RESEARCH ARTICLE

Effects of grade and mass distribution on the mechanics of trotting in dogs

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SUMMARY

Quadrupedal running on grades requires balancing of pitch moments about the center of mass (COM) while supplying sufficient impulse to maintain a steady uphill or downhill velocity. Here, trotting mechanics on a 15 deg grade were characterized by the distribution of impulse between the limbs and the angle of resultant impulse at each limb. Anterior–posterior manipulation of COM position has previously been shown to influence limb mechanics during level trotting of dogs; hence, the combined effects of grade and COM manipulations were explored by adding 10% body mass at the COM, shoulder or pelvis. Whole body and individual limb ground reaction forces, as well as spatiotemporal step parameters, were measured during downhill and uphill trotting. Deviations from steady-speed locomotion were determined by the net impulse angle and accounted for in the statistical model. The limbs exerted only propulsive force during uphill trotting and, with the exception of slight hindlimb propulsion in late stance, only braking force during downhill trotting. Ratios of forelimb impulse to total impulse were computed for normal and shear components. Normal impulse ratios were more different from level values during uphill than downhill trotting, indicating that the limbs act more as levers on the incline. Differential limb function was evident in the extreme divergence of forelimb and hindlimb impulse angles, amplifying forelimb braking and hindlimb propulsive biases observed during level trotting. In both downhill and uphill trotting, added mass at the up-slope limb resulted in fore–hind distributions of normal impulse more similar to those of level trotting and more equal fore–hind distributions of shear impulse. The latter result suggests a functional trade-off in quadruped design: a COM closer to the hindlimbs would distribute downhill braking more equally, whereas a COM closer to the forelimbs would distribute uphill propulsion more equally. Because muscles exert less force when actively shortening than when lengthening, it would be advantageous for the forelimb and hindlimb muscles to share the propulsive burden more equally during uphill trotting. This functional advantage is consistent with the anterior COM position of most terrestrial quadrupeds.

INTRODUCTION

From pronghorn antelope (*Antilocapra*) on North American plains to goral (*Naemorhedus*) on Himalayan precipices, quadrupeds occupy virtually every terrestrial habitat on Earth. Pronghorn antelope, which rely on unrivaled speed for escape, prefer flat or rolling terrain of less than 5% grade (Kindschy et al., 1978) whereas goral readily traverse steep rock cliffs and boulder fields (Lekagul and McNeely, 1977). Most quadrupeds, including gray wolves (*Canis lupus*), which occupy an impressive variety of habitats in the Northern Hemisphere (Nowak and Walker, 1991), are generally capable of traversing all but the most precipitous terrain. Although some excellent kinematic data are available (e.g. Carlson-Kuhta et al., 1998; Hoyt et al., 2002; van Oldruitenborgh-Ooste et al., 1997; Smith et al., 1998; Nyakatura et al., 2008; Nyakatura and Heymann, 2010), relatively few studies have reported individual limb forces of quadrupeds during downhill and uphill locomotion. These studies include data from trotting horses (Dutto et al., 2004), trotting opossums (Lammers et al., 2006; Lammers, 2007), trotting and galloping goats (Lee et al., 2008), and geckos running on vertical surfaces (Autumn et al., 1999; Autumn and Peattie, 2002).

Because most quadrupeds encounter moderate to steep terrain in their habitats, locomotor systems designed largely for economical locomotion on flat terrain must be capable of adjusting to variable grades. The net work and power requirements of ascending and descending necessitate increased actuation by muscles. It is well known that skeletal muscles can produce greater force when actively lengthening and less force when shortening compared with isometric contraction (Close, 1972; Katz, 1939). Given that braking can employ active lengthening and propulsion cannot, it follows that propulsive force should require recruitment of a greater muscle cross-section than braking force of the same magnitude. Although its effect could be partially compensated for by altering musculoskeletal transmissions, this fundamental difference in muscle contractile mechanics has unavoidable consequences. As is typical of cursorial mammals, most of a dog's limb muscle is composed of its proximal retractors and, to a lesser extent, protractors (Pasi and Carrier, 2003; Williams et al., 2009a; Williams et al., 2009b) that actuate the limbs as levers. Hence, it is predicted that the limbs will function more as levers during uphill than downhill trotting (prediction 1).

The bias of forelimbs toward braking and hindlimbs toward propulsion during level quadrupedal locomotion has been known for several decades (Cavagna, 1977; Heglund et al., 1982; Jayes and Alexander, 1978). It is predicted that this functional differentiation will be maintained or amplified during grade running. Specifically, forelimbs will brake more strongly during downhill trotting, and hindlimbs will be more strongly propulsive during uphill trotting (prediction 2). This is most clearly expressed by

individual limb impulse angles, determined from the quotient of shear and normal impulse. Impulse angles reported for level trotting of dogs are –3.3 deg in the forelimb and 5.8 deg in the hindlimb (Lee et al., 2004). Published values of shear and vertical impulse in other quadrupeds suggest that hindlimb impulse angle may be more propulsive during 6 deg incline than during level trotting in horses (Dutto et al., 2004), whereas no such pattern is evident in opossums ascending a 30 deg grade, nor is the predicted braking impulse angle evident during descent (Lammers et al., 2006).

In the present study, experimental center of mass (COM) manipulations were designed to provide insight into the functional consequences of quadrupedal body form variation during grade running. The effects of experimental COM manipulations on level trotting have been described previously in dogs (Lee et al., 2004). On the basis of these results, two effects of load distribution during downhill and uphill trotting are predicted here. By shifting the COM position upslope, hind-loading during downhill trotting and fore-loading during uphill trotting should result in a distribution of normal impulse more similar to that of level trotting (prediction 3) and a more equal distribution of shear impulse between the forelimbs and hindlimbs (prediction 4).

Although typically not measured from the same stride by multiple force platforms, an expected consequence of quadrupedal grade running is that force is redistributed from the upslope to the downslope limb or limbs. This redistribution can be expressed as the fraction of normal impulse exerted by the forelimb (i.e. the forelimb component of normal impulse divided by the sum of forelimb and hindlimb normal impulse). In agreement with this prediction, horses trotting up a 6 deg incline show a decreased forelimb fraction of mean vertical force of 0.52 compared with 0.57 on the level (Dutto et al., 2004). Likewise, in opossums running up and down a 30 deg grade, the forelimb fraction of mean vertical force decreased to 0.51 uphill and increased to 0.82 downhill compared with 0.67 on the level (Lammers et al., 2006). These investigators compared vertical rather than normal force distributions between level and grade locomotion. Yet, on a grade, vertical force includes a shear force component in the direction of travel, so vertical impulse ratios represent something mechanically distinct in grade *versus* level locomotion. The disparity between vertical and normal impulse distributions might reasonably be ignored in the case of slight grades, where the sine of the grade angle is approximately equal to the grade angle, but should generally be considered in comparisons of grade and level locomotion. Mean normal force distributions have been reported in goats running up and down a 15 deg grade, where the forelimb fraction of mean normal force decreased to 0.53 uphill and increased to 0.72 downhill compared with 0.65 on the level (Lee et al., 2008). The consensus of previous quadrupedal grade running studies is a substantial decrease in the fraction of forelimb support during uphill running and an increase during downhill running.

