lift (E_p; filled circles) and accelerate (E_k; open circles) the center of mass (E_p=$0.088u^2-0.236u+0.332$, r^2=0.88; E_k=$-0.153u^2+0.412u-0.032$, r^2=0.88). (D) Phase difference between the fluctuations in E_p and E_k (phase=$-75.5u^2+62.7u+196.4$; r^2=0.44). Values are means ± S.E.M. for all of the dogs. Lines are least-squares regressions.

increased the z_{com}. The two pendulums had equal amplitudes in all cases.

When the two pendulums swung nearly synchronously (i.e. $\theta<5\%$, as in a walking pace or trot), the z_{com} was nearly as large as each individual pendulum displacement. In this case, mass distribution had little effect on the z_{com} (Fig. 6A). Alternatively, if the pendulums swung out of phase (i.e.
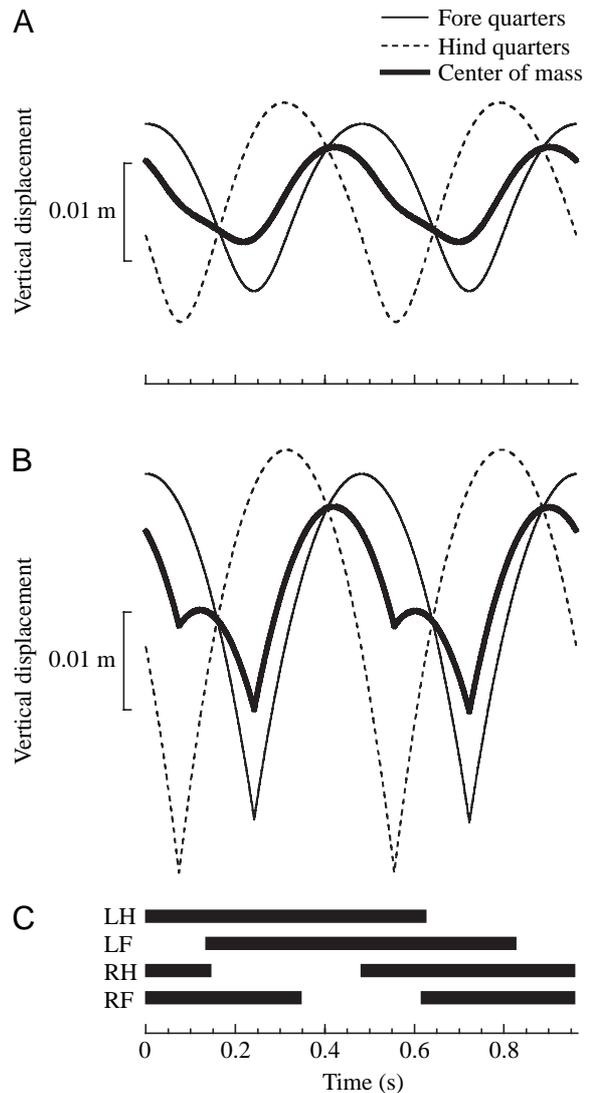

Fig. 4. Vertical displacements of the fore quarters, hind quarters and center of mass *versus* time for one typical walking stride at 0.8 m s^{-1}. The relative magnitudes and the timing of the actual displacement data (A) corresponded to the compass gait prediction (B). The similarities suggest that the fore and hind quarters actually vault over their support limbs like independent bipeds. The sharp transition points in the compass gait prediction (B) correspond to an instantaneous transfer from left to right limbs at the middle of double support. However, in a dog (A), this transition is smooth because it occurs over the entire period of double support. The dog's leg length and contact time were 0.54 m and 0.696 s, respectively, for the fore limbs and 0.45 m and 0.629 s, respectively, for the hind limbs. (C) The dog's actual footfall pattern from A; LH, left hind limb; LF, left fore limb; RH, right hind limb; RF, right fore limb.

$\theta \approx 25\%$), the z_{com} increased as the distribution of mass became less equal since the heavier pendulum had more influence on the center of mass movement (Fig. 6A).

The timing of the center of mass movements more closely followed the movements of the heavier pendulum. Mass distribution primarily determined the phase relationship between the peak z_{com} and the peak displacements of the fore and hind pendulums (ϕ) when the pendulums moved nearly synchronously (Fig. 6B). When the pendulums were more out of phase (i.e. θ approached 25%), both mass distribution and phase affected the relative timing of the center of mass movements. For equal distribution of mass between the two pendulums (i.e. M_f=0.5), the center of mass always reached its highest position at a time exactly halfway between the hind and fore pendulum maximum positions (ϕ=50%; Figs 5B, 6B).

All combinations of pendulum phase and mass distribution, except for that shown in Fig. 5D, resulted in two fluctuations of the center of mass despite four total pendulum fluctuations (two by each pendulum). This observation is consistent with what was observed in the dogs and the compass gait predictions.

