

ACCELERATION AND BALANCE IN TROTTING DOGS

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Summary

During quadrupedal trotting, diagonal pairs of limbs are set down in unison and exert forces on the ground simultaneously. Ground-reaction forces on individual limbs of trotting dogs were measured separately using a series of four force platforms. Vertical and fore–aft impulses were determined for each limb from the force/time recordings. When mean fore–aft acceleration of the body was zero in a given trotting step (steady state), the fraction of vertical impulse on the forelimb was equal to the fraction of body weight supported by the forelimbs during standing (approximately 60%). When dogs

accelerated or decelerated during a trotting step, the vertical impulse was redistributed to the hindlimb or forelimb, respectively. This redistribution of the vertical impulse is due to a moment exerted about the pitch axis of the body by fore–aft accelerating and decelerating forces. Vertical forces exerted by the forelimb and hindlimb resist this pitching moment, providing stability during fore–aft acceleration and deceleration.

Key words: locomotion, mechanical stability, running, quadruped, dog, acceleration, balance.

Introduction

The trot is a running gait employed by quadrupeds that exhibit upright or sprawling postures and can be observed in a diverse array of mammals and reptiles. In most canids, it is the preferred gait for moderate speeds. The diagonal pattern of limb support that distinguishes trotting from other quadrupedal running gaits has long been thought to provide mechanical stability during running (Hildebrand, 1985). Forces that tend to rotate the body about its pitch (transverse) axis can be opposed by the forelimb or hindlimb of a support pair, while forces that tend to rotate the body about its roll (sagittal) axis can be opposed by the right or left limb of a support pair. Footfalls of the diagonal limbs are so closely coupled in the trot that it is recognized by horse riders as a ‘two-beat’ gait (Hildebrand, 1965). In other words, there are two functional steps (defined by paired footfalls of diagonal limbs) per stride. The trot is considered to be a symmetrical gait because the right and left forelimbs, as well as the right and left hindlimbs, are set down in alternate trotting steps (i.e. they are half a stride cycle out of phase) and their duty factors (the ratio of foot contact time to stride period) are equal (Alexander, 1984). Just as in bipedal running, the body falls and rises once in each functional step and twice per stride.

This report examines the ground-reaction forces exerted by individual limbs and their effects on whole-body mechanics during quadrupedal trotting. Historically (and with good reason), the forces acting simultaneously on more than one limb of a quadruped have been summed and treated as a single force acting on the center of mass of the body. This approach

has been used to characterize the bouncing mechanism used by terrestrial runners (Cavagna et al., 1977) and has given rise to mathematical models of running based on the mechanics of simple spring-mass systems (Blickhan, 1989; McMahon and Cheng, 1990; Blickhan and Full, 1993).

The bouncing mechanism discovered in animals has been emulated in running robots (Raibert, 1986). Raibert and co-workers have designed and built dynamically stable quadrupedal robots that trot, pace and bound using a straightforward system for the control of forward velocity, body attitude and hopping height (Raibert, 1990). In so doing, they have raised several fundamental questions about the mechanical function and coordination of individual limbs in living quadrupeds. This report addresses the most basic of these questions: is the vertical force redistributed between the forelimb and hindlimb or does it remain distributed in some constant proportion during quadrupedal trotting?

During steady-state trotting, no net fore–aft force acts on the body, but whenever fore–aft forces cause acceleration or deceleration, a moment is exerted about the pitch axis of the body (Gray, 1968). Without a mechanism for balance, any step involving a net fore–aft acceleration would also involve a net rotation (nose-up or nose-down pitching of the body).

It is clear that dogs are capable accelerating or decelerating (in several consecutive steps or even abruptly) without rotating, but little is known about the mechanical function of the limbs in dynamic balance. Two methods of balancing have been tested in control systems for robotic or computer-

simulated trotting machines. The first includes algorithms for placement of the feet with respect to the center of mass and torques exerted by actuators at the shoulder and hip joints. In this case, the moment due to fore–aft acceleration of the body is balanced by a tipping moment due to placement of the feet too far behind or ahead of the shoulder and hip. Vertical force is distributed in a constant proportion between the fore- and hindlimb. This type of control has been used in trotting robots (Raibert, 1986, 1990). The second method of balancing includes algorithms for differential axial thrust of the limbs and torques exerted by actuators at the shoulder and hip joints. Here, the moment due to fore–aft acceleration of the body is balanced by a moment due to differential vertical forces on the limbs; vertical force is redistributed between the forelimb and hindlimb to provide balance. This type of control has been used only in simulations of a planar, quadrupedal model (Murphy and Raibert, 1985). In the present study, we used a series of force platforms to examine the way in which the body of dogs is balanced during acceleration or deceleration in individual trotting steps.

Materials and methods

Animals and data collection

Two groups of purebred dogs (*Canis familiaris*) were used in this experiment. The first group consisted of five Labrador retrievers, on loan from a guide dog training program and a local kennel. Their average age was 12 months and mean mass was 28.5 ± 1.91 kg. The second group consisted of seven 5-month-old greyhounds, also from a local kennel. Their mean mass was 17.7 ± 3.86 kg (means \pm s.d.). The dogs were led in hand or prompted verbally to trot the length of a runway with a series of four force platforms at its center. Data were collected for 2 s as the dogs crossed the platforms. Only data from uninterrupted trotting were saved. The dogs were weighed immediately before or after a session of data collection.

Force and velocity measurements

Force data were collected at 300 Hz from four rectangular force platforms positioned in series at the center of a 9.5 m runway. Each platform was 0.52 m long (the approximate distance between diagonal footfalls during trotting). Using platforms of this length increased the likelihood that simultaneous footfalls (i.e. footfalls of diagonal limbs) would occur on separate platforms, yielding independent force recordings for each limb. If foot placements did not meet this criterion, the data were discarded. The force platforms measured vertical, fore–aft and lateral forces, but only vertical and fore–aft forces are considered here. Vertical ground-reaction force acting upwards and fore–aft ground-reaction force acting in the direction of travel were considered to be positive. Vertical j_z and fore–aft j_y impulses (the areas under the force/time graphs) were determined from time-varying ground-reaction forces by numerical integration.