Although running up or down a grade at a steady speed requires no more force than level running (i.e. a vertical resultant force equal to body weight), a component of this force (i.e. shear force) acts in the direction of travel. During steady-speed, level trotting (Fig. 1A), the resultant ground reaction force is normal to the substrate and is distributed between the forelimbs and hindlimbs according to the craniocaudal position of the feet with respect to the COM. This determines the common center of pressure (COP) between the limbs. During steady-speed downhill or uphill running, the resultant ground reaction force has both a normal and shear component; however, the normal force distribution still defines the COP, which lies directly beneath the COM, on average, during steady-speed locomotion (Fig. 1B,C).
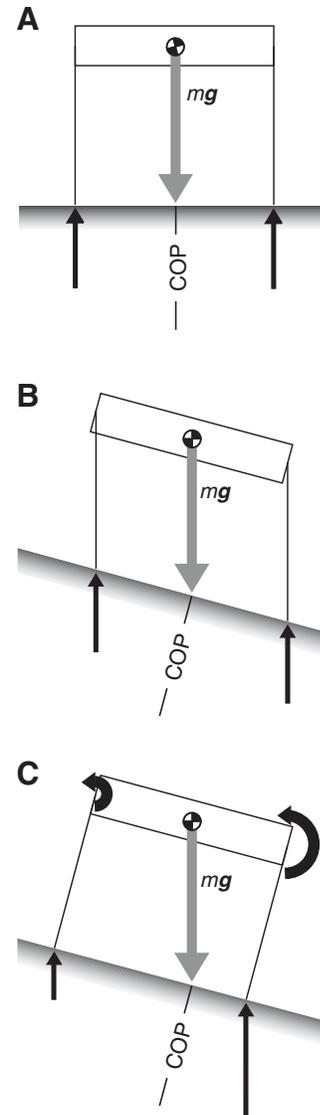

Fig. 1. A basic model with the center of mass (COM) equidistant between the shoulder and hip, showing fore–hind force distribution and center of pressure (COP) position during steady-speed trotting. On the level (A), normal force is distributed equally between the limbs. During grade running the limbs may be used collectively as simple telescoping struts (B) or as levers (C) to maintain steady-speed trotting uphill or downhill. In B, mean limb angles are adjusted to accommodate the grade and normal force remains equally distributed between the limbs. In C, moments are required about the proximal joints and normal force is redistributed to the downslope limb. The model assumes that the forelimbs and hindlimbs are retracted or protracted to the same degree as shown in B. In this case, the distance between forefoot and hindfoot contacts (*p*) would be consistent.

Shear force is required to maintain forward speed against the acceleration of gravity and is proportional to the sine of substrate angle in any steady-speed stride, whether downhill or uphill. During grade running, shear force may be provided by the angle of the limbs with respect to the substrate (Fig. 1B), such that the limbs only need to exert axial force (i.e. in line with the hip or shoulder). Hence, the limbs act purely as struts (Gray, 1968) and their normal force distribution and COP are unchanged from the level. Alternatively, shear force may be provided by hip and/or shoulder torques that tend to protract or retract the limbs (Fig. 1C). This is

referred to as action of the limbs as levers (Gray, 1944; Gray, 1968) and results in an altered distribution of normal force between the limbs [i.e. a redistribution to the down-slope limb(s)]. A further consequence of lever function is that shear impulse is distributed to the forelimbs and hindlimbs according to hip and shoulder torques. Relative hip and shoulder torques drawn in Fig. 1C are not an *a priori* prediction of this model; that is, any torque distribution providing the requisite net torque is possible, as long as it does not exceed the allowable shear force between the foot and ground.

Previous work shows that telescoping strut *versus* lever mechanics largely explain the different strategies used by dogs and turkeys during net accelerations on the level. Dogs tend to use their limbs as levers and redistribute normal force between the forelimbs and hindlimbs during moderate accelerations (Lee et al., 1999) whereas turkeys alter their limb angles as telescoping struts during extreme accelerations (Roberts and Scales, 2002). Unlike bipeds, which are generally constrained to use single limb support during running, quadrupeds are free to use lever mechanics without exerting a net pitching moment about the COM – provided that the CoP is kept between the supporting forefeet and hindfeet. These mechanisms are not mutually exclusive, so telescoping strut and lever mechanisms can be combined in the function of individual limbs. Furthermore, multi-legged runners can allocate telescoping strut and lever functions differentially to individual limbs during a stride. This, combined with the mechanism of resisting pitch moments, yields a greater scope of functional differentiation in the forelimbs and hindlimbs of quadrupeds compared with the limbs of bipedal striders or hoppers.

MATERIALS AND METHODS
Subjects and data collection

Three adult dogs (a pointer, a Weimaraner and a Labrador retriever) were used in this experiment. Subjects ranged in body mass from 27 to 34 kg and from 3 to 10 years of age. The dogs were borrowed from private owners for a period of 8 h or less and were never kept overnight. During data collection sessions, water was provided *ad libitum* and periodic rest breaks were given. The dogs trotted as they were led on a leash up and down a 15 deg grade, hard-packed soil runway in which two force platforms were positioned in series. Both downhill and uphill trotting were recorded. Force data were collected for 2 s as the dogs crossed the platforms. A video camera with VCR (PEAK[TM] Performance Technologies Inc.) acquired 120 images s[−1] in lateral view. Only data from uninterrupted trotting were saved. Data were collected while the dogs carried no load (unloaded, U) and under three loading conditions, in which tandem saddle bag packs were worn. Two small bags of lead shot totaling 10% body mass were inserted bilaterally in the anterior (fore-loaded, F), middle (mid-loaded, M) or posterior compartments (hind-loaded, H).

Force data were collected at 360 Hz from two strain gauge type force platforms (made by N. T. Heglund) positioned in series, using LabView[TM] software and a National Instruments[TM] data acquisition system (DAQCard AI-16-E4, SCXI 1000 chassis, SCXI 1121 strain/bridge modules and SCXI 1321 terminal blocks). Force and video acquisition were synchronized by connection of a manual switch to a PEAK[TM] Event Synchronization Unit, which simultaneously marked a video frame and triggered force acquisition *via* a breakout connector to the data acquisition card. Each force platform was 0.6 m long by 0.4 m wide. Using platforms of this length increased the likelihood that diagonal forefeet and hindfeet would strike separate force platforms simultaneously. Trials in which foot placements did not meet this criterion were discarded.

Furthermore, footfalls that struck the platform edges as evidenced by negative vertical force (i.e. a moment tending to lift the opposite end) were discarded. The force platforms measured normal ground reaction force (GRF) and shear GRF along the line of travel with separate double-cantilever transducers at each corner post. Normal GRF acting upward and shear GRF acting in the direction of travel were considered positive.

Parameters

Normal impulse j_n and shear impulse j_s were determined by numerical integration of GRF from a given limb over its contact time (t_c) or from a pair of diagonal limbs over their total contact time ($t_{c,total}$). Mean normal force on the COM during paired diagonal supports was determined from the total normal impulse ($j_{n,total}$) exerted by the limbs and was normalized to body mass:

$$\overline{F}_n = (j_{n,total} / t_{c,total})/m\boldsymbol{g}, \qquad (1)$$

where m is body mass (or 110% of body mass in loaded conditions) and $\boldsymbol{g}$ is gravitational acceleration.

Grade locomotion may be regarded as a repeatable means of eliciting net braking or propulsion but it suffers from the same non-steady variability as studies on level ground. Detecting net braking and propulsion in level strides or steps is as easy as measuring the mean force or impulse in the direction of travel – departures from zero indicate net accelerations – but grade locomotion requires consideration of the shear force component opposing gravity. Here, a simple dimensionless parameter is employed. When analyzing a stride, or half stride of a symmetrical gait, steady-speed locomotion yields a mean force vector opposing gravity (i.e. vertical) with a magnitude of one body weight. Hence, a steady-speed stride or step is identified by a mean force (or impulse) vector rotated from normal by the same angle as the grade; in other words, vertical (Fig. 2). Departures from steady-speed locomotion can then be quantified by the angular deviations of the total impulse vector from vertical, an approach that applies to level as well as grade locomotion (Lee et al., 2004). The net impulse angle for paired diagonal supports was determined with respect to normal from the ratio of total shear impulse ($j_{s,total}$) to total normal impulse ($j_{n,total}$):

$$\theta = \tan^{-1}(j_{s,total} / j_{n,total}). \qquad (2)$$

Likewise, forelimb impulse angle is determined as:

$$\theta_{fore} = \tan^{-1}(j_{s,fore} / j_{n,fore}), \qquad (3)$$

and hindlimb impulse angle is determined as:

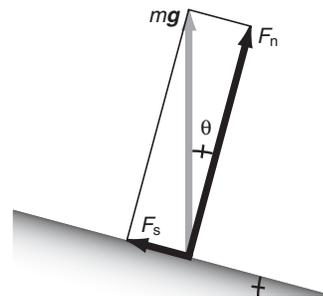$$\theta_{hind} = \tan^{-1}(j_{s,hind} / j_{n,hind}). \qquad (4)$$

Fig. 2. Mean resultant ground reaction force is vertical, opposing body weight during steady-speed downhill or uphill locomotion. This resultant force has a shear component (F_s) parallel to the grade and a normal component (F_n) perpendicular to the grade. A steady-speed trotting step is indicated by a net impulse angle (θ) equal to the angle of the grade.

The fore–hind distribution of normal impulse was expressed as the fraction of forelimb to total normal impulse. This quantity is referred to as the normal impulse ratio:

$$P_v = j_{n,fore} / j_{n,total}. \tag{5}$$

During level locomotion, R_n is equivalent to the vertical impulse ratio (Jayes and Alexander, 1978) in that it defines the relative position of the common COP between the feet. Nonetheless, level locomotion is a special case whereas R_n defines the COP on any non-level substrate plane.