Comparison of dogs to model predictions

The two-pendulum model predicted that quadrupeds would walk with a flat center of mass trajectory if they used a 25% limb phase and had equal body mass distribution between the fore and hind quarters (Figs 1, 5D). The center of mass trajectory of walking dogs, however, was not flat; the vertical displacement was 53±6% (mean ± S.D., N=3) of the mean fore and hind quarters displacement (e.g. Fig. 4A). Dogs attained significant fluctuations of the center of mass by deviating from the flat-trajectory assumptions (i.e. 25% limb phase and equal mass distribution) of the two-pendulum model.

We found that each fore limb lagged the hind limb on the same side of the body by, on average, 15% of stride time at all speeds in the dogs (Fig. 7; P=0.09 for limb phase *vs* speed, repeated-measures ANOVA). The two-pendulum model
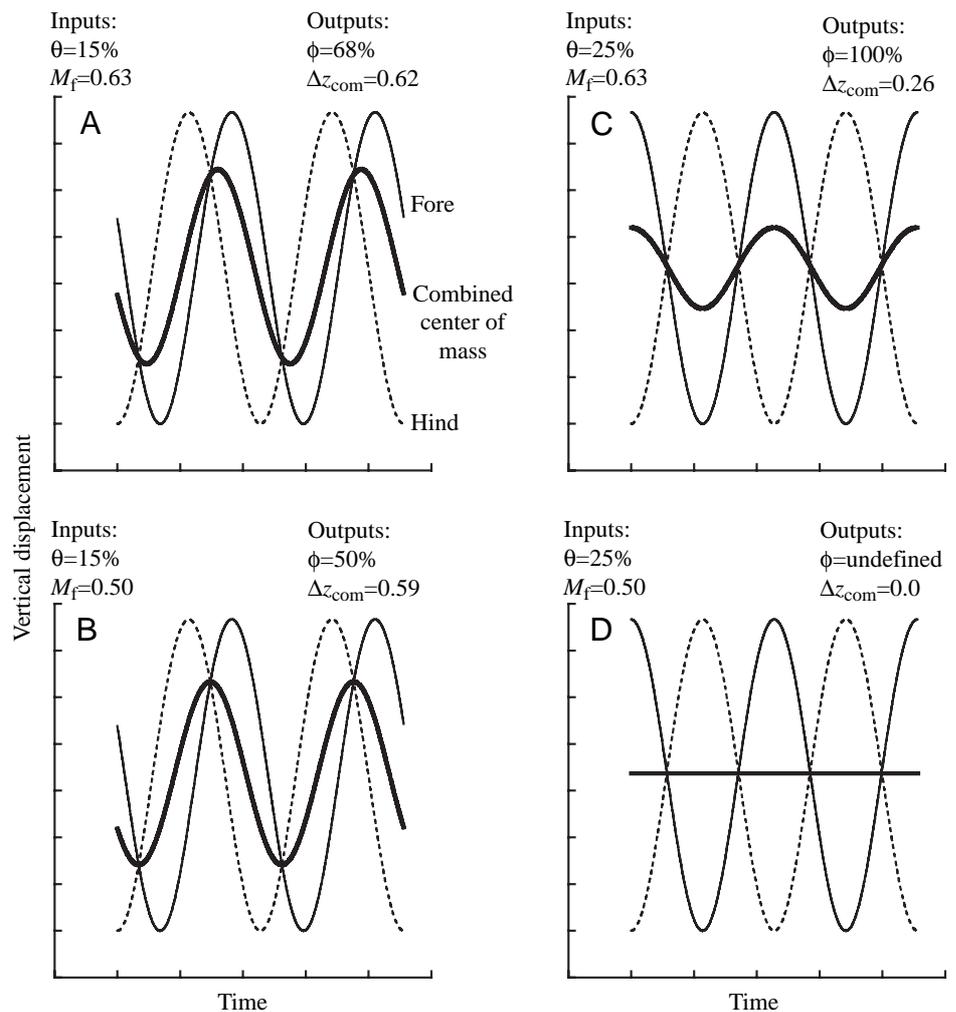

Fig. 5. Vertical displacement of the fore pendulum, hind pendulum and system center of mass *versus* time for specific examples from the two-pendulum model of quadrupedal walking. The model consists of two identical independent pendulums representing a quadruped's fore and hind quarters with a variable phase relationship (θ) and mass distribution (M_f). θ is the percentage of stride time that the fore pendulum displacement lags the hind pendulum displacement (analogous to the phase between a dog's ipsilateral fore and hind limbs), and M_f is the ratio of fore pendulum mass to the combined mass of both pendulums (equivalent to the fraction of body weight supported by the fore limbs). The time interval shown is equivalent to a complete dog stride. Δz_{com} is the magnitude of the center of mass vertical displacement relative to the pendulum displacement, and ϕ is the time interval between the peak center of mass vertical displacement and the peak hind pendulum vertical displacement, expressed as a percentage of time between peak hind and fore pendulum displacements. A represents the pendulum phase and mass distribution combination actually used by the dogs, and D represents the phase and mass distribution shown in the hypothetical diagram of Fig. 1. B and C represent intermediate patterns.

predicted that if limb phase decreased to 15% with equal mass distribution, the magnitude of the center of mass displacement would increase to 59% of each pendulum displacement (Figs 5B, 6A). This prediction was slightly greater than the observed 53% displacement in walking dogs.