Mean forward velocity was determined directly from the

force recording by a method similar to that used by Jayes and Alexander (1978), except that the mean velocity was first calculated for a complete stride (a full cycle of footfalls), instead of a partial stride. The time and distance between subsequent footfalls of a given foot were determined from vertical force recordings of the individual force platforms in the four-platform series. Mean forward velocity in the stride was calculated as the quotient of the distance between the centers of pressure in subsequent footfalls of the same foot and the time between corresponding vertical force maxima. This manner of defining a stride by maximum vertical force instead of initial foot contact is explained more completely by Bertram et al. (1997). The ‘raw’ fluctuations in forward velocity were determined from the integral of fore–aft acceleration with respect to time (assuming an initial velocity of zero). The mean value of the velocity fluctuations during the stride was subtracted from the mean forward velocity to determine the initial forward velocity (at the beginning of the stride); this accounted for any net velocity changes. Initial velocity was then used as an integration constant in the calculation of actual instantaneous velocities during the stride. Mean forward velocity \bar{u} was then determined independently for each trotting step by averaging instantaneous velocities in each step period. To account for size differences between individuals, mean velocities were expressed as dimensionless Froude numbers \bar{U} :

$$\bar{U} = \bar{u}/\sqrt{gb}, \quad (1)$$

where g is gravitational acceleration and b is body height, as defined in the following section on videographic measurements.

In addition to measuring ground-reaction forces during locomotion, force platforms were used to determine the fraction of total body weight supported by the forelimbs during standing. The dogs stood as quietly as possible with the fore- and hindlimbs on separate platforms, and data were collected for 10 s. Mean values of the forelimb and hindlimb vertical force recordings were used to calculate standing weight ratios. Standing measurements were acquired from two of the Labradors used in this study and from four greyhounds, which were not the same animals as those used in the analysis of trotting. Three standing measurements were made on each dog. Other investigators have used sets of scales to determine fore–hind weight distributions in standing dogs (Kruger, 1943; Kimura et al., 1979).

Videographic measurements

Shoulder height s , hip height h , trunk length l and body height b were measured from video images of the dogs trotting on the force platforms. Video images were acquired using a CCD (Sony RGB) video camera and video recorder (Panasonic AG-1960), and then digitized on a Macintosh computer (Quadra 900) running NIH Image (v. 1.57). A background grid at the lateral edge of the platforms was used to calibrate the images. All measurements were made from video frames corresponding to mid-step, where the shoulder was positioned directly over the supporting forefoot. Shoulder and hip heights

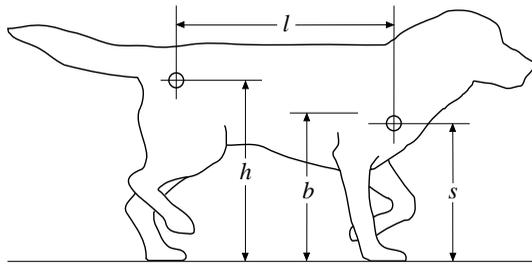


Fig. 1. A schematic diagram of linear measurements made from video images of trotting dogs in mid-step. Shoulder height s and hip height h are the vertical distances from the ground to the scapulo-humeral and coxofemoral joints, respectively. Trunk length l is the horizontal distance between the scapulo-humeral and coxofemoral joint. Body height b was used in Froude number calculations; its measurement is explained in the text.

are the vertical distances from the ground to the shoulder (scapulo-humeral joint) and from the ground to the hip (coxofemoral joint), respectively (Fig. 1). Trunk length is the horizontal distance between the shoulder and hip joints. These measurements were normalized to trunk length: $S=s/l$, $H=h/l$ and $L=l/l=1$. Froude number normalization of velocity required an estimate of the size of the animal. For this purpose, body height was measured as the sum of the vertical distance from the ground to the elbow (cubital joint) and one-third of the vertical distance from the elbow to the top-line of the back. This measurement was chosen because it is easier to identify than any point on the scapula, which could not be visualized in the films.

Results

The morphological data for the two groups of dogs, determined from the video images, are presented in Table 1. During quadrupedal trotting, diagonal fore- and hindlimbs act in pairs, exerting forces on the ground simultaneously. Vertical and fore-aft ground-reaction forces, measured simultaneously using serial force platforms, on the fore- and hindlimb of a diagonal pair are shown in Fig. 2. The combined action of

Table 1. Mean values of videographic measurements

	Labradors	Greyhounds
s (cm)	31.2±2.08	39.0±2.13
h (cm)	47.0±0.95	52.3±3.31
l (cm)	50.5±2.72	54.1±2.68
b (cm)	36.2±0.88	38.3±2.61
S (s/l)	0.62±0.041	0.72±0.047
H (h/l)	0.93±0.054	0.97±0.046
L (l/l)	1.00	1.00

Values are means ± S.D.

s , shoulder height; h , hip height; l , trunk length; b , body height.

Shoulder height (S), hip height (H) and trunk length (L) are also expressed as fractions of trunk length.