However, shear impulse of the forelimbs and hindlimbs are equal and opposite during steady-speed level trotting, making the net shear impulse zero. The predominance of braking or propulsion during grade running, however, allows the fore–hind distribution of shear impulse to be determined as the ratio of forelimb to total shear impulse:

$$P_s = j_{s,fore} / j_{s,total}. \tag{6}$$

A Fourier method (Hamming, 1973) adapted for the analysis of GRF by Alexander and Jayes (Alexander and Jayes, 1980) was used to quantify the shape of the force-time curves. This method decomposes a complex waveform into five simple sinusoids of progressively higher frequency. These sinusoids are known as Fourier terms and each term has a coefficient, the magnitude of which indicates its influence on the shape of the waveform. The five coefficients generated by this analysis are a_1, b_2, a_3, b_4 and a_5, where a indicates a cosine term and b indicates a sine term. Upon Fourier analysis to determine the steady-speed values of these coefficients, representative force curves were reconstructed for forelimbs and hindlimbs during downhill and uphill trotting under each loading condition. The three lowest frequency Fourier terms were included in these Fourier reconstructions:

$$F(t) = a_1\cos(\pi t / t_c) + b_2\sin(2\pi t / t_c) + a_3\cos(3\pi t / t_c), \tag{7}$$

where t is time.

The COP on each force platform was determined by comparing the normal force from independent transducer elements at the fore and aft of the force platform. The two platforms were calibrated on a continuous scale to facilitate the computation of distance between footfalls on separate platforms (Bertram et al., 1997). The COP for each foot was determined by force-averaging over the duration of foot contact. In other words, instantaneous COPs were weighted according to the instantaneous normal force values, summed and then divided by the summation of normal force over t_c. This avoided the confounding effect of an extreme COP measurement during toe-off, for example, when the normal force is quite small. During paired diagonal contacts, the forefeet and hindfeet struck separate platforms allowing calculation of the distance between their mean COPs along the line of travel (p).

Mean velocity in the direction of travel $\bar{v}_s$ was determined directly from the force record by a method similar to that of Jayes and Alexander (Jayes and Alexander, 1978), except that time and distance parameters were computed from normal force peaks rather than initial foot contacts. The times (step period, t_{step}) and distances (step length, d) between subsequent forelimb supports and subsequent hindlimb supports were determined from the times of normal force peaks and the corresponding COP positions of each foot. Mean velocity $\bar{v}_s$ is the ratio of d to t_{step}. Because the paired diagonal supports of interest were preceded by a single forelimb support and followed by a single hindlimb support, forelimb and hindlimb values of $\bar{v}_s$, d and t_{step} were averaged to provide the best estimates of these parameters. The

aforementioned t_{step} is one half of the stride period ($2t_{step}$) during trotting. For consistency with previous work, $2t_{step}$ was used to normalize individual foot and paired diagonal foot contact times. The ratio of foot contact time to stride period is termed the duty factor DF and was computed as:

$$DF_{total} = t_{c,total} / 2t_{step}, \tag{8}$$

$$DF_{fore} = t_{c,fore} / 2t_{step}, \tag{9}$$

$$DF_{hind} = t_{c,hind} / 2t_{step}. \tag{10}$$

In addition, the ratio of forefoot to hindfoot contact time ($t_{c,fore}/t_{c,hind}$) was computed.

The timing of initial hindfoot contact with respect to initial forefoot contact was also expressed as a fraction of $2t_{step}$. This quantity, referred to as the hindfoot phase (α_{hind}), was computed as:

$$\alpha_{hind} = (t_{i,hind} - t_{i,fore}) / 2t_{step}, \tag{11}$$

where $t_{i,fore}$ and $t_{i,hind}$ are initial contact times for the forelimbs and hindlimbs, respectively. A negative value of α_{hind} indicates that hindlimb contact occurred before forelimb contact.

Statistics

A general linear model (GLM) with three categorical effects [slope (downhill or uphill), loading condition (U, M, F or H) and subject (1, 2 or 3)] and two continuous effects (impulse angle θ and mean velocity $\bar{v}_s$) was used to evaluate locomotor parameters in JMP 8.0™ software. Considering the effect of subject in the GLM permitted multiple runs to be considered from each subject, while assessing the significance of inter-subject differences. For certain parameters, one or more non-significant ($P>0.05$) effect was dropped from the model, as noted in the Results. GLM predictions with 95% confidence intervals were determined at $\theta\approx0$ (i.e. steady speed) and $\bar{v}_s=2.38\,m\,s^{-1}$, except where one of these effects was non-significant. All of the parameters presented in the Results were assessed by the GLM, except Fourier coefficients and DF (supplementary material Tables S1 and S2), which were predicted by multiple regression at steady-speed velocities of $2.59\,m\,s^{-1}$ (downhill) and $2.18\,m\,s^{-1}$ (uphill).

RESULTS
Fourier reconstructions of normal and shear force-time curves

Steady-speed Fourier coefficients of normal and shear force–time curves were predicted at $2.59\,m\,s^{-1}$ (downhill) and $2.18\,m\,s^{-1}$ (uphill) (supplementary material Table S1). These coefficients were used to reconstruct steady-speed normal and shear force–time curves for downhill and uphill trotting under each loading condition (Fig. 3). As expected, normal GRF was always positive (i.e. pushing against the foot) during downhill and uphill trotting. With the exception of very slight hindlimb propulsion late in the step, shear GRF was entirely braking during downhill trotting and entirely propulsive during uphill trotting. Hindlimb phase (Fig. 4B), duty factors (supplementary material Table S2) and step periods (Table 2) were also used in these force–time reconstructions.

Step characteristics

Before proceeding with a description of step parameters, it is important to note that $\bar{v}_s$ in the direction of travel was significantly greater in downhill than uphill trotting (Table 1). Hence, an intermediate velocity of $2.38\,m\,s^{-1}$ was chosen to make both
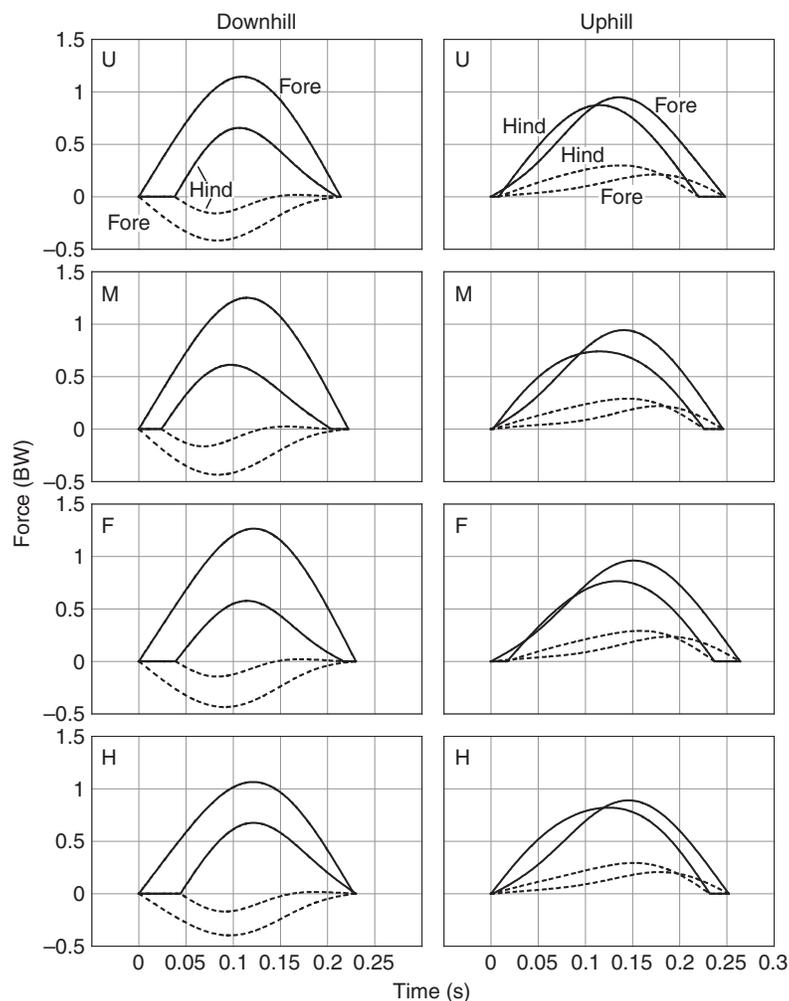
Fig. 3. Ground reaction force curves reconstructed from steady-speed Fourier coefficients (see Materials and methods and supplementary material Table S1) for each loading condition during downhill (2.59 m s^{-1}) and uphill (2.18 m s^{-1}) trotting. Solid lines indicate normal force and broken lines indicate shear force. F, fore-load; H, hind-load; M=mid-load; U, unloaded. BW, body weights.

downhill and uphill predictions in the general linear model (GLM). Step length and step period were thus predicted at the same velocity for downhill and uphill trotting (Table 2), revealing significant differences (d, P=0.0021; t_{step}, P<0.0001) between downhill and uphill locomotion. Because velocity is the quotient of d and t_{step}, the same velocity (i.e. 2.38 m s^{-1}) is achieved by long, slow steps during uphill trotting as by shorter, quicker steps during downhill trotting. Effects of load and θ were non-significant and were, therefore, dropped from the GLM for these two parameters.