We also found that body mass was not distributed equally in dogs: the fore limbs supported 63% of body mass during standing and at all walking speeds (P=0.88, repeated-measures ANOVA). The 63:37 mass distribution between the fore and
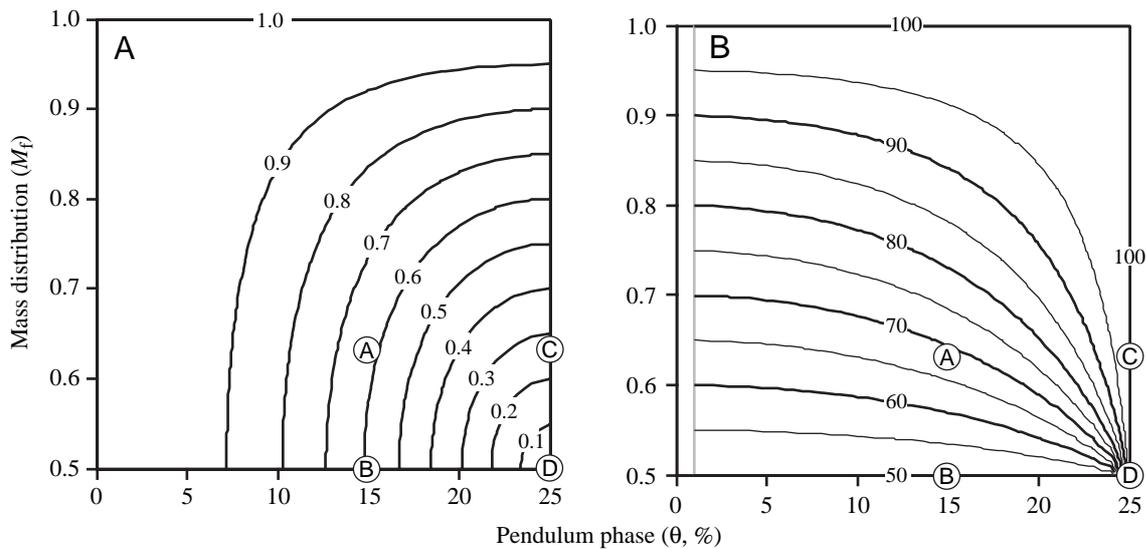
Fig. 6. Contour plots of the magnitude of the center of mass vertical displacement relative to the pendulum vertical displacement (Δz_{com}; A) and the phase relationship between the center of mass and the hind pendulum vertical displacement (ϕ; B) for the two-pendulum model of walking. These data are plotted as a function of the relative mass of the fore pendulum, M_f, and the phase difference between the fore and hind pendulums, θ. Both pendulums have the same amplitude in all cases. The circled letters correspond to the combinations of phase and mass distribution in Fig. 5A–D.

hind quarters was similar to the differences in maximum vertical ground reaction forces under the fore and hind limbs at 0.8 m s^{-1} (0.60× vs 0.35×W_b, respectively; Fig. 8). The two-pendulum model predicted that altering mass distribution away from the equal distribution of Fig. 5D and to the
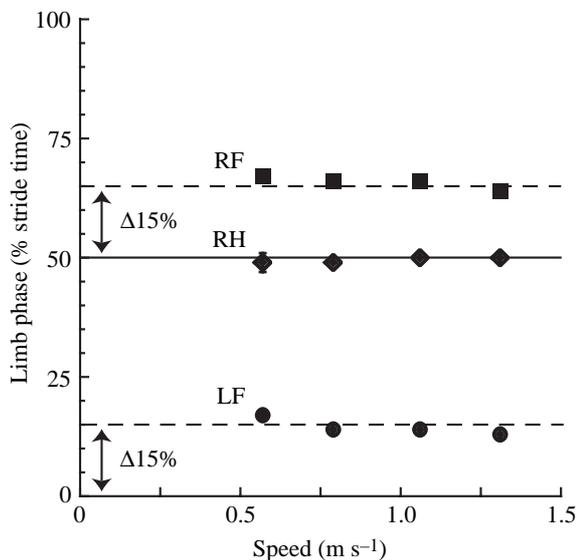

Fig. 7. Limb phase $versus$ speed. Each limb phase was calculated relative to the left hind limb (i.e. left hind limb phase=0%). At all speeds, each fore limb contacted the ground approximately 15% of the stride time after the ipsilateral hind limb. Hildebrand defined this limb phase and footfall pattern as a lateral sequence walk (Hildebrand, 1968, 1976). The order of footfalls was left hind (LH), left fore (LF), right hind (RH) and right fore (RF). Values are means ± S.E.M. for all of the dogs. Error bars are too small to be visible in most cases.

distribution observed in dogs, without altering limb phase (i.e. M_f=0.63 and θ=25%; Fig. 5C), would increase the vertical displacement of the center of mass to 26% of each pendulum displacement. This center of mass displacement was still much less than that observed in the dogs (53%). However, when both mass distribution and limb phase were matched for the dog values (i.e. M_f=0.63 and θ=15%; Fig. 5A), the predicted center of mass displacement was 62% compared with 53% observed in the dogs.