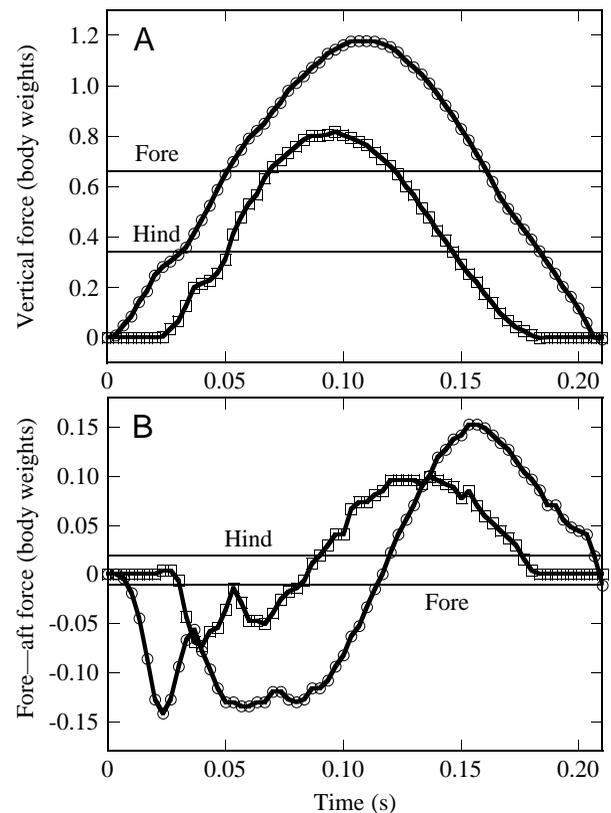


Fig. 2. Vertical (A) and fore-aft (B) ground-reaction forces during a single trotting step are plotted against time. Circles indicate forelimb force and squares indicate hindlimb force. Initial and final contacts of the step are indicated by the left and right borders in both graphs. Contact time t_c of the functional step is 0.210 s. Horizontal lines, labeled 'Fore' and 'Hind', indicate the mean ground-reaction forces on the limbs during the functional step. Impulse can be determined from the area beneath the mean force line or the area beneath the force/time plot. Force is measured in multiples of body weight.

these limbs represents a single functional step with a time of contact t_c equal to the collective contact time of the two limbs. The forelimb usually delimited the final contact, but initial contact was as likely to be delimited by the hindlimb as the forelimb (Bertram et al., 1999). This report is concerned only with the average effect of ground-reaction forces during the step (Fig. 2). Mean forces were determined in the contact time of the functional step, allowing the kinetics of the individual limbs and the entire body to be considered together.

During a complete stride, vertical accelerations of the center of mass must integrate to zero if the body is to follow a level trajectory (Cavagna et al., 1977). During individual trotting steps, vertical accelerations integrate to zero when there are no overlaps or flight periods between adjacent steps. Mean vertical accelerations \bar{A}_z were calculated for each trotting step from the summed vertical impulse j_z of diagonal limbs and expressed in dimensionless terms:

$$\bar{A}_z = (j_z/t_c)/mg - 1, \quad (2)$$

where m is body mass. In the 226 trotting steps analyzed here,

\bar{A}_z was -0.008 ± 0.077 (mean \pm s.d.). Deviations from zero were largely due to overlap and flight periods associated with different trotting speeds. The mean forward velocity \bar{u} was $2.42 \pm 0.29 \text{ m s}^{-1}$, and the mean Froude number \bar{U} was 1.27 ± 0.15 (means \pm s.d.).

To quantify the fraction of vertical load supported by the forelimb during locomotion, Jayes and Alexander (1978) calculated the ratio of the forelimb vertical impulse to the sum of the fore- and hindlimb vertical impulses. The same ratio, referred to here as vertical impulse ratio R , was calculated for each trotting step as:

$$R = j_{z,\text{fore}}/j_z, \quad (3)$$

where j_z is the sum of the diagonal fore- and hindlimb vertical impulses. During trotting, R is also equal to the fraction of the mean vertical force on the forelimb, because the mean vertical force was calculated by dividing both impulse values by the contact time of the functional step. A plot of R versus Froude number did not have a significant slope in this sample of steps, nor has such a relationship been found by other workers (Jayes and Alexander, 1978). This indicates that R is unaffected by mean forward velocity during normal trotting.

In contrast to vertical accelerations, fore-aft accelerations need not integrate to zero in the limits of a stride. This is obvious in the first few strides of a sprint, where fore-aft accelerations of the body are almost entirely in the forward direction (Cavagna et al., 1971). When the mean fore-aft acceleration in a complete stride is zero, there is no change in forward velocity and the motion is considered 'steady state'. Mean fore-aft accelerations in trotting steps can be treated similarly. Mean fore-aft accelerations \bar{A}_y were calculated for each trotting step from the summed fore-aft impulses of diagonal limbs j_y and expressed in dimensionless terms:

$$\bar{A}_y = (j_y/t_c)/mg. \quad (4)$$

It is important to note that \bar{A}_y is equal to the mean fore-aft force expressed in multiples of body weight. For this reason, it will sometimes be referred to as an accelerating or decelerating force. Mean fore-aft acceleration varied substantially above and below zero; mean \bar{A}_y was -0.020 ± 0.051 (mean \pm s.d., $N=226$). It was not significantly correlated with Froude number or mean vertical acceleration but, as will be shown, was closely related to R .

The functional relationship between R and mean fore-aft acceleration was estimated using the reduced major axis, a method of Model II regression (Sokal and Rohlf, 1995) (Fig. 3A). Simple regression is inappropriate in this case because the data are bivariate and error variations are unknown (Rayner, 1985). Steady-state vertical impulse ratio R_0 is the y-intercept of the reduced major axis regression of R on \bar{A}_y . At steady state, the forelimbs of Labradors exerted a greater fraction of the total vertical impulse [$R_0=0.643 \pm 0.005$ ($\pm 95\%$ confidence interval, C.I.)] than those of greyhounds [$R_0=0.558 \pm 0.007$ ($\pm 95\%$ C.I.)], in good agreement with the fraction of body weight supported by the forelimbs during standing, 0.647 ± 0.013 (mean \pm s.d., $N=6$) and 0.555 ± 0.022

