Mechanics of dog walking compared with a passive, stiff-limbed, 4-bar linkage model, and their collisional implications

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Summary

Here, we present a simple stiff-limbed passive model of quadrupedal walking, compare mechanics predicted from the model with those observed from forceplate measurements of walking dogs and consider the implications of deviation from model predictions, especially with reference to collision mechanics. The model is based on the geometry of a 4-bar linkage consisting of a stiff hindleg, back, foreleg and the ground between the hind and front feet. It uses empirical morphological and kinematic inputs to determine the fluctuations in potential and kinetic energy, vertical and horizontal forces and energy losses associated with inelastic collisions at each foot placement. Using forceplate measurements to calculate centre of mass motions of walking dogs, we find that (1) dogs may, but are not required to, spend periods of double support (one hind- and one forefoot) agreeing with the passive model; (2) legs are somewhat compliant, and mechanical energy fluctuates during triple support, with mechanical energy being lost directly after hindfoot placement and replaced following forefoot placement. Footfall timings and timing of mechanical energy fluctuations are consistent with strategies to reduce collisional forces, analogous to the suggested role of ankle extension as an efficient powering mechanism in human walking.

Key words: collision, inverted pendulum, walk, quadruped.

Introduction

Walking with relatively stiff limbs, vaulting the hips (or hips and shoulders in the case of quadrupeds) over incompliant legs, presents a strategy for limiting the cost of locomotion. With this gait, mechanical energy forms interchange for 'free' – potential energy converts to kinetic as the centre of mass (COM) falls, and returns to potential as it rises again – so walking in bipeds is often described in terms of an 'inverted pendulum' (e.g. Cavagna et al., 1977). While fluctuations in kinetic and potential energy of the COM are also largely out of phase in walking quadrupeds (Cavagna et al., 1977) including dogs (Griffin et al., 2004), the mechanics of quadrupedal walking is generally less clear: although kinetic and potential energy oscillations can be broadly out of phase, the degree to which limbs can be treated as stiff, inverted pendulums is uncertain.

Consideration of passive dynamic walking for bipeds (McGeer, 1990; Garcia et al., 1998) and quadrupeds (Smith and Berkemeir, 1997) subjectively shows remarkably life-like motions with simple stiff-limbed machines powered only by changes in potential energy due to walking down a gentle slope in order to overcome collisional losses. The relevance of the energetic cost of collisions at each limb placement is being increasingly understood in a variety of locomotory systems, including bipedal walking (Kuo, 2002; Donelan et al., 2002; Collins et al., 2005), gibbon brachiation (Usherwood and Bertram, 2003) and horse galloping (Ruina et al., 2005). Here, we discuss some of the implications of minimising or managing collisions in quadrupedal walking and their potential use in accounting for observed footfall patterns and powering strategies.

As highlighted by Aristotle, 'Again, why do quadrupeds move their legs criss-cross? We have to examine the reasons for all these facts, and others cognate to them; that the facts are such is clear from our Natural History, we have now to ask reasons for the facts.' In an effort to approach this issue in the case of quadrupedal walking, we present a passive model based on the geometry of a 4-bar linkage to show (1) the fluctuations in potential and kinetic energy, (2) the vertical and horizontal forces, and (3) the mechanical energy losses that would be associated with each foot placement for a stiff-limbed, walking quadruped represented as a pair of inverted pendulums linked by a stiff, incompressible back. This model is not intended to accurately predict the kinetics, forces or energetics of actual quadrupedal walking; rather, it provides a reductionist position, from which the observed deviations from the passive, stiff-limbed case can be highlighted and their implications discussed.

Materials and methods

Here we present methods for: (1) a simple model of quadrupedal walking based on the geometry of a 4-bar linkage, predicting fluctuations in potential and kinetic energies, and horizontal and vertical accelerations, for passive, stiff-limbed quadrupeds; (2) extension of the model to derive energy losses due to collision as functions of limb phase and powering strategy; (3) empirical determination of fluctuations in potential and kinetic energies, horizontal and vertical accelerations, and power from forceplate and kinematic measurements; and (4) quantitative comparison of the model and observed fluctuations in potential and kinetic energies to determine the degree to which quadrupedal walking is passive (with a high 'energy recovery') and stiff-limbed (with a high value of the novel parameter 'compression ratio'). Further comparisons between model and empirical observations in this manuscript are qualitative.