The relative timing of the center of mass fluctuations (ϕ) was affected by the unequal mass distribution of dogs as predicted by the two-pendulum model. When more mass was concentrated in the fore pendulum to match the dog's mass distribution, the center of mass of the two-pendulum model tracked the fore pendulum more closely (ϕ=68%). This observation suggests that the center of mass followed the fore limbs more closely in the dogs (ϕ=66%) because they supported more weight than the hind limbs.

Although we focused on the vertical component of the ground reaction force to determine the mass distribution between the fore and hind quarters, the dog's unequal mass distribution was also evident in the fore–aft and lateral components of the ground reaction force. Both the fore limbs and hind limbs generated a braking ground reaction force followed by a propulsive force (Fig. 8). However, the fore limbs spent more time braking than the hind limbs (55% vs 40% of their respective ground contact times). Furthermore, the fore limbs generated a greater peak braking force (–0.11× vs –0.06×W_b, fore vs hind limbs) and a greater peak propulsive force (0.10× vs 0.07×W_b) than the hind limbs. As a result, the fore limbs generated ~75% of the total braking impulse and 50% of the total propulsive impulse. The fore and hind limbs
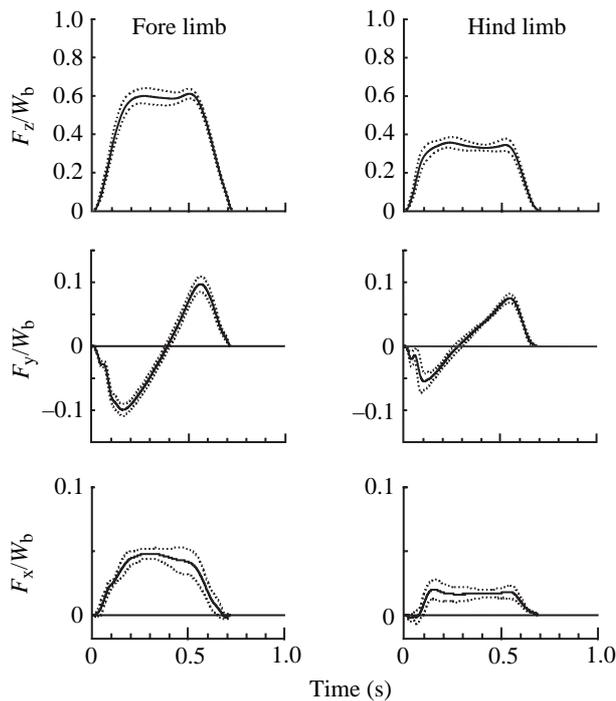
Fig. 8. Individual limb vertical (F_z), fore–aft (F_y) and lateral (F_x) ground reaction force components for the fore and hind limbs *versus* time for dogs walking at 0.8 m s^{-1}. Forces are expressed as a fraction of body weight (W_b). The fore limb forces were much larger than the hind limb forces. The solid line represents the mean trace for the six dogs, and the broken lines are ±1 S.D. Note that the y-axis scales differ. Positive values correspond to up (F_z), forward (F_y) and medial (F_x).

contributed equally to the propulsive impulse because the greater peak fore limb forces were offset by the shorter time over which the fore limbs generated propulsive forces. Similarly, the fore limbs generated 2–3 times greater peak lateral forces than the hind limbs. For all limbs, the peak lateral ground reaction force was directed medially (i.e. toward the body mid-line) and was less than 0.06× and 0.03×W_b for the fore and hind limbs, respectively. These small lateral forces help explain why the lateral movements of the center of mass had only a small effect on the total E_k.

Discussion

Center of mass movements

The center of mass movements of a walking human and dog are not easily distinguished. Both animals cyclically convert E_p into E_k and *vice versa* twice during a stride. Walking dogs behave like two humans walking one in front of the other. In dogs, the fore and hind quarters each reach their highest position near mid-stance of their respective support limbs (Fig. 4A), just like bipedal inverted pendulums. We find that two factors can explain how dogs, and probably many other quadrupedal animals, can produce inverted pendulum-like movements. First, dogs walk with a limb phase of 15% rather than 25%, which prevents the fore and hind quarters from

moving exactly out of phase. Second, dogs support more than half of their body weight with their fore limbs so that the center of mass vertical movements more closely follow the movements of the fore quarters. Together, these factors cause the center of mass to rise and fall twice per stride, like a walking biped.

Nearly all combinations of pendulum phase and mass distribution result in two fluctuations of the center of mass despite four total pendulum fluctuations (two by each pendulum). This finding makes sense mathematically since the addition of two sine waves of equal frequency results in a third wave of the same frequency. Thus, when applied to dogs or other walking quadrupeds, the center of mass will undergo two oscillations per stride as long as the fore and hind limbs each undergo two oscillations per stride. The one case when this does not occur is when the fore and hind quarters oscillate exactly out of phase and mass is distributed equally (Fig. 5D), a combination that results in no oscillation of the center of mass.