Values of p can be expressed in dimensionless terms as a fraction of d. The ratio p/d, predicted by the GLM, was significantly greater during uphill trotting (P<0.0001; Fig. 4A). Given that d was also greater during uphill trotting (Table 2), this indicates a greater absolute and relative fore–aft distance between paired diagonal footfalls. Although individual limb angles were not measured here, this difference is likely due to a more retracted hindlimb angle during uphill trotting. The effect of θ was non-significant and was dropped from the GLM for this parameter.

Hindlimb phase (α_{hind}) quantifies the time of initial hindfoot contact with respect to initial forefoot contact. Downhill α_{hind} was significantly greater (i.e. later contact of the hindfoot; P<0.0001) than uphill α_{hind}. Fore-loading elevated α_{hind} significantly above unloaded values (Fig. 4B).

The ratio of forelimb to hindlimb contact time ($t_{c,fore}/t_{c,hind}$) was significantly greater (P<0.0001) during downhill than uphill trotting (Fig. 5A). The effect of subject was non-significant and was dropped

from the GLM for this parameter. During grade trotting, fore-loading significantly increased $t_{c,fore}/t_{c,hind}$ whereas mid- and hind-loading significantly decreased $t_{c,fore}/t_{c,hind}$ with respect to the unloaded condition (Fig. 5A).

Normal force

Mean normal force (F_n) for the contact time of paired diagonal footfalls ($t_{c,total}$) ranged from 0.9 to 1.05 body weights with no significant difference between downhill and uphill trotting (Fig. 4C).

Normal impulse distribution

Steady-speed normal impulse ratio ($R_{n,0}$) indicates the fraction of normal impulse on the forelimb during steady-speed trotting (i.e. θ=0). The effect of velocity was non-significant and was dropped from the GLM for this parameter. $R_{n,0}$ was significantly reduced during uphill compared with downhill trotting (P<0.0001; Fig. 5B). Without lever function (Fig. 1A,B), $R_{n,0}$ would remain similar to level trotting values. On average, downhill values were 0.06 greater whereas uphill values were 0.11 less than level. Hence, the fraction of normal impulse on the forelimb was increased with respect to level during downhill trotting, but not to the extent that it was decreased during uphill trotting. As discussed later, this supports prediction 1, that the limbs will tend to act more as levers during uphill than during downhill trotting.

In all three loading conditions, $R_{n,0}$ was significantly different from unloaded (Fig. 5B). In agreement with prediction 3, loading
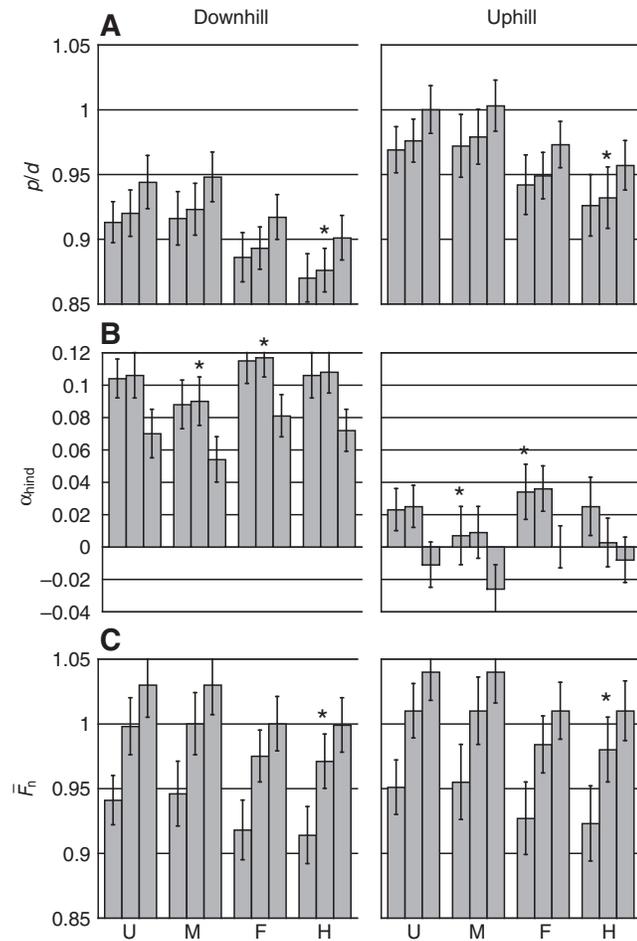
Fig. 4. Steady-speed values of (A) distance between forefeet and hindfeet as a fraction of step distance (p/d), (B) hindlimb phase shift (α_{hind}) and (C) mean normal force F_n for each loading condition during downhill and uphill trotting. Columns represent each of the three subjects. Error bars indicate 95% confidence intervals and * indicates steady-speed values significantly different ($P<0.05$) from the unloaded condition (U). F, fore-load; H, hind-load; M, mid-load. Subjects are 1, 2 and 3 from left to right.

the upslope limb resulted in normal impulse distributions more similar to level. During downhill trotting, hind-loading decreased $R_{n,0}$ to within 0.025 of the unloaded level value (grey horizontal line in Fig. 5B) and, during uphill trotting, fore-loading increased $R_{n,0}$ to within 0.07 of the unloaded level value.

Shear impulse distribution
Steady-speed shear impulse ratio ($R_{s,0}$) indicates the fraction of shear impulse at steady-speed. Presented in bar plots and also graphically by impulse vectors in Fig. 5C, $R_{s,0}$ was significantly greater during downhill than during uphill trotting ($P<0.0001$). Patterns of $R_{s,0}$ across loading conditions were similar to those of $R_{s,0}$, with the exception that mid-loaded condition was not significantly different from the unloaded condition. As discussed later, loading the upslope limb resulted in a more equal fore–hind distribution of shear impulse (prediction 4). Specifically, hind-loading during downhill trotting reduced $R_{s,0}$ whereas fore-loading during uphill trotting increased $R_{s,0}$ (Fig. 5C).

Table 1. Mean forward velocity ($\bar{v}_s$) and impulse angle (θ) during downhill and uphill trotting in dogs

Loading condition	Downhill		Uphill	
	$\bar{v}_s$ (m s^{-1})	θ (deg)	$\bar{v}_s$ (m s^{-1})	θ (deg)
U	2.85±0.064[†]	0.54±0.28[†]	2.41±0.083[†]	−0.44±0.37[†]
M	2.57±0.097[*,†]	0.23±0.43[†]	2.14±0.105[*,†]	−0.75±0.37[†]
F	2.49±0.082[*,†]	0.20±0.36[†]	2.05±0.086[*,†]	−0.78±0.38[†]
H	2.49±0.082[*,†]	−0.04±0.36[†]	2.06±0.097[*,†]	−1.02±0.43[†]

General linearized model (GLM) predictions (±95% CI). Significant differences ($P<0.05$) from the unloaded condition are indicated by * and between downhill and uphill by [†].
F, fore-loaded; H, hind-loaded; M, mid-loaded; U, unloaded.