Model construction

Phase

As walking can be considered a symmetrical gait, the footfall pattern can be described usefully in terms of phase (ϕ), expressed as a percentage throughout, where

$$\phi = T_{H1-F1} / T . \tag{1}$$

T_{H1-F1} is the time period between the first hindfoot and the first forefoot making contact with the ground as a proportion of the complete stride time (T) (the period between successive contacts with the same foot – double the period of a step). We assume symmetry between left and right throughout: the first hind foot hits the ground at 0% of stride period, the first front foot at ϕ% and the second hind foot at 50%. As an example, an evenly spaced Hind-Fore-Hind-Fore-Hind (H-F-H-F-H) footfall pattern would have a phase of 25%. Phases less than 25% are biased towards H-F–H-F–H. Note that, with this definition, left and right make no difference; a stride can begin with either left hind- or right hindfoot. Note that the model uses a subtly different form of phase [the 'geometric phase' (ϕ_{geom}), see below], but this has an imperceptible bearing on the results.

Numerical 4-bar model

The model reduces quadrupedal walking to a 4-bar linkage (Fig. 1) that continuously conserves mechanical energy (although see the 'collisions calculations' section on powering strategies). The geometry of the path of the hips and shoulders is determined by a compass gait for hind- and forelimbs, and a linkage between hips and shoulders provided by an incompressible, rigid back. This can be viewed as a 4-bar linkage consisting of a mass-less hindleg, a back with a distributed mass, a mass-less front leg and the static ground between the front and hind feet. This geometry determines the height, and thus potential energy, of the COM at every hindleg angle (θ) (taken from the vertical). Swing legs are disregarded. We calculate the appropriate geometry for the 4-bar linkage for the full range of hindlimb angles from $-\theta_{hind}$ to $+\theta_{hind}$ (repeated to make two steps, or one stride, Fig. 1B). For

each small change in hindlimb angle (a 125th of θ_{hind}, so approximately 0.18° in our simulations), the time interval is calculated that results in the appropriate linear and angular velocities required for the kinetic energies to combine with potential energy to result in a constant total mechanical energy (see Usherwood and Bertram, 2003). With the additional assumption that the limbs sweep through equal angles before and after the vertical, the only required inputs are as follows. Morphological: hind- and foreleg lengths (L_{hind}, L_{fore}); body mass (m_b); bias of body mass towards the shoulders [p, which we take as 60% following Jayes and Alexander (Jayes and Alexander, 1978), Lee et al. (Lee et al., 1999) and Griffin et al. (Griffin et al., 2004)]; and body moment of inertia about the COM (I). Kinematic: the mean horizontal velocity $\mathbf{V}$, which with stride period T is used to determine θ_{hind} (below) and the limb phase (ϕ). By iteration, the total mechanical energy of the system is found that results in the observed net forward velocity ($\mathbf{V}$).

The maximum angle swept from the vertical of the hindlimb (θ_{hind}) is given by:

$$\theta_{hind} = \sin^{-1} (\mathbf{V}T / 4L_{hind}) . \tag{2}$$
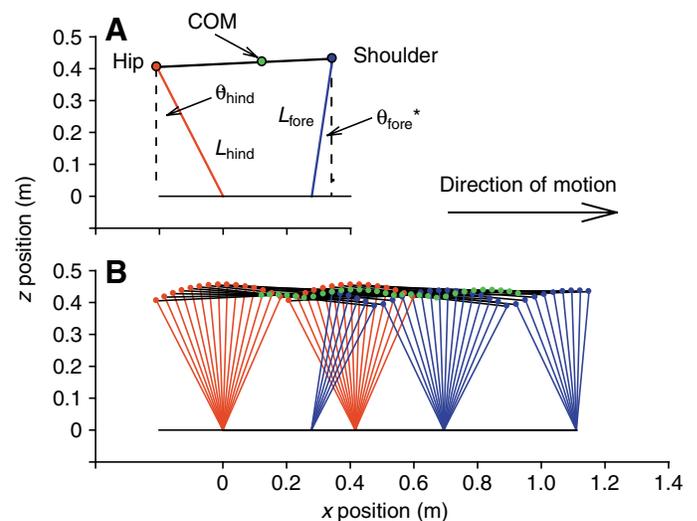
Fig. 1. Model geometry. (A) A 4-bar linkage consisting of a stiff hindleg (red, length L_{hind}), back, foreleg (blue, length L_{fore}) and the ground between the hind and front feet. The path of the body centre of mass (COM) and its rotations are calculated from purely geometric considerations as the hindleg vaults over the vertical (B). The stride begins at the instant of hindfoot placement. Both hind- and foreleg angles are assumed to sweep an equal angle before and after vertical. The initial foreleg angle θ_{fore}* is determined from the phase. The hindlimb angle is incremented, changing COM position (green dots) and body angle, and the appropriate time step for each increment throughout the stride is calculated such that the total mechanical energy is constant (although see the 'powering strategies' section). Interchanges between mechanical energy components (potential, kinetic and rotational kinetic energies), velocities and accelerations were thus calculated from the 4-bar linkage geometry as a function of time. Total mechanical energy was adjusted so that the model and observed mean horizontal velocities corresponded.