Determinants of the vertical displacements of the fore and hind quarters

We find that a dog's fore and hind quarters each reach their highest position near mid-stance of their respective support limbs. This finding assumes that the vertical movements of the fore and hind quarters are mechanically independent of each other, as reasoned by us and other authors (Alexander and Jayes, 1978a; Jayes and Alexander, 1978). Although this assumption may not allow precise predictions of the pectoral and pelvic girdle displacements, our goal was to understand the basis for the pattern of center of mass movement. Consequently, our overall conclusions are not likely to be affected by small deviations from this assumption.

The vertical displacement patterns of the fore quarters, hind quarters and center of mass of a dog are remarkably similar to the patterns for a compass gait. However, the displacement magnitudes in a dog are half of the compass gait prediction (Fig. 4; Jayes and Alexander, 1978). This difference could be due to subtle non-strut-like limb behavior. For example, the stance limb of walking humans does not actually behave like an incompressible strut; joint flexion and the resulting limb compression reduces the vertical displacement of the center of mass (Lee and Farley, 1998).

In dogs, the difference between the compass gait prediction and the observed displacement could be reconciled if the fore and hind limbs compressed by 3.4% and 4.6%, respectively, of limb length at mid-stance. For comparison, dogs compress their limbs by ~20% of limb length during trotting (Farley et al., 1993). The limbs probably undergo some compression during walking since the shoulder, elbow, knee and ankle joints flex by ~20° during the stance phase (Goslow et al., 1981). We could increase the accuracy of our predictions of the absolute displacements of the fore quarters, hind quarters and center of mass by adding a limb compression component to the compass gait model. However, this refinement does not appear to be necessary to gain insight into the determinants of the movement patterns of the center of mass since the rigid-leg

model accurately predicts the relative magnitude and timing of the dog's center of mass movements.

If limb compression primarily affects absolute, but not relative, displacements then it is unlikely to explain the greater relative center of mass displacement predicted by the two-pendulum model (62%) compared with that observed in dogs (53%). Instead, this difference may be due to our method of calculating limb phase. Hildebrand (1976) proposed that when the fore and hind foot contact times are unequal, as in dogs, it may be more functionally relevant to calculate limb phase based on the intervals between mid-stance times of the limbs rather than touchdown times. This alternative may indeed be functionally important for understanding the center of mass vertical displacement pattern in walking dogs since the fore and hind quarters each reach their highest position at mid-stance of their respective support limbs. With this alternative method, limb phase is 17% rather than 15%. In the two-pendulum model, this limb phase value and the observed mass distribution (i.e. θ=17% and M_f=0.63), leads to a center of mass displacement that is 53% of the pendulum displacement – the same value observed in dogs.
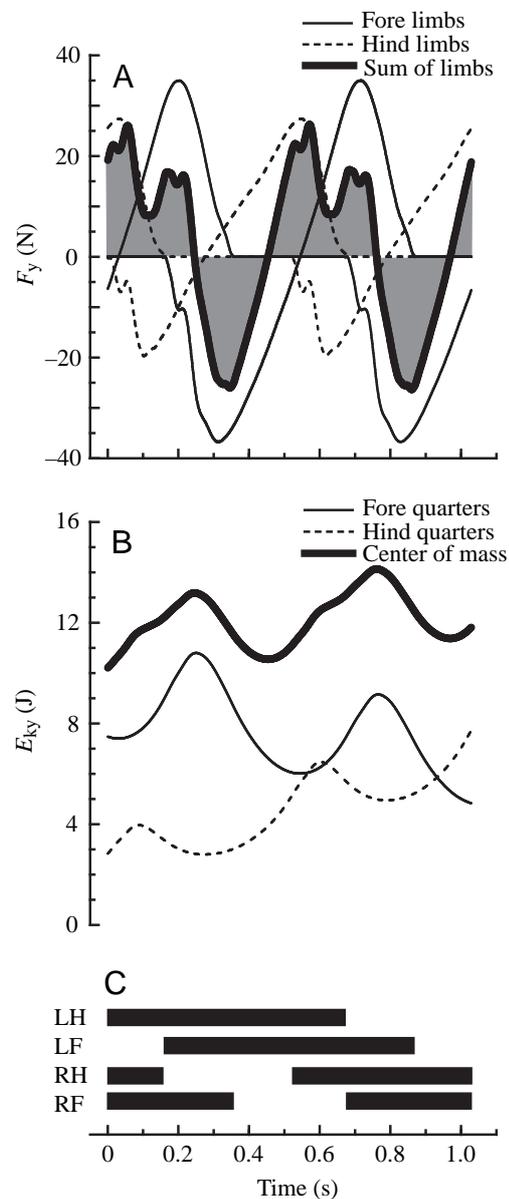
Determinants of the fore–aft movements of the fore and hind quarters

For effective inverted pendulum-like exchange, the magnitude of the E_p and E_k fluctuations must be closely matched. To what extent do limb phase and mass distribution – factors that affect the E_p fluctuations – determine the E_{ky} fluctuations of the center of mass? We cannot answer this question using the two-pendulum model because it assumes independent pendulum movement but, in dogs, the trunk probably transmits fore–aft forces between the fore and hind quarters. We can, however, gain insight into the factors that affect the fore–aft movements of the center of mass by examining the interaction between the fore and hind quarters.