Individual limb impulse angles
Impulse angles of the forelimb (θ_{fore}) and hindlimb (θ_{hind}) are dimensionless expressions of a limb's braking or propulsive function. Extreme and highly significant ($P<0.0001$) differences between downhill and uphill trotting were evident in both θ_{fore} (Fig. 6A) and θ_{hind} (Fig. 6B). In addition to bar plots, angles are illustrated for subject 1 and the level, unloaded angle is drawn from Lee et al. (Lee et al., 2004) (Fig. 6). The braking angle of forelimbs is greatly amplified during downhill (−17.8 deg) compared with level trotting (−3.3 deg). Conversely, the propulsive angle of hindlimbs is greatly amplified during uphill (19.4 deg) compared with level trotting (5.8 deg). Both of these results are consistent with prediction 2 – that the fore–hind functional differentiation of braking–propulsive function will be maintained or amplified during grade running – but this is only relevant in the downslope limbs because the usual braking or propulsive functions of the upslope limbs are reversed during grade running.

Compared with the unloaded condition, fore-loading significantly reduced forelimb braking angle during downhill trotting and significantly increased forelimb propulsion angle during uphill trotting (Fig. 6A). A corresponding effect was seen in the hindlimb: hind-loading significantly increased hindlimb braking angle during downhill trotting and significantly decreased hindlimb propulsion angle during uphill trotting (Fig. 6B). No other loading effects on θ_{fore} or θ_{hind} were seen in the forelimb or hindlimb.

DISCUSSION
Step parameters
A prominent characteristic of uphill trotting is a significant increase in t_{step} with respect to downhill trotting (Table 2). Step length (d) also increased significantly, indicating longer, slower steps during uphill trotting at a given velocity. Because $\bar{F}_n$ was statistically similar

Table 2. Step period (t_{step}) and step length (d) of the three subjects during downhill and uphill trotting

Subject	Downhill		Uphill	
	t_{step} (s)	d (m)	t_{step} (s)	d (m)
1	0.232±0.0035[†]	0.541±0.0092[†]	0.240±0.0045[†]	0.558±0.0117[†]
2	0.251±0.0033[†]	0.589±0.0086[†]	0.260±0.0036[†]	0.606±0.0095[†]
3	0.242±0.0035[†]	0.571±0.0092[†]	0.250±0.0037[†]	0.589±0.0097[†]

Three adult dogs were used – a pointer (subject 1), a Weimaraner (subject 2) and a Labrador retriever (Subject 3).
GLM predictions (±95% CI). Significant differences ($P<0.05$) between downhill and uphill are indicated by [†]. Loading conditions had no significant effect and were dropped from the GLM.
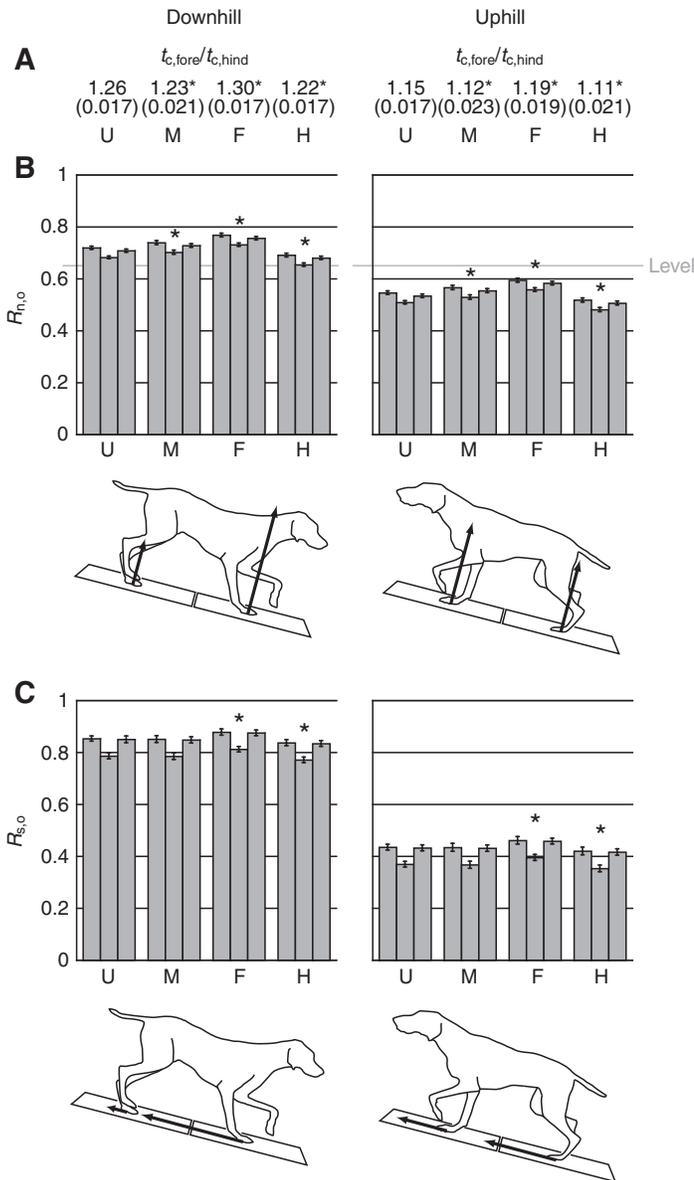
Fig. 5. Time and impulse parameters across loading conditions during downhill and uphill trotting. Columns represent each of the three subjects. (A) The ratio of forefoot to hindfoot contact times ($t_{c,fore}/t_{c,hind}$). (B) Normal impulse ratios with a horizontal bar indicating unloaded level normal impulse ratios from Lee et al. (Lee et al., 2004). (C) Shear impulse ratios. Error bars indicate 95% confidence intervals and * indicates steady-speed values significantly different ($P<0.05$) from the unloaded condition (U). F, fore-load; H, hind-load; M, mid-load. Subjects are 1, 2 and 3 from left to right.
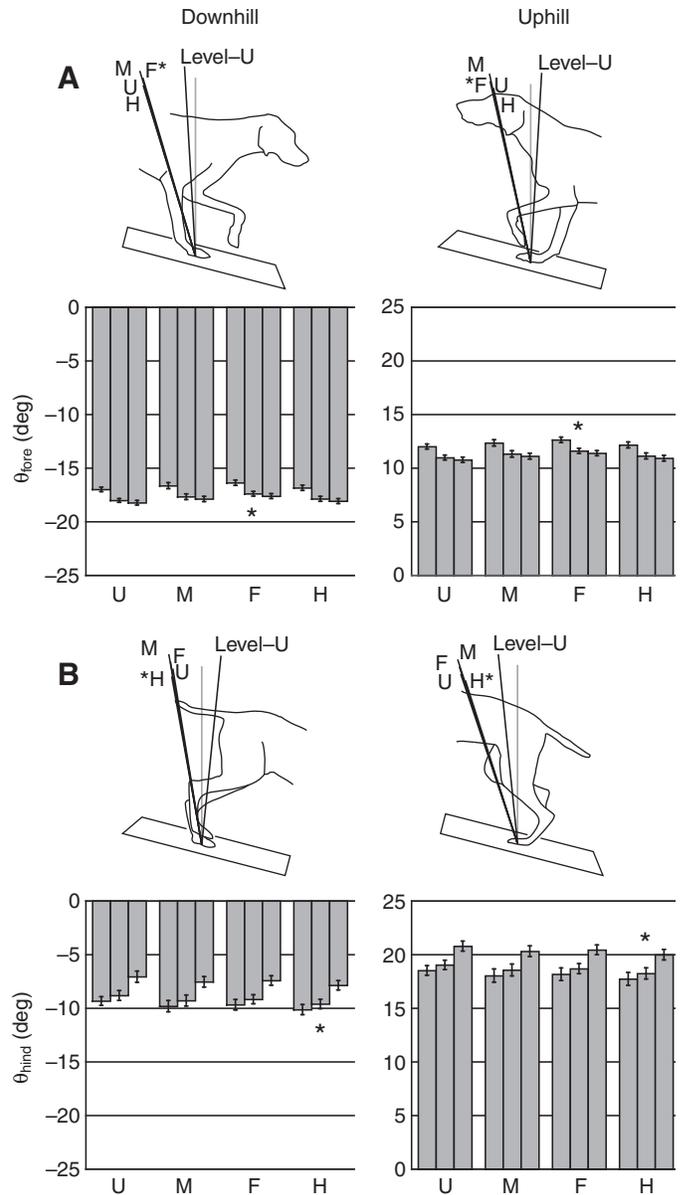

Fig. 6. Forelimb (A) and hindlimb (B) impulse angles across loading conditions during downhill and uphill trotting. Columns represent each of the three subjects. Level unloaded (Level–U) values from Lee et al. (Lee et al., 2004) are shown for comparison. Vertical (grey) lines are drawn for reference and * indicates steady-speed values significantly different ($P<0.05$) from the unloaded condition (U). F, fore-load; H, hind-load; M, mid-load. Subjects are 1, 2 and 3 from left to right.

between downhill and uphill trotting, the present data indicate that the diagonal $t_{c,total}$ remained a constant proportion of t_{step} at the steady-speed velocity of $2.38\,\mathrm{m\,s^{-1}}$. Increasing t_{step} with respect to level is a common response to uphill trotting in quadrupeds, although stride period ($2t_{step}$) is normally reported. Horses trotting on treadmills inclined by 3.4 or 5.7 deg showed increases in t_{step} with respect to level (Hoyt et al., 2000; van Oldruitenborgh-Ooste et al., 1997). Stride period has also been found to increase during uphill locomotion in other quadrupeds at various gaits (Gillis and Biewener, 2002; Pierotti et al., 1989; Roy et al., 1991). If duty factors are consistent, greater step periods provide a clear advantage of

increased contact time in which to exert force. This is not always the case, however, as no consistent change in stride period or hindlimb contact time was observed in squirrel monkeys walking or running up a treadmill inclined by 8, 16 or 28 deg (Vilensky et al., 1994). Also, small lizards walking and running up a treadmill inclined by 30 deg showed decreased stride periods and contact times (Jayne and Irschick, 1999).

