Ground forces applied by galloping dogs

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Summary

The gallop differs from most other quadrupedal gaits in that each limb plays a unique role. This study compares the ground forces applied by the four limbs and uses force differences between limbs to address the question of why the gallop is the fastest quadrupedal gait. Individual ground forces were recorded from each of the four limbs as six dogs galloped down a runway at constant speed. Trials were videotaped at high speed using a camera positioned perpendicular to the runway, and velocity was measured using photosensors. The trailing forelimb applied greater peak vertical forces than the lead forelimb, however the vertical impulses from the two forelimbs were similar because the lead forelimb had a longer contact interval. The trailing forelimb and lead hindlimb applied greater peak accelerating forces and accelerating force impulses than their contralateral limbs despite their tendency to have shorter contact intervals. The accelerating impulse of both forelimbs combined did not differ significantly from that of both hindlimbs. The forelimbs applied a greater decelerating impulse than the hindlimbs, such that their net fore-aft impulse was decelerating whereas that of the hindlimbs was accelerating. The greater accelerating impulse applied by the trailing forelimb and greater decelerating impulse applied by the lead forelimb are consistent with the forelimbs acting as elastic struts rather than being actively retracted. In contrast, greater accelerating forces were produced by the lead hindlimb while the center of mass was lifted, suggesting that the hindlimbs are more actively extended or retracted during stance. The differences in ground forces measured between paired limbs suggest that the lead forelimb and trailing hindlimb are limited in their ability to apply forces by their positions in the stride cycle rather than by their muscular capacity. Although a bound or half-bound would allow more limbs to produce their maximal forces, a gallop may generate higher speeds because it is more efficient. Galloping could be more efficient than other gaits involving sagittal bending if the increased number of ground contact intervals decreased either the decelerating forces applied at the onset of ground contact or the vertical motion of the center of mass.

Key words: locomotion, gallop, ground force, gait, biomechanics, dog.

Introduction

High-speed running in mammals is characterized by sagittal bending of the trunk. This flexion and extension of the trunk augments speed by increasing the stride length and the propulsive impulse applied by the hindlimbs. It was calculated that a limbless cheetah could attain speeds of 10 km h⁻¹ through sagittal bending alone (Hildebrand and Goslow, 2001). Whereas the bound, half-bound and gallop all take advantage of sagittal bending, the gallop is the high-speed gait of the fastest mammalian runners (Gambaryan, 1974; Hildebrand, 1977). There is no clear consensus in the literature, however, as to what advantages the gallop holds over the bound or half-bound.