The fore and hind limbs of dogs generate braking and propulsive forces simultaneously throughout the entire stride (Fig. 9A). Consequently, the net braking and propulsive forces acting on the center of mass are smaller than those generated by the individual limbs. Another consequence is that the amplitude of the E_{ky} fluctuations is smaller for the center of mass than for both the fore and hind quarters (Fig. 9B). Because limb phase affects the relative timing of the E_{ky}

Fig. 9. Average fore–aft ground reaction forces (F_y) and kinetic energy fluctuations (E_{ky}) for all dogs walking at 0.8 m s^{-1}. (A) The limbs generated propulsive and braking forces simultaneously throughout most of the stride. Consequently, the summed limb fore–aft force was smaller than the individual limb forces. Shaded areas indicate the net propulsive and braking impulses, which determine the velocity fluctuations of the center of mass. Limb phase was 15% of stride time, as observed in dogs. (B) Kinetic energy fluctuations were smaller for the center of mass than for the fore and hind quarters because the nearly out-of-phase fluctuations of the fore and hind quarters partly offset each other. Data assume that (1) the fore and hind quarters were, respectively, 63% and 37% of the total body mass (37.8 kg), (2) the fore and hind quarters each had a mean velocity of 0.8 m s^{-1} and (3) the velocity fluctuations of the fore and hind quarters were determined completely by their respective fore–aft ground forces. The first two assumptions are reasonable, but the third assumption is likely to be false because forces transmitted *via* the trunk probably play a role. The fore and hind limbs generate net braking and propulsive forces, respectively, so trunk forces would presumably counteract these net forces. Otherwise, the net propulsive ground reaction force on the hind quarters would cause them to overtake the fore quarters. The trunk is most likely loaded in compression during steady-speed walking because the hind quarters must, on average, push the fore quarters forward, and the fore quarters must, on average, push backwards on the hind quarters over a complete stride. If these trunk interaction forces were accounted for, we would expect the kinetic energy values of the fore and hind quarters to return to their respective initial values at the end of the stride instead of having net changes as shown in B. (C) The dogs' average footfall pattern; LH, left hind limb; LF, left fore limb; RH, right hind limb; RF, right fore limb.
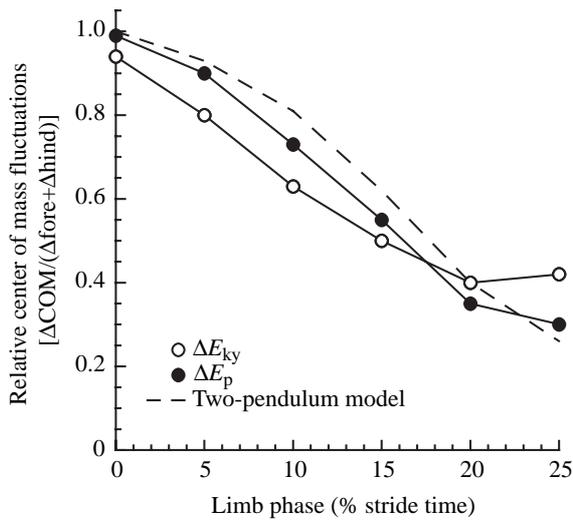
Fig. 10. Decreasing limb phase increased gravitational potential energy (ΔE_{p}) and fore–aft kinetic energy (ΔE_{ky}) fluctuations of the center of mass relative to those of the fore and hind quarters. As limb phase approached 0%, the vertical and fore–aft movements of the fore and hind quarters were more synchronous. These changes were similar to those predicted by the two-pendulum model. We assumed that (1) the fore and hind quarters were, respectively, 63% and 37% of the total mass (37.8 kg) and (2) limb phase did not affect the ground reaction force. Values were calculated using mean individual limb ground reaction force data for dogs walking at 0.8 m s^{-1} (Fig. 8) and time-shifting the data to simulate a range of limb phases. The values for 15% limb phase correspond to the example in Fig. 9.

fluctuations of the fore and hind quarters, it is likely that limb phase has a large impact on the amplitude of the E_{ky} fluctuations of the center of mass.

Indeed, limb phase appears to affect the E_{ky} fluctuations to a similar extent as it affects the vertical displacement (Fig. 10). As limb phase approaches 0% (e.g. walking pace or trot), the E_{ky} fluctuations of the center of mass increase since the fore and hind quarter fluctuations are nearly in phase with each other. These results, however, are subject to the assumptions discussed in Fig. 9B and they also assume that limb phase does not affect the fore–aft ground reaction force pattern. It is difficult to test this last assumption since the dogs used the same limb phase across speed; a broader comparative study of animals that naturally vary in limb phase may be needed to evaluate this assumption. Overall, the data suggest that limb phase modulates the magnitude of E_{k} and E_{p} fluctuations to allow for inverted pendulum-like energy exchange across a range of limb phases.