This definition of θ_{hind} is appropriate for use in the 4-bar model as the model assumes symmetry about the vertical and a duty factor (DF) of 0.5 (as the legs are infinitely stiff). True maximum sweep values are larger because the DF is >0.5 during walking, and are somewhat biased so that the hindfoot travels further back than it does forwards with respect to the hip. However, the aim of the model is to make the simplest 'default' position, with which to contrast empirical observation.

We calculate an approximation of the moment of inertia (second moment of mass) of the body about the COM with the following assumptions: the mass distribution behind the COM is even and the distribution after the COM towards the shoulders is also even, but the mass is biased towards the shoulders such that p=0.6. It turns out that modelled changes in rotational kinetic energy account for only a very small proportion of energy interchange (the amplitude in our simulations is typically 18 times less than for potential energy); therefore, we consider this very basic approximation for the moment of inertia to be adequate for the purposes of this study, and do not consider rotational kinetic energy further.

The model uses a geometric form for phase (ϕ_{geom}) as an input for the geometry:

$$\phi_{geom} = (\theta_{fore} + \theta_{fore}*) / 4\theta_{fore} , \qquad (3)$$

where θ_{fore} is the maximum angle from vertical swept by the forelegs, and $\theta_{fore}*$ is the angle of the forelegs from vertical at the instant of hindfoot placement (Fig. 1). As the magnitude of the velocity varies little throughout a stride, despite fluctuations in kinetic energy, the two forms for phase (Equations 1 and 3) give indistinguishable (<1% difference) values.

Collision calculations

The instantaneous change in velocity at each foot-on of the stiff-legged walking model is associated with a collision [see (Ruina et al., 2005) for extensive discussion of collision mechanics]. Treating this collision as inelastic, a mechanical energetic cost of these collisions can be calculated from the velocity of the COM immediately before foot-on (**v**) and the step change in direction of the COM (γ) (Fig. 2):

$$\mathbf{v}' / \mathbf{v} = \cos(\gamma) , \qquad (4)$$

where $\mathbf{v}'$ is the velocity directly after the collision, before any energy return has taken place. From this, the ratio of post- and pre-collision kinetic energies (E_k' and E_k, respectively) can be calculated:

$$E_k' / E_k = \cos^2(\gamma) . \qquad (5)$$

Therefore, the energy lost with each sudden redirection of the COM trajectory at both hind and front foot placement can be calculated from the stiff-limbed 4-bar linkage model described above:

$$\Delta E_{coll} = E_k - E_k' = \tfrac{1}{2} m_b \mathbf{v}^2 [1 - \cos^2(\gamma)] . \qquad (6)$$

It is worth noting that, although the magnitude of the accelerations (and so forces) at each collision is high
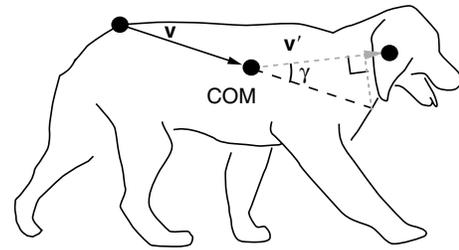
Fig. 2. Collision geometry at foreleg contact. A component of the centre of mass (COM) velocity just prior to collision **v** can be maintained after the collision (**v**′) despite an inelastic redirection through an angle γ determined from the 4-bar linkage geometry. The collisional energy loss calculated at each leg contact is dependent on both velocity and the angle γ with which the COM path is suddenly deflected.

(approaching infinite with a stiff-limbed model) and dependent on the simulation step size, energy losses associated with collision are finite and relatively insensitive to simulation step size.