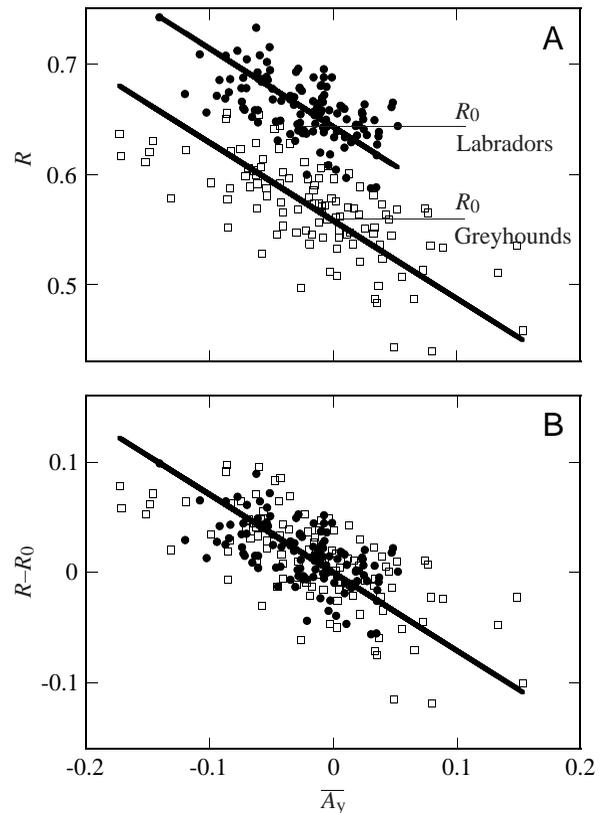


Fig. 3. (A) Vertical impulse ratio R as a function of mean fore-aft acceleration of the body \bar{A}_y in Labradors (filled circles) and greyhounds (open squares). The slopes of the two reduced major axis regressions are very similar: -0.709 ± 0.109 (mean \pm 95% confidence interval, C.I.) for Labradors and -0.707 ± 0.103 (mean \pm 95% C.I.) for greyhounds. The y-intercepts of the reduced major axis lines are the steady-state vertical impulse ratios R_0 . These values are significantly different: 0.643 ± 0.005 (mean \pm 95% C.I.) for Labradors and 0.558 ± 0.007 (mean \pm 95% C.I.) for greyhounds. (B) $R - R_0$ as a function of \bar{A}_y in Labradors (filled circles) and greyhounds (open squares). The slopes of the two reduced major axis regressions are unchanged, but the y-intercepts have been shifted to zero by subtracting R_0 .

(mean \pm s.d., $N=12$) for Labradors and greyhounds, respectively. Steady-state and static weight distributions are equivalent because both are determined by the craniocaudal mass distribution in the body. Despite different values of R_0 in the two breeds, the slopes of the reduced major axis regressions were nearly identical. This implies a functional relationship independent of R_0 .

The functional relationship between R and \bar{A}_y can also be expressed as a relationship between $R - R_0$ (change in R from the steady-state condition) and \bar{A}_y . The reduced major axis regressions shown for the Labradors and greyhounds can be made coincident by subtracting their respective values of R_0 , such that their y-intercepts are zero (Fig. 3B). Positive and negative values of $R - R_0$ indicate a redistribution of vertical impulse to the forelimb and hindlimb, respectively. An increase in vertical impulse on the forelimb, for example, must

always be accompanied by an equal decrease in vertical impulse on the hindlimb – such that the mean vertical acceleration of the body is kept approximately equal to zero.

Angular momentum balance

In the preceding section, it was shown that changes in R are related to mean fore–aft accelerations of the body. Gray (1968) has discussed the effects of fore–aft acceleration on vertical force distribution in the limbs of quadrupeds. When animals accelerate or decelerate, a non-zero mean fore–aft force is exerted on the limbs, resulting in a moment about the pitch (transverse) axis of the body. During trotting, this moment can be resisted by a redistribution of vertical impulse between the forelimb and hindlimb, just as a table resists tipping when it is unevenly loaded. If the body is to be prevented from rotating (i.e. undergoing a net angular acceleration) when the animal accelerates or decelerates, the moment due to net vertical forces on the fore- and hindquarters must be equal and opposite to the moment due to the net fore–aft force causing acceleration or deceleration.

Mean moments about the center of mass can be estimated from simple equations when it is assumed that the body remains approximately horizontal during the step and that the shoulder and hip are (on average) centered above the forefoot and hindfoot, respectively. These assumptions are reasonable for the range of fore–aft accelerations considered here, but probably not for very large accelerations. At the moderate trotting speeds considered here, flight periods between steps are very small or absent. Since angular momentum is conserved during flight, swinging of the limbs could cause the body to rotate. This effect is minimized during trotting because diagonal limb pairs swing 180° out of phase (one pair is retracted while the other is protracted). Because of the very short flight times and out-of-phase limb movement, rotation of the body during flight was considered to be negligible. Symmetrical limb movements and minimal flexion of the spine also keep the center of mass in a nearly constant position with respect to the thorax. Asymmetrical gaits, such as galloping, would violate this assumption.

The forequarters and hindquarters are subjected to the downward force of their own weight and to the upward ground-reaction force exerted on the feet. During steady-state locomotion, these forces are equal and opposite, such that $R=R_0$; however, during acceleration or deceleration, $R \neq R_0$ and net vertical forces are exerted on the fore- and hindquarters. If R is greater than R_0 , forelimb ground-reaction force is greater than the weight of the forequarters and the hindlimb ground-reaction force is less than the weight of the hindquarters. Hence, a net upward force $\bar{F}_{z,fore}$ is exerted on the forelimb and a net downward force $\bar{F}_{z,hind}$ is exerted on the hindlimb. The dimensionless mean forces $\bar{F}_{z,fore}$ and $\bar{F}_{z,hind}$ are given by:

$$\bar{A}_{z,fore} = (R - R_0)(1 + \bar{A}_z) \quad (5)$$

and

$$\bar{A}_{z,hind} = (-R + R_0)(1 + \bar{A}_z), \quad (6)$$

respectively. The factor $1 + \bar{A}_z$ is necessary to correct for step-

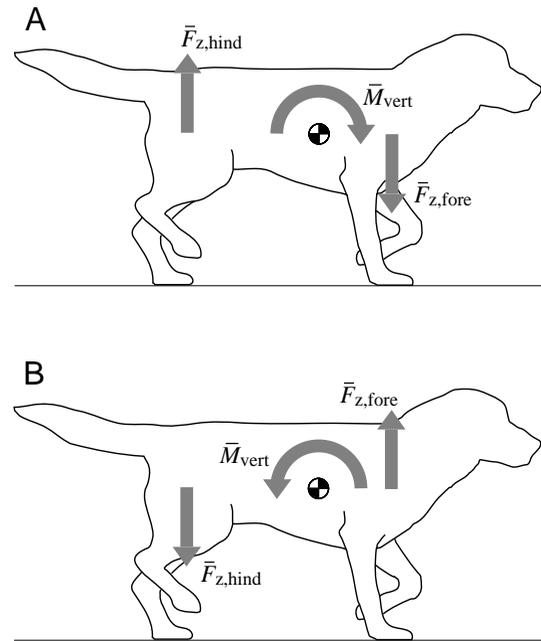


Fig. 4. Diagrams showing the mean moment \bar{M}_{vert} about the pitch axis of the body due to redistribution of the vertical impulse between the fore- and hindlimbs. This moment is exerted by net forces acting on the forequarters $\bar{F}_{z,fore}$ and hindquarters $\bar{F}_{z,hind}$. Showing both the moment and force is redundant, but facilitates comparisons with Fig. 5. (A) During acceleration, the vertical impulse is shifted from the forelimb to the hindlimb, exerting a negative (nose-down) moment. (B) During deceleration, the vertical impulse is shifted from the hindlimb to the forelimb, exerting a positive (nose-up) moment.

to-step variability in the mean vertical acceleration; its effect is minimal because $\bar{A}_z \approx 0$. $\bar{F}_{z,fore}$ and $\bar{F}_{z,hind}$ describe a force couple because they are parallel, equal in magnitude and opposite in sign (Fig. 4). Force couples have the unique property of exerting the same moment about any point, so the dimensionless mean moment \bar{M}_{vert} exerted about the center of mass by these forces is independent of the position of the center of mass. \bar{M}_{vert} tends to rotate the body about its pitch axis and is given by:

$$\bar{M}_{vert} = \bar{F}_{z,fore}L, \quad (7)$$

where $L=l/l=1$ is the dimensionless trunk length. The moment exerted by the force couple is equal to the product of $\bar{F}_{z,fore}$ and the perpendicular distance between the lines of action of $\bar{F}_{z,fore}$ and $\bar{F}_{z,hind}$ (trunk length L). Negative (nose-down) moments were associated with acceleration (Fig. 4A), and positive (nose-up) moments were associated with deceleration (Fig. 4B).

Fore–aft accelerating and decelerating forces act in the ground plane, exerting mean pitching moments \bar{M}_{f-a} about the center of mass. Accelerations exerted positive (nose-up) moments (Fig. 5A), and decelerations exerted negative (nose-down) moments (Fig. 5B). If the body is to be kept from undergoing a net rotation during each step of

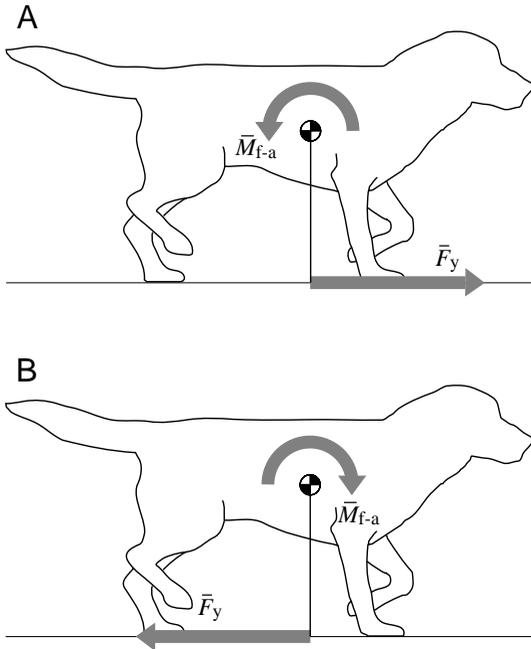


Fig. 5. Diagrams showing the mean moment \bar{M}_{f-a} about the pitch axis of the body due to a mean fore-aft accelerating force \bar{A}_y . The moment is shown for comparison with Fig. 4 (its inclusion here is redundant). (A) During acceleration, \bar{A}_y exerts a positive (nose-up) moment. (B) During deceleration, \bar{A}_y exerts a negative (nose-down) moment. \bar{M}_{vert} and \bar{M}_{f-a} act in opposite directions during acceleration (Figs 4A, 5A) and deceleration (Figs 4B, 5B). These moments sum to zero (i.e. no net rotation) if the center of mass height is D (see equation 7).

acceleration or deceleration, \bar{M}_{vert} and \bar{M}_{f-a} must sum to zero; therefore:

$$\bar{M}_{vert} = -\bar{M}_{f-a} = -\bar{A}_y D, \quad (8)$$

where $D=d/l$ is the dimensionless height of the center of mass (the ratio of the fore-aft moment arm d to the effective vertical moment arm l) and the moment arm of the fore-aft accelerating force \bar{A}_y about the center of mass. Equation 8 describes a line of slope D ; the magnitude of D was determined from the slope of the reduced major axis regression of \bar{M}_{vert} on \bar{A}_y (Fig. 6). Thus, the height of the center of mass was estimated from kinetic, not kinematic, variables. The resulting values of D were 0.691 ± 0.106 ($\pm 95\%$ C.I.) for Labradors and 0.743 ± 0.109 ($\pm 95\%$ C.I.) for greyhounds. In both breeds, the predicted center of mass height was slightly dorsal to the shoulder joint; the values of D determined from the reduced major axis regressions in Fig. 6 were not significantly different from videographic measurements of shoulder height expressed as a fraction of trunk length (Table 1).