These gaits that employ sagittal bending are called asymmetrical gaits because the ground contacts of the two limbs of each pair (fore- or hindlimbs) are not evenly or symmetrically spaced in time (Hildebrand, 1977). The gallop differs from the bound and half-bound in that contralateral limbs of both pairs contact the ground at different times (Fig. 1). In the rotary gallop, which is used by dogs at high speed, the trailing forelimb contacts the ground first, followed by the lead forelimb (the lead forelimb 'leads' in that it lands in front of the trailing forelimb). Thereafter, liftoff of the trailing forelimb occurs, followed by that of the lead forelimb. An airborne phase with the limbs gathered beneath the body then precedes hindlimb contact. The hindlimbs then follow the same pattern of trailing and leading contact and takeoff, using the opposite limbs as the lead and trail. Finally an airborne phase with the limbs extended precedes the forelimb contact of the next stride (Fig. 1). The transverse gallop, which is used by dogs at lower speeds and by horses at all galloping speeds, is similar to the rotary gallop. However, in the transverse gallop the right and left hindlimbs land in the same order as the forelimbs rather than the reverse (Hildebrand, 1977).
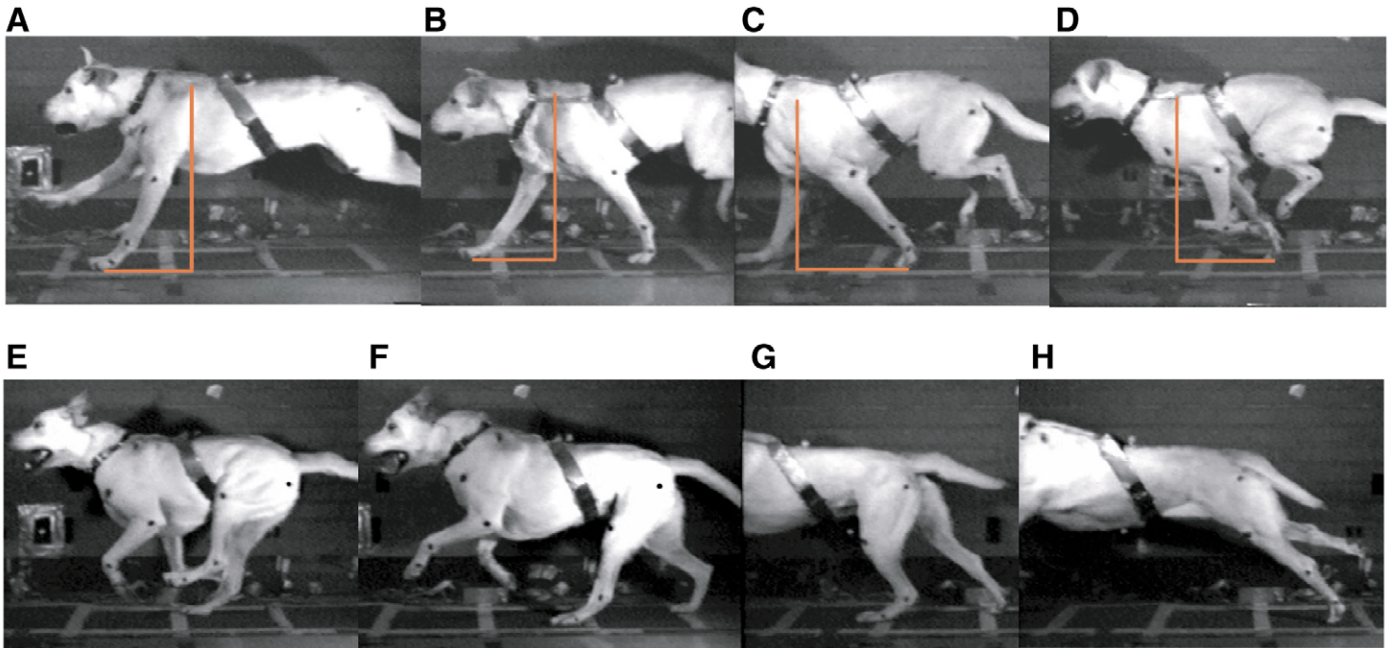
Fig. 1. Stance phases in a rotary gallop for Dog E. (A) Beginning of trailing forelimb stance. (B) Beginning of lead forelimb stance. (C) End of trailing forelimb stance. (D) End of lead forelimb stance. Orange lines show vertical and horizontal distances between the forelimb axis of rotation and the ground contact point. (E) Beginning of trailing hindlimb stance. (F) Beginning of lead hindlimb stance. (F) End of trailing hindlimb stance. (G) End of lead hindlimb stance.

Howell noted that it would be disadvantageous for the two forelimbs of large animals to land simultaneously, as occurs in the bounding gait of small mammals, because it would be difficult to overcome the decelerating impulse (Howell, 1944). He does not explain, however, why the forelimbs would create a greater decelerating impulse if they landed together rather separately. Ruina and colleagues proposed that a four-beat gait, in which each of the limbs impacts the ground independently, should be the most energy-efficient gait as it would minimize the energy lost at ground impact (Ruina et al., 2005). They envision this running gait as a rimless wheel, where maximizing the number of spokes would lead to greatest efficiency. Similarly, according to their model, spacing out the ground contact periods of the four limbs decreases the supporting impulse each limb applies while it is angled in opposition to the direction of travel and thereby decreases the decelerating impulse (Ruina et al., 2005).

Due to the unique timing of their ground contacts in a gallop, contralateral limbs need not be functionally equivalent, as they are in a bound or trot. In fact, due to differences in velocity and center of mass height at the time of ground contact, it is not possible for them to be identical in all locomotor parameters. Cantering horses apply greater decelerating impulses with their lead limbs and greater accelerating impulses with their trailing limbs (Merkens et al., 1993). A previous study on galloping dogs found the same pattern in the forelimbs whereas differences between hindlimbs were not significant (Bryant et al., 1987). Inherent differences in the positions and ground forces between lead and trailing limbs could affect agility by favoring turning in one direction rather than the other. In turns, galloping mammals prefer to use the inside forelimb as the lead limb (Hildebrand, 1977). Differences in bone and muscle strain between lead and trailing limbs could be of clinical importance as they might make galloping mammals more prone to injury on a particular side. Both racing dogs and horses develop more injuries in the right forelimb than in the left, although these differences, as well as any asymmetries in the limb bones due to remodeling or breeding for track racing, may be attributed to the turn direction of racetracks (Boudrieau et al., 1984; Rooney, 1977; Palmer, 1986). Subtle differences in ground forces between leading and trailing limbs might also lead to the evolution of unique anatomical specializations in the preferred leading and trailing limbs. Asymmetries in limb bone lengths and diameters have been reported in horses, although these may be adaptations to the turn direction of racetracks (Pearce et al., 2005; Watson et al., 2003; Hanson and Markel, 1994). Due to these factors, a greater understanding of the interlimb differences in ground forces during the high-speed gallop is of interest.