Model powering strategies

For steady speed walking to be maintained, the energetic losses due to COM collision at each foot placement must be recovered over the stride cycle. The timing of energy return has a bearing on the collision energy losses and/or the speed that can be achieved for a given cost. For the completely stiff-limbed walker, energy should ideally be put into the system only directly following a collision event, as this allows the greatest period at highest speed for a given collisional energy loss; any other energy input strategy would require higher velocities at the instant of collision (and so higher collisional energy losses) if the same average horizontal velocity was to be achieved. We therefore study the collision energy losses associated with three extreme energy input strategies: first, an immediate recovery of each energy loss directly after each collision (this is the strategy assumed in all previous sections); second, a recovery of energy only directly after forelimb contact (resulting in a reduced total mechanical energy between hindfoot contact and forefoot contact); third, a recovery of energy only directly after hindlimb contact. Note that, for fair comparison, the initial energy conditions are adjusted so that the mean speed is the same in each case.

Empirical measurements

Dogs and forceplate and integrations

Five sound pet dogs covering a moderate range of sizes and proportions (Table 1) were walked over a forceplate, following procedures approved by the Royal Veterinary College. Speeds were selected at which each dog appeared to walk steadily without breaking into a trot or pausing. Non-dimensionalised speeds (Froude numbers $Fr = \mathbf{V}^2/gL_{hind}$, where g is the acceleration due to gravity) were calculated following Alexander and Jayes (Alexander and Jayes, 1983), using the hindlimb length (floor to hip during standing) as the

Table 1. *Morphology and key kinematic variables for the five dogs*

	Dog 1	Dog 2	Dog 3*	Dog 4	Dog 5[†]
Breed	Labrador	Australian shepherd	Australian shepherd	Springer spaniel	Bull terrier
Sex	Male	Male	Female	Male	Male
Mass (kg)	33.8	25.3	21.7	18.1	13.0
Hindlimb (m)	0.46	0.51	0.46	0.40	0.36
Back (m)	0.59	0.63	0.52	0.53	0.37
Forelimb (m)	0.48	0.48	0.47	0.40	0.33
Number of trials	6	5	6	8	10
Mean ± 1 s.d. θ_{hind} (°)	25.3±2.2	26.7±1.2	23.4±1.6	25.4±1.7	18.2±0.9
Mean phase ± 1 s.d. (%)	16.5±0.9	12.9±1.6	11.6±1.8	9.6±1.6	15.8±1.5

*The dog for which example trials of very slow, slow and moderate walking (Fig. 3) were taken.

[†]Excluded from Fig. 4 as energy recovery was <50% throughout the Froude number range; this dog exhibited a 'bouncing gait' even when kinematically walking.

representative length. Basic two-dimensional kinematic parameters (from 240 Hz 5-camera Qualisys system; Qualisys, Gothenberg, Sweden) and ground reaction forces (from a Kistler 9827BA; Kistler Instruments Ltd, Alton, UK) recording at 1000 Hz and low-pass filtered at 25 Hz with a zero-lag digital fourth-order Butterworth filter were repeatedly recorded for single steps. Mean horizontal velocity, required as a model input and for forceplate integration (see below), was derived from motion of a marker sited on the trunk at approximately halfway down the seventh rib. Foot-on timings (required for limb phase, an input of the model) and foot-off timings (to show periods of triple support) were assessed from kinematic markers on the feet.

Motions of the COM were calculated from the measured ground reaction forces, as were the associated changes in potential and kinetic energy, following the principles described by Cavagna (Cavagna, 1975). In order to minimise drift due to integrating or double-integrating over long periods, we used measurements for single steps (we use from hind-on to the contralateral hind-on) and duplicated the derived values, assuming walking to be a symmetrical gait, to provide results for a complete stride (two steps). In addition, it was assumed that there is no net change in COM height over a step (mean vertical velocity is zero), the mean horizontal velocity is that observed from kinematics and there is no net horizontal acceleration or deceleration. Unlike Cavagna (Cavagna, 1975), we include vertical kinetic energy in our calculation of kinetic energy. COM power (external mechanical power) is calculated from the changes in the sum of potential and kinetic energies for a small time-step (Δt):