Fore-aft forces on the forelimbs and hindlimbs

\bar{A}_y is the sum of dimensionless mean fore-aft forces on the forelimb $\bar{F}_{y,fore}$ and hindlimb $\bar{F}_{y,hind}$ of a diagonal pair (Fig. 2). So far, it has been unnecessary to consider these forces individually because their fore-hind distribution does not

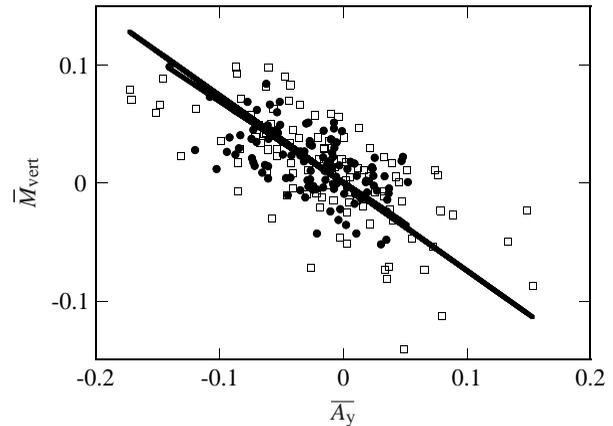


Fig. 6. Mean moment \bar{M}_{vert} due to redistribution of vertical impulse as a function of mean fore-aft acceleration \bar{A}_y in Labradors (filled circles) and greyhounds (open squares). The slopes of the two reduced major axis regressions are -0.691 ± 0.106 (mean $\pm 95\%$ confidence interval, C.I.) for Labradors and -0.743 ± 0.109 (mean $\pm 95\%$ C.I.) for greyhounds. These slopes determine the magnitude of D , which approximates the ratio of the height of the center of mass to the length of the trunk (see equation 8). The y -intercept of both regressions is zero.

influence the net pitching moment about the center of mass. $\bar{F}_{y,fore}$ and $\bar{F}_{y,hind}$ followed well-defined patterns in both Labradors and greyhounds (Fig. 7); their relationships to \bar{A}_y were described by least-squares linear regression. At steady state ($\bar{A}_y=0$), $\bar{F}_{y,fore}$ and $\bar{F}_{y,hind}$ were found to have opposite, non-zero values. The forelimb imparted a decelerating force, while the hindlimb imparted an accelerating force to the body. Similar fore-hind acceleration patterns have been reported during walking and trotting in dogs and sheep (Jays and Alexander, 1978) and during running in hexapedal arthropods (Full et al., 1991).

Both $\bar{F}_{y,fore}$ and $\bar{F}_{y,hind}$ were positive linear functions of their sum \bar{A}_y (Fig. 7). These relationships show that the fore- and hindlimbs work together to accelerate or decelerate the body. Their slopes, however, are notably different. In both Labradors and greyhounds, the slope of $\bar{F}_{y,fore}$ was found to be significantly greater than that of $\bar{F}_{y,hind}$ ($P < 0.05$); the sum of the two slopes is, of course, unity. The forelimb and hindlimb slopes are roughly proportional to R_0 and $1-R_0$, respectively, suggesting a relationship between vertical loading of the limbs and the fore-aft forces that they exert during acceleration and deceleration. This is expected because fore-aft forces are limited by the magnitude of vertical force and the coefficient of friction between the foot and ground.

Discussion

Acceleration and balance

Our data clearly show that the vertical impulse is redistributed between the fore- and hindlimb during acceleration and deceleration. This finding supports the long-standing supposition that a diagonal pattern of limb support

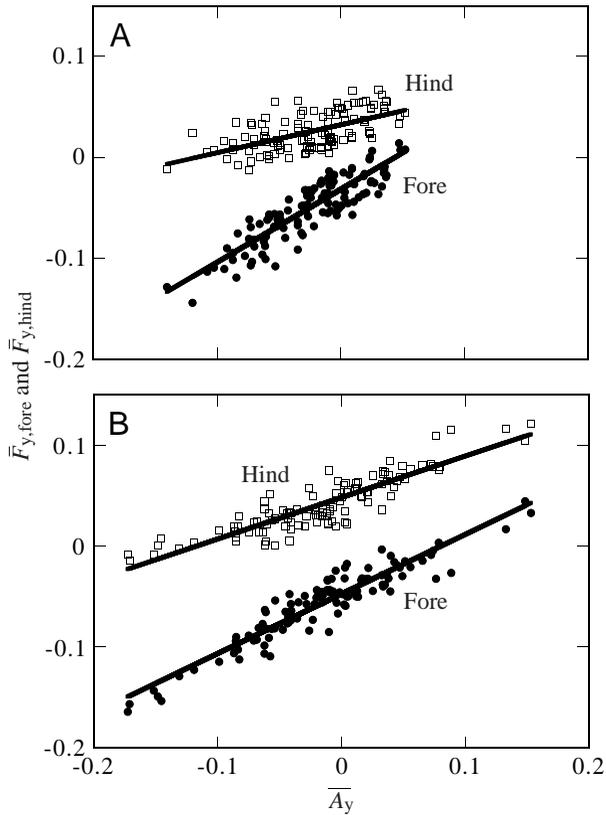


Fig. 7. Mean fore–aft forces imparted to the body by the forelimb $\bar{F}_{y,fore}$ (circles) and hindlimb $\bar{F}_{y,hind}$ (squares) of a diagonal pair. These forces are expressed as a function of their sum \bar{A}_y , and least-squares regression lines are shown. (A) Labradors: fore- and hindlimb regressions, respectively, have y-intercepts of -0.032 ± 0.003 and 0.032 ± 0.003 (mean \pm 95% confidence interval, C.I.) and slopes of 0.723 ± 0.072 and 0.277 ± 0.072 (mean \pm 95% C.I.). (B) Greyhounds: fore- and hindlimb regressions, respectively, have y-intercepts of -0.048 ± 0.003 and 0.048 ± 0.003 (mean \pm 95% C.I.) and slopes of 0.590 ± 0.042 and 0.410 ± 0.042 (mean \pm 95% C.I.).

provides mechanical stability during quadrupedal trotting. This stability is probably an important factor in the preponderance of trotting gaits among quadrupeds. For cursorial quadrupeds with relatively long limbs and laterally compressed bodies, pitch stability is most important, but for sprawling quadrupeds, roll stability is equally important.