By modulating the magnitude of mechanical energy fluctuations, limb phase appears to affect the mechanical work of walking; the relative mechanical energy fluctuations of the center of mass at a 25% limb phase are less than half those at a 0% limb phase (Fig. 10). However, the magnitude of the total mechanical energy increments of the center of mass does not account for all sources of limb mechanical work. For example, two limbs perform mechanical work against each other if

one limb performs positive work while another limb simultaneously performs negative work on the center of mass (Alexander and Jayes, 1978b; Donelan et al., 2002a). Our analysis suggests that, as limb phase approaches 25%, the periods of simultaneous braking and propulsive force generation increase and likely lead to greater amounts of inter-limb work. Therefore, the smaller fluctuations in center of mass total mechanical energy as limb phase approaches 25% may be offset by an increase in inter-limb work. In general, limbs probably work against each other to a much greater extent in quadrupeds than bipeds because limbs work against each other for 100% of the stride in dogs but only ~30% of the stride in humans.

Predicting center of mass movements: effect of morphology and limb phase

Based on the results of the two-pendulum model, the limb pair (e.g. fore or hind) that supports more weight and generates the largest forces will primarily determine the movements of the center of mass. Because the force distribution is similar for standing as for walking, it is possible to make predictions about which limbs most influence the center of mass movements for most walking quadrupedal animals by simply measuring the body weight supported by the fore and hind limbs during standing. However, this approach and the results of the two-pendulum model may not apply to animals with heavy heads or tails that do not move in synchrony with the fore or hind quarters, respectively.

Animals use a wide range of limb phases and, according to our two-pendulum model, these different phase values can lead to profound changes in the displacement of the center of mass. If ipsilateral fore and hind limbs or contralateral fore and hind limbs strike the ground together, such as in a walking pace or walking trot, the center of mass vertical displacement equals the displacement of the fore and hind quarters since their movements do not offset each other. Conversely, the center of mass displacement decreases dramatically if the limbs strike the ground at more evenly spaced time intervals (i.e. approaching 25% limb phase). Given the great number of limb phase measurements of walking animals (Hildebrand, 1976), it may be possible to make broad predictions about the relative center of mass movements of diverse animals. These predictions, however, do not appear to correlate with the extent to which animals utilize inverted pendulum-like energy exchange. Diverse animals such as lizards (Farley and Ko, 1997) and horses (Minetti et al., 1999) use vastly different limb phases – 50% (equivalent to 0% in our model) and 22%, respectively – and they recover similar percentages of energy *via* the inverted pendulum mechanism (~50%).

For most animals, each species' fore and hind limb lengths and duty factors are similar (Hildebrand, 1976), which led us to assume equal fore and hind pendulum displacements and frequencies in our model. Yet even if the limb lengths were slightly different, as they probably are in most animals, it would have a negligible effect on our conclusions since the natural frequency of a swinging pendulum varies with $L^{-0.5}$,

where L is leg length. Although vertical displacement is proportional to limb length, the fore limb length would have to be >1.8 times the hind limb length (for an equal mass distribution) to cause the center of mass displacement to follow the fore limb displacement to the same extent as when the mass distribution is 65:35 between the fore and hind quarters.

Conclusions

The inverted pendulum-like behavior of walking is observed in many phylogenetically and morphologically diverse animals, and our study provides some insight into the mechanical factors responsible for this convergent behavior. The center of mass movements of a walking biped are primarily determined by the mechanical behavior of the limb. Our study demonstrates that changing limb phase or the distribution of weight supported among a quadruped's limbs can alter the center of mass dynamics without changing the behavior of individual limbs. Thus, a quadruped has more options for altering the dynamics of walking than a biped.

Previous models of quadrupedal walking (Alexander, 1980; Alexander and Jayes, 1978b) suggest that animals can minimize the work performed by each limb by generating ground force patterns that cause the fore and hind quarters to vault over their respective stance limbs, like inverted pendulums. These predicted force patterns are similar for a wide range of limb phases and mass distributions. The results from these previous models, when combined with our findings, suggest that animals can modulate their center of mass movements over a wide range without deviating from the strut-like limb behavior that is predicted to be most economical.

Unlike our hypothetical example with equal mass distribution and footfalls evenly spaced through a stride, we found that the center of mass of a walking dog does not maintain a flat trajectory because (1) the fore limbs lag the hind limbs by less than 25% of the stride time and (2) the fore limbs support more than half of body weight. In fact, our model demonstrates that many combinations of limb phase and/or unequal fore:hind quarter mass distribution will produce two fluctuations of the center of mass per stride if the fore and hind quarters vault over their stance limbs like inverted pendulums. This insensitivity to changes in limb phase and mass distribution may help explain how animals as diverse as lizards and dogs achieve similar center of mass dynamics (i.e. two fluctuations of the center of mass per stride) despite vastly different limb postures (sprawled *vs* upright) and limb phases (50% *vs* 15%) (Farley and Ko, 1997). Future studies of other species with different combinations of limb phase and fore:hind mass distribution will provide further insight into how gait pattern, morphology and limb mechanical behavior determine the center of mass dynamics in walking.