$$P_{COM} = \Delta(E_p + E_k) / \Delta t . \quad (7)$$

Energy recovery and compression ratio

To provide a quantitative assessment of the degree to which walking quadrupeds follow stiff-limbed, passive walking, we use both the widely discussed term 'energy recovery' (e.g. Cavagna et al., 1977; Griffin et al., 2004) and a new term, which we describe as a compression ratio (*CR*). Energy recovery describes the proportion of combined potential and kinetic energy fluctuation that could be achieved passively:

$$ER = 1 - \Sigma E_m / (\Sigma E_k + \Sigma E_p) = \\ (\Sigma E_k + \Sigma E_p - \Sigma E_m) / (\Sigma E_k + \Sigma E_p) , \quad (8)$$

where E_m is the total instantaneous mechanical (E_p+E_k) energy. A value of 1 would suggest perfect E_k-E_p-E_k interchange and a constant zero P_{COM}.

The *CR* is based on the variations in potential energy that *would* occur *if* the quadruped was stiff-limbed, using the observed morphology and foot kinematics. It is based on the amplitude of changes in energy, and takes no account of timing. It can be used as a measure of the degree to which limbs can be viewed as being stiff:

$$CR = a_{E_p,obs} / a_{E_p,mod} , \quad (9)$$

where $a_{E_p,obs}$ is the amplitude of the forceplate-derived variation in potential energy, and $a_{E_p,mod}$ is that derived from the stiff-limbed model. A value of zero would show that the COM travelled in a completely level path; a value of 1 suggests that the COM changes height exactly as calculated from the rigid 4-bar linkage model. Note that this metric is only useful for walking: values near 1 *can* be achieved with trotting, but it should not then be inferred that stiff limbs are being used. Also note that for a walking biped, this would be simply

$$CR_{biped} = a_{E_p,obs} / m_b g L [1 - \cos(\theta)] , \quad (10)$$

where L is the leg length and θ the maximum leg angle from vertical.

Results and discussion

Model- and forceplate-derived results for three trials of one dog (Dog 3, an Australian Shepherd; Table 1) are shown in Fig. 3. The appropriate observed kinematic inputs (**V**, θ, *T*) from each trial were used as inputs to the model. These three trials were selected as they cover very slow, slow and moderate walking speeds, and deviations from the zero acceleration assumption used in the forceplate integrations were small

(impulses over the integration period would have accounted maximally for a change in 0.06 m s^{-1} or 0.07 m s^{-1} in horizontal and vertical velocity, respectively). Each trace shows values for a complete stride, adjusted to start at hindfoot contact (derived from kinematics). Results for three of the four additional dogs broadly matched those for the 'moderate' example trial (Fig. 3iii). The remaining dog, also the smallest, locomoted at an appropriate range of Froude numbers (0.23–0.46) for walking dogs; however, this dog appeared to use a bouncing gait at these Froude numbers, with the energy recovery values often below 50%.

Fluctuations in E_p and E_k: energy recovery and the compression ratio

At low speeds, fluctuations in potential energy approach those predicted by the stiff-limbed geometry (Fig. 3iA, and the *CR* of Fig. 4). However, this is associated with energy input as the COM rises, and loss as it falls again (Fig. 3iE), as indicated by the power profile, the low amplitude of the E_k fluctuations (Fig. 3iB) and the diminished energy recovery [Fig. 4, matching the observations of Griffin et al. (Griffin et al., 2004)]. At intermediate speeds, observed fluctuations in E_p are of a lower amplitude and match the stiff-limbed model less well, presumably indicating that the limbs compress to a greater extent. However, E_k-E_p-E_k energy interchange is more effective during periods of double support (one hind- and one forefoot), suggesting passive stiff-limbed or 'inverted pendulum' mechanisms are effective: COM powers are low during this period (Fig. 3iiE), and energy recovery is at a maximum (Fig. 4) at these speeds. At higher walking speeds, the observed E_p fluctuations flatten further, and *COM* powers are consistent with spring-like behaviour of the forelimbs, with mechanical energy lost during the first half of stance and recovered during the second half. This theme continues with increasing speed, with a reduction in both energy recovery (suggesting more spring-like behaviour and less stiff-limbed or inverted-pendulum energy interchange) and the *CR* (indicating that limbs compress to a greater extent).