We have shown that pitching moments due to fore–aft acceleration are balanced primarily by redistributing the vertical impulse between the fore- and hindlimbs. Angular momentum balance yields a good approximation of the center of mass height (equation 8), indicating that most of the moment due to fore–aft acceleration is balanced in this way. Two methods of balance during fore–aft acceleration were mentioned in the Introduction. The first involves skewed placement of the feet; the second involves redistribution of vertical force between the fore- and hindlimbs. We have shown that the latter method accounts for most of the balancing moment during moderate accelerations and decelerations at a trot. Nevertheless, the two methods could be used simultaneously.

Skewed foot placement may become important during larger fore–aft accelerations or when different gaits are used. It is unlikely, however, that foot placement alone could balance the body during large fore–aft accelerations. Experiments with quadrupedal robots have shown that fore–aft accelerations are limited by the geometry of the physical legs. In this case, foot placement is used for balance during acceleration, and the diagonal legs are constrained to exert equal forces and have equal excursions (legs that function this way are termed force-equalizing virtual legs) (Raibert, 1986, 1990). This method of balance during acceleration is illustrated in Fig. 8B, which represents the mean angle of the legs and the mean resultant ground-reaction force during a trotting step. Because of force equalization, the center of pressure is kept half-way between the fore- and hindfoot. The resultant force passes through the center of mass because its fore–aft component is determined by the mean inclination of the legs during contact.

Redistribution of vertical force can balance the body during large accelerations because the balancing moment is not limited by the physical legs. This method of balance is illustrated in Fig. 8A, which represents the mean angle of the legs and the mean resultant ground-reaction force during a trotting step. The center of pressure is adjusted with respect to the feet when the vertical force is redistributed between the

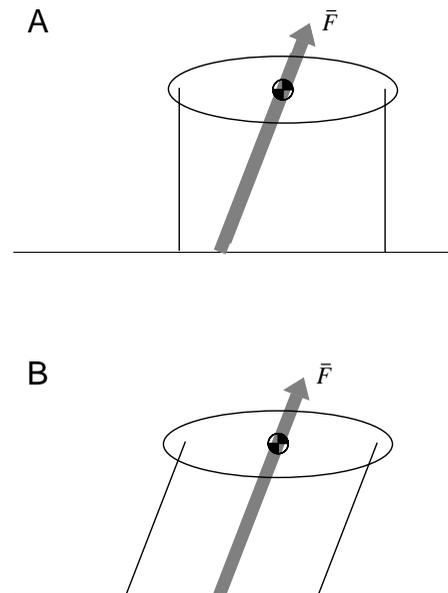


Fig. 8. Two methods of balancing the body during fore–aft acceleration. This simple model represents a trotting quadruped with center of mass half-way between the shoulder and hip. (A) The mean angle of the legs is vertical, and the mean center of pressure is shifted by redistribution of vertical impulse; this keeps the mean resultant force \bar{F} in line with the center of mass. Net torques about the shoulder and hip are responsible for the fore–aft component of \bar{F} . (B) The mean angle of the legs is inclined to the horizontal, and the mean center of pressure remains half-way between the feet because vertical impulse is distributed equally between the legs. The fore–aft component of \bar{F} is determined by the mean inclination of the legs, keeping the mean resultant force in line with the center of mass.

fore- and hindfeet. The legs are not horizontally inclined (i.e. their excursions are symmetrical), so the fore-aft component of the resultant force must be due to torques (retraction or protraction of the legs) exerted at the shoulders and hips. Excellent accelerating and balancing performance has been achieved using this method in simulations of a planar model; the model accelerated from 0 to 2 m s^{-1} in just two trotting steps (Murphy and Raibert, 1985). The body was balanced precisely and its trajectory was not skewed, as it is when foot placement algorithms are used. Murphy and Raibert (1985) emphasize another important advantage of this method: angular momentum can be adjusted during the entire stance, not just at initial foot placement. The method of force redistribution also seems to be much more suitable for locomotion on rough terrain where precise foot placement would be precluded.

The mean fore-aft accelerations analyzed in this report are small; they represent subtle changes in forward running speed that occur during a single trotting step. The largest mean fore-aft accelerations measured were approximately ± 0.18 (18% of gravitational acceleration), representing an increase or decrease in trotting speed of approximately 0.35 m s^{-1} in a single step (0.2 s). Nevertheless, estimates of maximum mean fore-aft accelerations can be extrapolated from the relationships in Fig. 3A. If $R_0=0.6$, the largest mean acceleration would be 0.86 (at $R=0$) and the largest mean deceleration would be -0.56 (at $R=1$). Such fore-aft accelerations would increase or decrease forward velocity by 1.7 m s^{-1} and -1.1 m s^{-1} , respectively, in one trotting step. This suggests that dogs can easily accelerate to a moderate trotting speed and come to a complete stop in two steps. Although we did not measure starting and stopping performance, it is clear that vertical force redistribution would be a sufficient means of balance during fore-aft accelerations of this magnitude. It is likely, however, that skewed foot placements or even a change in gait (to a bounding or galloping pattern) would be important during very large accelerations and decelerations.

Limbs as levers

If the mean angle of the limbs were precisely vertical, as in Fig. 8A, all the fore-aft acceleration of the body would be attributable to the action of limbs as levers in the sense of Gray (1968). In other words, mean accelerating and decelerating forces would be the result of net retracting and protracting torques exerted about the shoulders and hips by their extrinsic muscles (i.e. muscles attaching the limbs to the trunk). Retracting and protracting torques appear to be the primary means of moderate fore-aft acceleration in trotting dogs. Murphy and Raibert's (1985) simulation of a trotting quadruped also accelerated by exerting torque between the body and leg.