List of symbols

E_{com}	total mechanical energy of the center of mass
E_k	kinetic energy of the center of mass
E_{ky}	fore–aft component of kinetic energy of the center of mass
E_p	gravitational potential energy of the center of mass
F_x	medio-lateral component of the ground reaction force
F_y	fore–aft component of the ground reaction force
F_z	vertical component of the ground reaction force
L	leg length
M_f	dimensionless fraction of total mass located in the fore quarters (or pendulum)
M_h	dimensionless fraction of total mass located in the hind quarters (or pendulum)
$t_{peak,com}$	time of peak vertical displacement of the center of mass
$t_{peak,fore}$	time of peak vertical displacement of the fore quarters
$t_{peak,hind}$	time of peak vertical displacement of the hind quarters
u	speed
W_b	body weight
z_{com}	vertical displacement of the center of mass
z_{fore}	vertical displacement of the fore quarters (or endulum)
z_{hind}	vertical displacement of the hind quarters (or pendulum)
Δz_{com}	dimensionless magnitude of the maximum center of mass vertical displacement relative to Δz_{pend}
Δz_{pend}	maximum vertical displacement of the fore and hind pendulum in the two-pendulum model
$\Sigma\Delta E_{com}$	sum of the positive increments in E_{com} over the stride
$\Sigma\Delta E_k$	sum of the positive increments in E_k over the stride
$\Sigma\Delta E_p$	sum of the positive increments in E_p over the stride
ϕ	percent time of peak center of mass vertical displacement relative to the time interval between $t_{peak,fore}$ and $t_{peak,hind}$
ϕ'	phase shift of center of mass vertical displacement relative to the fore pendulum
θ	phase shift between the fore and hind pendulums as a percentage of stride time
θ'	phase shift between the fore and hind pendulums
ω	pendulum frequency

Appendix 1. Details of the two-pendulum model

We modeled the vertical displacements of the fore and hind quarters as two independent simple pendulums because this closely approximated the vertical movement patterns of the fore and hind quarters observed in dogs. For small angles, the vertical displacement patterns of two pendulums and their combined center of mass can be calculated mathematically by a series of cosine waves. The hind pendulum vertical displacement was given as:

$$z_{hind}(t) = \Delta z_{pend}\cos(\omega t) , \qquad (A1)$$

where Δz_{pend} is the maximum vertical displacement of the fore

and hind pendulum, ω is the pendulum frequency, which was kept constant at 1 rad s^{-1}, and t is time. The fore pendulum vertical displacement was given by:

$$z_{\text{fore}}(t) = \Delta z_{\text{pend}} \cos(\omega t - \theta') , \qquad (A2)$$

where θ' is the phase shift between the fore and hind pendulums. Stride time was 4π to include two full cycles for each pendulum, representing the movements caused by the left and right limbs within a stride.

Accounting for the mass distribution between the fore and hind pendulums, we calculated the displacement of the system center of mass, which was expressed as a fraction of the maximum pendulum vertical displacement (Δz_{pend}):

$$z_{\text{com}}(t) = M_{\text{h}} \cos(\omega t) + M_{\text{f}} \cos(\omega t - \theta') , \qquad (A3)$$

where M_{h} and M_{f} are the fractions of the total mass (0–1.0) located in the hind and fore pendulum, respectively. Although mass does not affect the movements of an individual pendulum, the mass distribution determines the effect of each pendulum on the system center of mass motion. Note that z_{com}, M_{h} and M_{f} are dimensionless. We simplified equation A3 to:

$$z_{\text{com}}(t) = \Delta z_{\text{com}} \cos(\omega t + \phi') , \qquad (A4)$$

where Δz_{com} is equal to the magnitude of the maximum center of mass displacement relative to the maximum pendulum vertical displacement, and ϕ' is the phase shift of the center of mass displacement relative to the fore pendulum. We determined the solutions for Δz_{com} and ϕ' by representing equation A4 graphically as the sum of two vectors (Ruina and Pratap, in press) and using the law of sines and cosines:

$$\Delta z_{\text{com}} = (M_{\text{f}}^2 + M_{\text{h}}^2 + 2M_{\text{f}}M_{\text{h}} \cos\theta')^{0.5} , \qquad (A5)$$

$$\phi' = \sin^{-1} [(M_{\text{h}} \sin\theta')/\Delta z_{\text{com}}] . \qquad (A6)$$

To define ϕ' in the same manner as equation 2, i.e. the percentage time that the peak center of mass vertical position lags the peak hind pendulum vertical position, we made the following modification:

$$\phi = [(\theta' - \phi')/\theta'] \times 100 . \qquad (A7)$$

Thus, ϕ is defined exactly as in the walking dogs and can be interpreted in the same way as equation 2.

To directly compare the limb phase values in the dogs and the phase shift values between the fore and hind pendulums in the model, we expressed the model's phase shift as a percentage of stride time:

$$\theta = (\theta'/4\pi) \times 100 , \qquad (A8)$$

where θ is the percentage of total stride time that the peak vertical displacement of the fore pendulum lagged the peak vertical displacement of the hind pendulum. Thus, θ equaled 25% when the fore pendulum lagged the hind pendulum by π (since stride time was 4π).

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