These results show the value of the term 'energy recovery' and the proposed term 'compression ratio' in the study of walking. Although energy recovery has proved effective in indicating the potential for passive E_p-E_k-E_p interchange, it is unable to provide an indication of how important this interchange is. Consider a large animal walking with a near-'Groucho' gait (with a level, constant speed COM) that fluctuates E_p and E_k by only a very small amount. If this small fluctuation happened to be exactly out of phase, consideration of energy recovery alone might suggest that it was walking efficiently, while each limb performed massive internal negative and positive works [and, presumably, at high metabolic cost (Ortega and Farley, 2005)]. Without resorting to leg-by-leg forceplate measurements and analysis, the *CR* provides an indication of the energy fluctuations that would be associated with stiff-limbed walking, and therefore how much weight to put on the consideration of the energy recovery term. So, there are two key questions to be asked when studying a walking animal: what proportion of the E_k-E_p-E_k interchanges may be considered passive and to what extent might this be achieved using stiff limbs. Although a full inverse dynamics

Fig. 3. Observed and model energy fluctuations (A,B), accelerations (C,D) and powers (E) for three example walking strides ranging from very slow (i) through slow (ii) to moderate (iii). Model outcomes, derived using empirical kinematic inputs and the stiff-limbed, constant energy (the immediate energy recovery strategy) model are shown in blue; values derived from forceplate measurements and kinematics are shown in red. Model accelerations go off-scale at the instants of each foot initial contact. Foot contact timings (F) can be used to identify periods of double and triple support.

Fig. 4. Combined summary results for four walking dogs over a range of speeds. Solid outlines relate to the left axis [compression ratio (*CR*)] and represent the observed fluctuations in potential energy as a proportion of those calculated from stiff-limbed 4-bar linkage geometry. Symbols with grey outlines relate to the right-hand axis [energy recovery (*ER*)] and represent the effectiveness of 'energy interchange' between kinetic and potential energies (1 being perfect). Lines show quadratic fits.

assessment of the walking animal is required to answer these questions fully, we consider energy recovery and *CR* to provide broad metrics for these two questions. Each of these terms indicates necessary *but not adequate* conditions for passive,

stiff-limbed walking. High values of each can potentially be achieved with near-Groucho (*ER*) or 'bouncing' (*CR*) walking. High values for both, however, provide strong evidence for passive, stiff-limbed walking mechanics without the requirement of a full inverse dynamics analysis.

Observed and model accelerations (forces)

Deviations between observed and model vertical and horizontal accelerations can be broadly understood by consideration of a certain degree of limb compliance, increasing with speed. The model predicts very high accelerations (or forces) at the instant of each foot placement; forceplate records show that there is a delay between foot placement and peak force, and the force peaks are smoothed. Once this is taken into account, the model is effective in accounting for both horizontal and vertical accelerations, particularly during periods of double (one hind-, one forefoot) stance (Fig. 3C,D).