Gregersen et al. (1998) have shown that extensor muscles of the hip (coxo-femoral) and shoulder (scapulo-humeral) joints are responsible for more than two-thirds of the work done by actively shortening muscles during steady-state trotting. They showed that the semimembranosus shortens actively,

extending the hip and retracting the hindlimb during the first 40% of contact time. This muscle clearly functions as a torque actuator. Although the work done by hip extensors is only 12% of the total external work during steady-state trotting (Gregersen et al., 1998), these muscles are responsible for much of the positive external work required for forward acceleration and jumping (Alexander, 1974).

Fore-aft forces on the fore- and hindlimb

Opposing mean fore-aft forces on diagonal limbs must act to compress the trunk, but the moments they exert about the shoulder and hip depend on the average orientation of the limbs and body. Assuming that the mean centers of pressure of the fore- and hindfoot are directly beneath the shoulder and hip, respectively, and that the limbs are of equal length, $F_{y,fore}$ and $F_{y,hind}$ would exert equal and opposite torques about the pitch axes of the shoulder and hip during steady-state trotting. This would create a bending moment that tends to dorsiflex the spine. Gray (1968) has explained that the spine (a flexible structure suspended between the limbs) tends to ventroflex as a result of the mass of the trunk, and has shown how torques exerted by the extrinsic muscles about the shoulder and hip can reduce the loading of the ventral musculature. This explanation for opposing fore- and hindlimb forces is cogent, but cannot be addressed here for lack of detailed limb kinematic data.

The tendency of mean fore-aft forces on the fore- and hindlimb to act in opposite directions can be explained (at least qualitatively) in terms of the expected function of the limbs during extreme fore-aft accelerations. During large accelerations, much of the vertical impulse is shifted to the hindlimb. If mean acceleration were just large enough to keep the forelimb off the ground ($R=0$), all the acceleration would have to be imparted by the hindlimb. Likewise, if mean deceleration were large enough to keep the hindlimb off the ground ($R=1$), all the deceleration would be imparted by the forelimb. As already mentioned, such extreme mean fore-aft accelerations were not measured in this study.

Opposing fore-aft forces on the fore- and hindlimb during trotting are reflected to some extent in the extrinsic musculature of the limbs. The hindlimb retractors are substantially more massive than the protractors, suggesting a greater capacity for acceleration from the hindlimb. The forelimb, however, has a more equal distribution of retractor and protractor muscle mass, with no obvious predominance of protractors, as its function in trotting would predict.

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References

- Alexander, R. McN.** (1974). The mechanics of jumping by a dog. *J. Zool., Lond.* **173**, 549–573.
- Alexander, R. McN.** (1984). The gaits of bipedal and quadrupedal animals. *Int. J. Robotics Res.* **3**, 49–59.
- Bertram, J. E. A., Lee, D. V., Case, H. N. and Todhunter, R. J.** (1999). The effect of body form on canine locomotion: A multiple force platform analysis of the trot in the Labrador Retriever and Greyhound. *Am. J. Vet. Res.* (in press).
- 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.
- Blickhan, R.** (1989). The spring-mass model for running and hopping. *J. Biomech.* **22**, 1217–1227.
- Blickhan, R. and Full, R. J.** (1993). Similarity in multilegged locomotion: bouncing like a monopode. *J. Comp. Physiol.* **173**, 509–517.
- Cavagna, G. A., Heglund, N. C. and Taylor, C. R.** (1977). Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. *Am. J. Physiol.* **233**, R243–R261.
- Cavagna, G. A., Komarek, L. and Mazzoleni, S.** (1971). The mechanics of sprint running. *J. Physiol., Lond.* **217**, 709–721.
- Full, R. J., Blickhan, R. and Ting, L. H.** (1991). Leg design in hexapedal runners. *J. Exp. Biol.* **158**, 369–390.
- Gray, J.** (1968). *Animal Locomotion*. London: Weidenfeld & Nicolson.
- Gregersen, C. S., Silvertown, N. A. and Carrier, D. R.** (1998). External work and potential for elastic storage of energy at the limb joints of running dogs. *J. Exp. Biol.* **201**, 3197–3210.
- Hildebrand, M.** (1965). Symmetrical gaits of horses. *Science* **150**, 701–708.
- Hildebrand, M.** (1985). Walking and running. In *Functional Vertebrate Morphology* (ed. M. Hildebrand, D. M. Bramble, K. F. Liem and D. B. Wake), pp. 38–57. Cambridge, London: Belknap Harvard.
- Jayes, A. S. and Alexander, R. McN.** (1978). Mechanics of locomotion of dogs (*Canis familiaris*) and sheep (*Ovis aries*). *J. Zool., Lond.* **185**, 289–308.
- Kimura, T., Okada, M. and Ishida, H.** (1979). Kinesiological characteristics of primate walking: its significance in human walking. In *Environment, Behavior and Morphology: Dynamic Interactions in Primates* (ed. M. E. Morbeck, H. Preuschoft and N. Gomberg), pp. 297–311. New York: Gustav Fischer.
- Kruger, W.** (1943). Über die Beziehungen zwischen Schwerpunktslage und Stärke der Substantia Compacta einzelner Gliedmaßenkochen bei vierfüßigen Säugetieren. *Morph. Jahrb.* **88**, 377–396.
- McMahon, T. A. and Cheng, G. C.** (1990). The mechanics of running: how does stiffness couple with speed? *J. Biomech.* **23**, 65–78.
- Murphy, K. N. and Raibert, M. H.** (1985). Trotting and bounding in a planar two-legged model. In *Theory and Practice of Robots and Manipulators, Proceedings of the RoManSy '84* (ed. A. Morecki, G. Bianchi and K. Kedzior), pp. 411–420. Cambridge, MA: MIT Press.
- Raibert, M. H.** (1986). *Legged Robots that Balance*. Cambridge, MA: MIT Press.
- Raibert, M. H.** (1990). Trotting, pacing and bounding by a quadruped robot. *J. Biomech.* **23**, 79–98.
- Rayner, J. M. V.** (1985). Linear relations in biomechanics: the statistics of scaling functions. *J. Zool., Lond.* **206**, 415–439.
- Sokal, R. R. and Rohlf, F. J.** (1995). *Biometry* (third edition). New York: W. H. Freeman & Co.