In stark contrast to most quadrupeds, humans decrease their stride periods during uphill running. For example, stride period decreased when running up treadmills inclined by 16.7 deg (Swanson and Caldwell, 2000) and 2.9–8.5 deg (Minetti et al., 1994). These results

are surprising, given that shorter stride periods require higher rates of force generation, provided that the duty factor is unchanged. This, in turn, might require greater muscle recruitment because of the force–velocity relationship and/or the recruitment of faster muscle fibers, both of which increase metabolic cost (Close, 1972). In guinea fowl on a treadmill inclined by 16 deg, stride period decreased, as in humans, but contact time actually increased due to greater duty factors during uphill than during level running (M. A. Daley, personal communication) – a result consistent with an increased time for muscle force generation. The question of why humans, and perhaps bipeds in general, employ shorter stride periods on an incline remains open.

A notable feature of downhill trotting is delayed hindlimb contact, as indicated by a greater hindlimb phase (α_{hind}) than during level trotting (Fig. 4C). The common COP depends upon the position of the feet with respect to the COM and the distribution of normal force between the forelimb and the hindlimb (Fig. 1). During downhill trotting, the common COP is the same as the forelimb COP until the hindlimb is set down. By delaying hindlimb contact, the COP remains farther forward and the resultant force (which is applied at the COP) can have a greater braking component without exerting a nose-down pitching moment about the COM. Hence, later hindlimb contact permits greater braking force during the first 20% of forelimb contact when normal force is relatively low (Fig. 3). Applying the same initial braking force with the hindlimb and a sufficient delay of forelimb contact could send the dog somersaulting nose down. Nose-down pitching is exacerbated during fore-loading by moving the COM more cranially but a significant increase in α_{hind} counteracts this effect. As expected, the risk of nose-up pitching during uphill trotting is substantially less, given the cranial COM position of most quadrupeds.

Grade trotting is also characterized by an increase in the $t_{c,fore}/t_{c,hind}$ ratio during downhill trotting and a decrease in $t_{c,fore}/t_{c,hind}$ during uphill trotting compared with level trotting (Fig. 5A) (Lee et al., 2004). A decrease in hindlimb duty factor with respect to level has also been shown in cats descending 26.6, 36.9 and 45.0 deg grades; however, no significant effect was found at 14 deg (Smith et al., 1998). In another study, decreases in stride period and hindlimb contact time, but not forelimb contact time, suggest that $t_{c,fore}/t_{c,hind}$ might increase in squirrel monkeys descending a range of grades from 4.6 to 15.6 deg (Vilensky et al., 1994). The present data suggest that an increase in $t_{c,fore}/t_{c,hind}$ during downhill trotting and a decrease during uphill trotting are related to redistribution of normal and shear impulse to the downslope limb (Fig. 5).

Normal and shear impulse distributions

Lever and telescoping strut actions of the limbs were detected by measuring the steady-speed normal impulse ratio $R_{n,0}$. If the legs acted purely as telescoping struts and the degree of protraction or retraction of the forelimbs and hindlimbs were similar, $R_{n,0}$ would be unchanged from that of level trotting (Fig. 1B) and, as lever action became more prominent, $R_{n,0}$ would increasingly diverge from that of level trotting (Fig. 1C). Using the previously reported relationship between R_n and mean fore–aft acceleration for dogs ($r^2=-0.71$) (Lee et al., 1999), $R_{n,0}$ is predicted to increase by 0.18 during 15 deg downhill trotting and decrease by 0.18 during 15 deg uphill trotting if the limbs are assumed to function strictly as levers to achieve braking or propulsion. The present data show that, with respect to level trotting, $R_{n,0}$ increases by 0.06 during downhill trotting and $R_{n,0}$ decreases by 0.11 during uphill trotting (Fig. 5B). Hence, the legs did not act purely as telescoping struts to maintain steady-speed downhill or uphill trotting. Nonetheless, the action of the legs as

levers (indicated by the divergence of $R_{n,0}$ from level) contributed only approximately half as much to the braking force during downhill trotting as to propulsive force during uphill trotting. In other words, more shear force was supplied by thrust in line with the legs (i.e. telescoping strut action) during downhill trotting whereas relatively more shear force was supplied by proximal joint torques (i.e. lever action) during uphill trotting. This result is in good agreement with prediction 1, which indicates greater lever function during uphill trotting. As explained in the Introduction, this prediction is based upon the fact that the majority of limb muscle mass in the proximal retractors, combined with the dogs' inability to exploit high-force lengthening (i.e. energy absorbing) contractions during uphill running.

Bolstering this explanation are a number of recent *in vivo* extrinsic muscle studies comparing level, downhill and uphill locomotion. In a report of hindlimb extrinsic muscle function of dogs (Schilling et al., 2009), hindlimb retractor recruitment increased dramatically (2 to 22 times level values) during uphill trotting at 10 and 14 deg. This significant increase in the mean rectified electromyogram is due to both increased magnitude and duration of muscle recruitment. In a study by Gillis and Biewener (Gillis and Biewener, 2002), greater stance-phase recruitment and shortening of the biceps femoris muscle were reported during uphill walking and running of rats on a treadmill inclined by 15 deg. These results provide evidence of greater hindlimb lever action during uphill running because the hip is extended through a greater angle by the shortening biceps, a major hindlimb retractor. *In vivo* data from forelimbs of dogs provide evidence of a less-pronounced lever function: retractor recruitment increases moderately during uphill (10 and 14 deg) trotting and protractor recruitment increases moderately during downhill (10 and 14 deg) trotting (Carrier et al., 2006). Although the present analysis shows greater net lever function uphill than downhill, an analysis of hip and shoulder joint dynamics would be required to ascribe more or less of this function to the forelimb or the hindlimb. Furthermore, kinematic data showing individual limb angles are needed to determine more precisely the relative contributions of telescoping strut and lever action to downhill braking and uphill propulsion. The distance between diagonal footfalls represented by p/d (Fig. 4A) shows an ~5% difference between downhill and uphill running, which could be explained by divergence of individual limb angles.

Effects of loading conditions on normal and shear impulse distributions

As expected from loading responses during level trotting (Lee et al., 2004), hind-loading during downhill trotting and fore-loading during uphill trotting yielded values of $R_{n,0}$ closer to those of steady-speed level trotting (prediction 3). Loading of the upslope limbs also yielded values of $R_{s,0}$ closer to 0.5, indicating a more symmetrical fore–hind distribution of shear impulse (prediction 4). It is reasonable, therefore, to suggest that quadrupeds with COM positions closer to the forelimbs would distribute propulsive force more equally between the forelimb and the hindlimb during uphill trotting. Conversely, quadrupeds with COM positions closer to the hindlimbs would distribute braking force more equally between the forelimb and the hindlimb during downhill trotting. This raises a basic question of quadrupedal design: what COM position allows adequate performance for both downhill and uphill locomotion? Here again, the explanation may be that muscle force during active lengthening (useful in braking but not propulsion) is much greater than that during active shortening (Close, 1972; Katz, 1939). Because less muscle is needed to supply a braking force of a given

magnitude, it is possible for the forelimb to provide a larger fraction of the required braking impulse during downhill trotting than the fraction of propulsive impulse the hindlimb can provide during uphill trotting (~0.84 *versus* ~0.60; Fig. 5C). Given that the COM is typically closer to the forelimb (Rollinson and Martin, 1981), terrestrial quadrupeds likely benefit from a more equal distribution of propulsive impulse between forelimbs and hindlimbs during uphill running, whereas the forelimbs easily provide most of the braking impulse during downhill running.