With increasing speeds, the model predicts larger components of the vertical impulse to be contained in the collision spikes. Mean vertical acceleration remains zero (mean vertical force = body weight) but, while the COM arcs along its trajectory, centripetal acceleration requirements become apparent – vertical accelerations during the majority of the stride fall below zero. The model indicates that this trend would continue with increasing speed until the dog requires vertical accelerations below -9.81 m s^{-2}; at this point there is insufficient gravity to keep the model dog in contact with the ground, and walking cannot be maintained. For the morphological and kinematic inputs of the 'medium' trial (θ_{hind}=24.8, φ=13.0%), this condition would occur at a Froude number of 0.84; with the same parameters but a phase of 0%
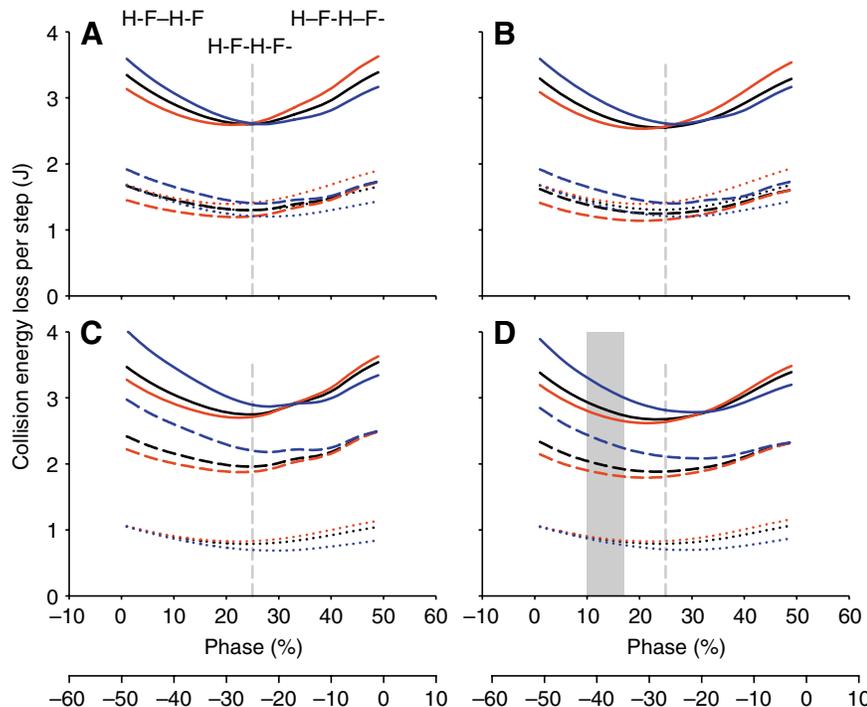
Fig. 5. Model collisional energy losses for a step with full ranges of forelimb–hindlimb phases. A ±25% limb phase suggests exactly even timing between hind- and forefoot contacts (H-F-H-F-, represented by vertical grey broken lines). Dotted lines represent energy lost at hind-foot contact; broken lines the energy lost at forefoot contact; solid lines the total energy lost for a step (one hind- and one forefoot contact). Three hypothetical powering strategies are shown: immediate recovery of energy loss (black); energy recovery only directly after forefoot contact (red) (most realistic); energy recovery only after hindfoot contact (blue). (A) Results for a fore-aft symmetrical walking dog with even fore- and hindleg lengths and a centre of mass (COM) mid-way along the body. (B) As for A, but with a realistic bias in leg lengths (foreleg = 0.47 m, hindleg = 0.46 m). (C) As for A, but with a realistic bias in mass position, with the COM towards the shoulders (*p*=0.6). (D) Results using realistic values of both limb length and mass bias. The underlying grey box represents the observed range of mean phases for walking dogs.

or 50% (pacing or trotting footfall pattern), at $Fr>0.76$; with a phase of 25%, at $Fr>0.84$. This phenomenon, therefore, occurs at speeds considerably greater than those tested in this study. This speed limitation to walking is largely equivalent to that described by Alexander (1989) and Usherwood (2005), traditionally understood using inverted pendulum mechanics to describe the centripetal acceleration requirements of stiff-limbed walking. However, even at moderate Froude numbers, limb compliance smoothes the COM trajectories, thus reducing both the impulses attributable to the collision spikes, and the centripetal acceleration requirements, effectively spreading the weight support across the stance.

Collision results

Results from the collision model (Fig. 5) indicate the implications of bias in front/back leg length, fore/aft mass distribution, powering strategy and phase. A realistic bias in front/back leg length (Fig. 5B) has little bearing on collisional energy losses compared with equal leg lengths. The mass bias (Fig. 5C), however, has a notable effect: the collisional energy loss due to hindfoot contact (dotted lines) is reduced, while that due to forefoot contact (broken lines) is increased, resulting in
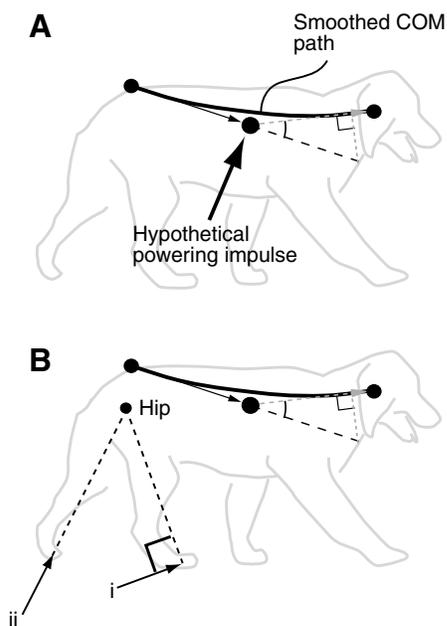
Fig. 6. Hypothetical propulsive impulses consistent with collision amelioration. If the mechanism for providing a powering impulse to the centre of mass (COM) also smoothes its path (A), powering is more efficient as collision losses are reduced. This may be achieved by two mechanisms (B): (i) hip torque while the hindleg is in early stance, or (ii) hindleg extension while the hindleg is late in stance. Either, or both, would have the effect of smoothing the path of the COM during forefoot placement, thus reducing the relatively high collision losses at this instant. Both of these mechanisms would be more effective, providing upward and forward impulses, with fore–hind phases of less than 25%.

a net increase in collisional energy losses. If the most life-like powering strategy, of returning lost energy directly after forefoot contact (red lines), is used, total collisional energy losses are reduced at low phases (H-F–H-F–H). The observed range of phases (grey bar in Fig. 4D), however, remains below those predicted by any of the collision models.

Collision discussion

It is clear that no walking animal is actually perfectly passive nor perfectly stiff-limbed. Equally, it is clear that there are never step changes in COM direction, and so there are not infinite forces, and energy losses calculated from a passive, stiff-limbed model should not be considered accurate. However, consideration of collisions, and especially their avoidance or potential amelioration, can provide insight into the selective pressures on both footfall timing [see Ruina et al. for horse galloping (Ruina et al., 2005)] and mechanisms of powering [see Kuo for bipedal walking (Kuo, 2002)] quadrupedal walking.

Collisional energy losses in our example walking quadruped (Fig. 5) are minimised at a phase of ±25% – an even spacing between each hindfoot and each forefoot placement. The reason behind this is twofold: first, the velocity at each collision is minimised if, when the front foot is being placed on the ground the hips are as high as possible and, when the hindleg is being placed on the ground, the shoulders are as high as possible. With this arrangement, achieved at phases of ±25%, the smallest possible proportion of mechanical energy is in the form of kinetic energy at each foot placement. Second, the deflection of the COM path at each foot placement is evenly divided; collision losses are reduced if the COM path is deflected by two intermediate changes rather than one large and one small (consider Equations 4–6). With our dogs, however, phases are approximately 10–17% (Table 1); in horses, the bias is also in this direction, accounting for their characteristic 'clip-clop–clip-clop' sound. Note that this theme is not, however, universal (see Hildebrand, 1968) for walking quadrupeds.

Let us first consider the effect of powering strategy given the observation that dogs (and horses) generally walk with a phase relationship of <25%. Fig. 5 suggests that the implications of realistic fore–hind leg length and mass distribution have relatively little bearing on the take-home message apparent in the fore-aft symmetrical case (Fig. 5A). That is, at phases less than 25% there is a benefit in terms of a reduction in collision energy losses (for walking at a given speed) to the powering strategy displayed in red: energy lost at hindfoot collision should not be replaced immediately; rather, the energy lost because of both hind- and forefoot collisions should be replaced directly after forefoot placement. The reason for this is as follows: with this powering strategy, at lower phases the effect of the energy lost at hindfoot placement on the overall mean speed becomes small because a relatively brief part of the step is spent at this reduced energy state. Meanwhile, the energy, and so the speed of the COM, is reduced for the instant of front foot placement, thus reducing the collisional losses because of front foot contact. Interestingly, this timing of

mechanical energy loss and recovery is consistent with that observed in all our forceplate measurements.

Let us next consider a potential selective pressure towards sub-25% phases from the phase described above as minimising collisional losses (25%). Here, we turn to the potential mechanisms for providing the required powering impulses. Kuo shows, for bipedal walking, some mechanisms of adding mechanical energy can be considerably more efficient than others (Kuo, 2002). In the bipedal case, powering with an ankle extension (presumably gastrocnemius action) late in stance may be 'four times less costly [than powering with a hip torque] because it decreases the collision loss at heel strike'; the collision geometry at foot placement can be smoothed by the lengthening of the trailing leg. We propose here two powering mechanisms with the potential for analogous path-smoothing benefits for quadrupeds (Fig. 6). Either a hip torque while the hindleg is early in stance or hindleg extension late in stance would contribute powering impulses with the concomitant effect of smoothing the COM path (deviating from the 4-bar linkage geometry) and reducing the collisional energy loss at front foot placement (the more significant collision because of the mass bias towards the front limbs, Fig. 5C,D).

So, *if* quadrupeds habitually power locomotion with their hindlimbs [as suggested by their muscle anatomy, and supported for trotting by forceplate measurements (Lee et al., 1999)], then powering with either hip torques or leg extension would be effective in reducing collision costs, particularly at phases less than 25%. Whether collision mechanics might explain why many quadrupeds power locomotion with their hindlimbs, or the tendency for quadrupeds to have a mass bias towards the forelimbs, is beyond the scope of this study, but deserves further attention.

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