Individual limb impulse angles

The tendency of forelimbs to supply more braking, and hindlimbs more propulsion, is typical of running quadrupeds (Cavagna, 1977; Heglund et al., 1982; Jayes and Alexander, 1978; Lee et al., 1999; Lee et al., 2004) and hexapods (Full et al., 1991). For comparisons across size, species and even between different locomotor behaviors within subjects, braking and propulsive functions are best described as dimensionless impulse angles. Here, the forelimb impulse angle (θ_{fore}) was predicted to be more strongly braking during downhill trotting, and the hindlimb impulse angle (θ_{hind}) more strongly propulsive during uphill trotting (prediction 2). Compared with level impulse angles (Lee et al., 2004), θ_{fore} increased ~14 deg in magnitude to -17.8 deg (Fig. 6A) and θ_{hind} increased ~14 deg in magnitude to 19.4 deg (Fig. 6B). Hence, the affinity of the forelimb to braking and the hindlimb to propulsion are not only maintained but also amplified during downhill and uphill trotting. Although the ultimate cause of these fore–hind functional differences may be the physical relationship between shear and normal force (e.g. front brakes are more effective than rear brakes and rear wheel propulsion is more effective than front wheel propulsion) (Gray, 1944; Gray, 1968; Lee et al., 1999), the proximate cause is likely the resulting specialization of forelimb and, to a greater extent, hindlimb structure. Evidence of such anatomical specialization is provided by the substantial fraction of muscle mass represented by hindlimb (propulsive) retractors (Pasi and Carrier, 2003; Payne et al., 2005a; Williams et al., 2007a) and, to a lesser extent, forelimb (braking) protractors (Payne et al., 2005b; Williams et al., 2007b). In addition to anatomical observations, the propulsive bias of hindlimbs and braking bias of forelimbs is reproduced by simple trotting simulations with knee-forward/elbow-back geometry (Lee and Meek, 2005). Together, pitch mechanics, limb geometry and limb anatomy explain the differential function of the forelimbs and hindlimbs of quadrupeds.

Comparisons with acceleration on the level

Principles of telescoping strut and lever function are applicable to both grade and level running, with the caveat that net lever function (Fig. 1C) can produce steady-speed grade running but would indicate acceleration on the level. Several recent studies have investigated net propulsive or braking accelerations of quadrupeds on the level. Walter and Carrier reported forelimb and hindlimb kinetics and kinematics during extreme propulsive accelerations of dogs, finding the fraction of forelimb shear impulse to be 0.43 (Walter and Carrier, 2009) – nearly equal to those reported here for steady-speed uphill trotting (Fig. 5C). The fraction of forelimb normal impulse in the present study, however, is considerably lower (0.43) compared with steady-speed uphill values between 0.5 and 0.6 (Fig. 5B). This discrepancy is likely associated with nose-up pitching during the accelerating strides (Walter and Carrier, 2009) due to greater propulsive forces and the use of a half-bound gait, which decouples forelimb and hindlimb footfalls. The authors conclude that lever function due to hip and shoulder retraction plays a primary role in

propulsive acceleration and that telescoping strut function, indicated by a more retracted angle of forelimbs and hindlimbs, plays a secondary roll (Walter and Carrier, 2009). Another recent study of acceleration in dogs focused on hindlimb mechanics (Williams et al., 2009a). These authors show that hindlimb propulsion is primarily due to hip extension (suggesting lever function) and ankle extension (suggesting telescoping strut function). Assuming only lever function, the same authors applied Gray's (Gray, 1944; Gray, 1968) model to help explain maximum propulsion and braking in greyhounds and polo ponies (Williams et al., 2009b). The data from the present study indicate a combination of lever (Fig. 1B) and telescoping strut (Fig. 1C) function to achieve steady-speed downhill and uphill trotting, with significantly greater lever function uphill. This also seems to be the consensus for quadrupedal propulsion on the level, although level braking mechanics are less studied.

CONCLUSIONS

As evidenced by steady-speed normal impulse ratios, the limbs act collectively more like levers during uphill than downhill trotting (prediction 1). Hence, uphill trotting requires greater proximal limb torques, recruiting the large retractor muscles of the hip and shoulder. These results are consistent with a well-known contractile property of skeletal muscle – a greater cross-section needs to be recruited to exert a given force during active shortening (uphill propulsion) than during active lengthening (downhill braking). As shown by individual limb impulse angles, differential fore–hind function during level trotting is amplified in forelimb braking during downhill trotting and in hindlimb propulsion during uphill trotting (prediction 2). During both dowhnhill and uphill trotting, the normal impulse distribution between the forelimbs and hindlimbs is closer to level values when the upslope limb is loaded (prediction 3). The forelimb exerts ~84% of the total braking impulse during downhill trotting whereas the hindlimb exerts only ~59% of the total propulsive impulse during uphill trotting. During both downhill and uphill trotting, loading of the upslope limb resulted in a more equal distribution of shear impulse between the forelimb and the hindlimb (prediction 4). This last result suggests a functional trade-off in quadruped design: a COM closer to the hindlimbs would distribute downhill braking force more equally whereas a COM closer to the forelimbs would distribute uphill propulsive force more equally. Considering the reduced force capacity of skeletal muscle during shortening *versus* lengthening contractions, the anterior COM position of most terrestrial quadrupeds provides a functional advantage during uphill running without substantial detriment to downhill running. The advantage of this mechanical design seems to extend level propulsion (Walter and Carrier, 2009; Williams et al., 2009b) and jumping (Alexander, 1974).

LIST OF SYMBOLS AND ABBREVIATIONS

COM	center of mass
COP	center of pressure
d	distance between forelimb and hindlimb COPs of adjacent steps (m)
DF	duty factor
$\bar{F}_n$	mean normal force (body weights, BW)
$\boldsymbol{g}$	gravitational acceleration
j_n	normal impulse (BW s^{-1})
j_s	shear impulse (BW s^{-1})
m	body mass
p	distance between diagonal foot COPs (m)
R_n	normal impulse ratio
R_s	shear impulse ratio
t_c	time of contact (s)

t_{step} time between forelimb and hindlimb normal force peaks of adjacent steps (s) (step period)

$\bar{v}_s$ mean velocity in the direction of travel (i.e. shear) (m s^{-1})

α_{hind} hindlimb phase-shift with respect to forelimb initial contact

θ impulse angle with respect to normal (deg)

REFERENCES

Alexander, R. M. (1974). The mechanics of jumping by a dog (*Canis familiaris*). *J. Zool.* **173**, 549-573.

Alexander, R. M. and Jayes, A. S. (1980). Fourier analysis of forces exerted in walking and running. *J. Biomech.* **13**, 383-390.

Autumn, K. and Peattie, A. M. (2002). Mechanisms of adhesion in geckos. *Integr. Comp. Biol.* **42**, 1081-1090.

Autumn, K., Hsieh, S. T., Dudek, D. M., Chen, J., Chitaphan, C. and Full, R. J. (1999). Function of feet in ascending and descending geckos. *Amer. Zool.* **38**, 84A.

Bertram, J. E. A., Lee, D. V., Todhunter, R. J., Foels, W. S., Williams, A. and Lust, G. (1997). Multiple force platform analysis of the canine trot: a new approach to assessing basic characteristics of locomotion. *Vet. Comp. Orthoped. Traumatol.* **10**, 160-169.

Carlson-Kuhta, P., Trank, T. V. and Smith, J. L. (1998). Forms of forward quadrupedal locomotion. II. A comparison of posture, hindlimb kinematics, and motor patterns for upslope and level walking. *J. Neurophysiol.* **79**, 1687-1701.

Carrier, D. R., Deban, S. M., Fischbein, T. (2006). Locomotor function of the pectoral girdle 'muscular sling' in trotting dogs. *J. Exp. Biol.* **209**, 2224-2237.

Cavagna, G. A. (1977). Storage and utilization of elastic energy in skeletal muscle. *Exerc. Sport Sci. Rev.* **5**, 89-129.

Close, R. I. (1972). Dynamic properties of mammalian skeletal muscles. *Physiol. Rev.* **52**, 129-197.

Dutto, D. J., Hoyt, D. F., Cogger, E. A. and Wickler, S. J. (2004). Ground reaction forces in horses trotting up an incline and on the level over a range of speeds. *J. Exp. Biol.* **207**, 3507-3514.

Full, R. J., Blickhan, R. and Ting, L. H. (1991). Leg design in hexapedal runners. *J. Exp. Biol.* **158**, 369-390.

Gillis, G. B. and Biewener, A. A. (2002). Effects of surface grade on proximal hindlimb muscle strain and activation during rat locomotion. *J. Appl. Physiol.* **93**, 1731-1743.

Gray, J. (1944). Studies in the mechanics of the tetrapod skeleton. *J. Exp. Biol.* **20**, 88-116.

Gray, J. (1968). *Animal Locomotion*. New York: Norton.

Hamming, R. W. (1973). *Numerical Methods for Scientists and Engineers*. New York: McGraw-Hill.

Heglund, N. C., Cavagna, G. A. and Taylor, C. R. (1982). Energetics and mechanics of terrestrial locomotion. III. Energy changes of the centre of mass as a function of speed and body size in birds and mammals. *J. Exp. Biol.* **97**, 41-56.

Hoyt, D. F., Wickler, S. J. and Cogger, E. A. (2000). Time of contact and step length: the effect of limb length, running speed, load carrying and incline. *J. Exp. Biol.* **203**, 221-227.

Hoyt, D. F., Molinari, M., Wickler, S. J. and Cogger, E. A. (2002). Effect of trotting speed, load and incline on hindlimb stance-phase kinematics. *Equine Vet. J. Suppl.* 330-336.

Jayes, A. S. and Alexander, R. M. (1978). Mechanics of locomotion of dogs (*Canis familiaris*) and sheep (*Ovis aries*). *J. Zool.* **185**, 289-308.

Jayne, B. C. and Irschick, D. J. (1999). Effects of incline and speed on the three-dimensional hindlimb kinematics of a generalized iguanian lizard (Dipsosaurus dorsalis). *J. Exp. Biol.* **202**, 143-159.

Katz, B. (1939). The relationship between force and speed in muscular contraction. *J. Physiol.* **96**, 45-64.

Kindschy, R., Sundstrom, C. and Yoakum, J. (1978). Range/wildlife interrelationships-pronghorn antelope. In *8th biennial pronghorn antelope workshop*, pp. 216-262. Jasper, AB. Edmonton, AB: Albertal Recreation, Parks, and Wildlife, Fish and Wildlife Division.

Lammers, A. R. (2007). Locomotor kinetics on sloped arboreal and terrestrial substrates in a small quadrupedal mammal. *Zoology* **110**, 93-103.

Lammers, A. R., Earls, K. D. and Biknevicius, A. R. (2006). Locomotor kinetics and kinematics on inclines and declines in the gray short-tailed opossum (*Monodelphis domstica*). *J. Exp. Biol.* **209**, 4154-4166.

Lee, D. V. and Meek, S. G. (2005). Directionally compliant legs influence the intrinsic pitch behavior of a trotting quadruped. *Proc. R. Soc. Lond. B* **272**, 567-572.

Lee, D. V., Bertram, J. E. A. and Todhunter, R. J. (1999). Acceleration and balance in trotting dogs. *J. Exp. Biol.* **202**, 3565-3573.

Lee, D. V., Stakebake, E. F., Walter, R. M. and Carrier, D. R. (2004). Effects of mass distribution on the mechanics of level trotting in dogs. *J. Exp. Biol.* **207**, 1715-1728.

Lee, D. V., McGuigan, M. P., Yoo, E. H. and Biewener, A. A. (2008). Compliance, actuation, and work characteristics of the goat foreleg and hindleg during level, uphill, and downhill running. *J. App. Phsyiol.* **104**, 130-141.

Lekagul, B. and McNeely, J. A. (1977). *Mammals of Thailand*. Bangkok: Sahakarnbhat.

Minetti, A. E., Ardigo, L. P. and Saibene, F. (1994). Mechanical determinants of the minimum energy cost of gradient running in humans. *J. Exp. Biol.* **195**, 211-225.

Nowak, R. M. and Walker, E. P. (1991). *Walker's Mammals of the World*. Baltimore, MD: Johns Hopkins University Press.

Nyakatura, J. A. and Heymann, E. W. (2010). Effects of support size and orientation on free-ranging tamarins of Amazonian Peru: implications for the functional significance of primate gait sequence patterns. *J. Hum. Evol.* **58**, 242-251.

Nyakatura, J. A., Fischer, M. S. and Schmidt, M. (2008). Gait parameter adjustments of cotton-top tamarins (*Saguinus oedipus*, Callitrichidae) to locomotion on inclined arboreal substrates. *Am. J. Phys. Anthropol.* **135**, 13-26.

Pasi, B. M. and Carrier, D. R. (2003). Functional trade-offs in the limb muscles of dogs selected for running vs. fighting. *J. Evol. Biol.* **16**, 324-332.

Payne, R. C., Hutchinson, J. R., Robilliard, J. J., Smith, N. C. and Wilson, A. M. (2005a). Functional specialisation of pelvic limb anatomy in horses (*Equus caballus*). *J. Anat.* **206**, 557-574.

Payne, R. C., Veenman, P. and Wilson, A. M. (2005b). The role of the extrinsic thoracic limb muscles in equine locomotion. *J. Anat.* **206**, 193-204.

Pierotti, D. J., Roy, R. R., Gregor, R. J. and Edgerton, V. R. (1989). Electromyographic activity of cat hindlimb flexors and extensors during locomotion at varying speeds and inclines. *Brain Res.* **481**, 57-66.

Roberts, T. J. and Scales, J. A. (2002). Mechanical power output during running accelerations in wild turkeys. *J. Exp. Biol.* **205**, 1485-1494.

Rollinson, J. and Martin, R. D. (1981). Comparative aspects of primate locomotion with special reference to arboreal cercopithecines. *Symp. Zool. Soc. Lond.* **48**, 377-427.

Roy, R. R., Hutchison, D. L., Pierotti, D. J., Hodgson, J. A. and Edgerton, V. R. (1991). EMG patterns of rat ankle extensors and flexors during treadmill locomotion and swimming. *J. Appl. Physiol.* **70**, 2522-2529.

Schilling, N., Fischbein, T., Yang, E. P. and Carrier, D. R. (2009). Function of the extrinsic hindlimb muscles in trotting dogs. *J. Exp. Biol.* **212**, 1036-1052.

Smith, J. L., Carlson-Kuhta, P. and Trank, T. V. (1998). Forms of forward quadrupedal locomotion. III. A comparison of posture, hindlimb kinematics, and motor patterns for downslope and level walking. *J. Neurophysiol.* **79**, 1702-1716.

Swanson, S. C. and Caldwell, G. E. (2000). An integrated biomechanical analysis of high speed incline and level treadmill running. *Med. Sci. Sports Exerc.* **32**, 1146-1155.

van Oldruitenborgh-Ooste, M. M. S., Barneveld, A. and Schamhardt, H. C. (1997). Effects of treadmill inclination on kinematics of the trot in Dutch warmblood horses. *Equine Vet. J. Suppl.* 71-75.

Vilensky, J. A., Moore, A. M. and Libii, J. N. (1994). Squirrel monkey locomotion on an inclined treadmill: Implications for the evolution of gaits. *J. Hum. Evol.* **26**, 375-386.

Walter, R. M. and Carrier, D. R. (2009). Rapid acceleration in dogs: ground forces and body posture dynamics. *J. Exp. Biol.* **212**, 1930-1939.

Williams, S. B., Payne, R. C. and Wilson, A. M. (2007a). Functional specialisation of the pelvic limb of the hare (*Lepus europeus*). *J. Anat.* **210**, 472-490.

Williams, S. B., Wilson, A. M. and Payne, R. C. (2007b). Functional specialisation of the thoracic limb of the hare (*Lepus europeus*). *J. Anat.* **210**, 491-505.

Williams, S. B., Usherwood, J. R., Jespers, K., Channon, A. J. and Wilson, A. M. (2009a). Exploring the mechanical basis for acceleration: pelvic limb function during acceleration in racing greyhounds (*Canis familiaris*). *J. Exp. Biol.* **212**, 550-565.

Williams, S. B., Tan, H., Usherwood, J. R. and Wilson, A. M. (2009b). Pitch then power: limitations to acceleration in quadrupeds. *Biol. Lett.* **5**, 610-613.