The present study extends the research of Bryant and colleagues by further investigating the extent to which the four limbs of a galloping dog differ in their contribution to a running stride. Here, a wider range of force parameters is investigated in dogs galloping at higher speeds. This allows for a comparison between the rotary gallop used by dogs at high speeds and the transverse gallop used by horses and provides maximum force data during the gallop for comparison with forces applied during other activities.

Table 1. *Description of the subjects*

Subject	Breed*	Mass (kg)	Mean velocity (m s^{-1})	Preferred lead
A	Labrador retriever	25.2	8.5±0.3	R[‡]
B	Pit bull/labrador retriever	23.3	9.6±0.4	NS
C	Hound/mixed breed	34.2	8.5±0.2	L[‡]
D	Hound/mixed breed	28.5	8.4±0.4	R[†]
E	Labrador retriever	33.1	10.2±0.1	R[‡]
F	Weimaraner	25.6	9.9±0.3	NS

*As many of the dogs were adopted from a local pound, all breeds are approximations based on subjects' appearance. For preferred lead, NS indicates that neither a right (R) nor a left (L) lead was significantly preferred. [†]Significance of lead preference was *P*<0.01; [‡]significance of preference *P*<0.001.

Materials and methods

Subjects and equipment

Six adult dogs of various breeds were used in this study (Table 1). These dogs were either privately owned pets or research dogs in training for another study. Dogs ran along a carpeted runway 40 m in length. Ground forces were recorded at 500 Hz with a 0.6×0.4 m Kistler 9281B SN force plate (Amherst, NY, USA) mounted flush with the runway 20 m from the start. Trials were videotaped at 250 Hz with a NAC HSV-500 camera (Tokyo, Japan) positioned perpendicular to the runway. To measure running velocity, laser sensors (Keyence LV-H41; Osaka, Japan) were positioned along the runway 2.5 m before and after the center of the force plate. A reflective band was placed around the thorax of each dog to activate the sensors as the dogs passed. A National Instruments 6034 A/D board (Austin, TX, USA) was used to import data from the laser sensors and force plate into the computer, where it was analyzed with Labview software (Austin, TX, USA).

Procedure

Dogs were encouraged to gallop along the runway as close as possible to maximum speed by having them chase either a tennis ball or an experimenter running with a hotdog. Dogs that did not appear to gallop with maximum effort after several practice trials were not used for this study. On each day in which trials were recorded, dogs performed trials until their velocity decreased due to fatigue or boredom. After the completion of each recording session, the dog was weighed on the force plate. Recording sessions were repeated on separate days for each dog until a sufficient number of acceptable 'maximal effort' trials were recorded for each limb.

Analysis

Trials were acceptable for analysis if they met the following criteria: (1) velocity was within 15% of the maximum measured for that dog, (2) the limb on which forces were analyzed landed fully on the force plate and no other feet contacted the plate during its stance period and (3) velocity measurements taken over the 2.5 m before and after the center of the force plate differed by less than 10%. Of the trials meeting these criteria, five trials for each limb (lead and trailing fore- and hindlimbs) were selected for analysis. These trials

were chosen so as to minimize the variation in velocity among the trials analyzed for each dog. Care was taken to ensure that velocity did not differ significantly between paired limbs in the trials analyzed for any dog. For one of the six dogs (dog C), only four trials for each limb were acceptable for analysis. The following parameters were measured for each trial analyzed: velocity, contact time, mean and maximum vertical, fore-aft and mediolateral forces and force impulses. Contact time was taken as the period over which dogs applied forces greater than or equal to 4% body weight to the plate.

Statistics

For each of the measured parameters, means for each limb of each dog were calculated. These means were then used in paired, two-tailed Student's *t*-tests in Microsoft Excel software to compare lead and trailing limbs of fore- and hindlimb pairs and both fore- *versus* both hindlimbs.

Results

Ground forces in the vertical, fore-aft and lateral directions were analyzed for 116 galloping trials from six dogs (Table 2; Fig. 2). The dogs used a rotary gallop and ran with a mean velocity of 9.2±0.3 m s^{-1}. The mean standard deviation in velocity among analyzed trials for an individual was 3.2% of the dog's mean velocity. Dogs tended to lead with the right forelimb, however this tendency was not significant (*P*=0.088). Of the six dogs, three showed a significant preference for the right lead and one showed a significant preference for the left lead (Table 1). Although the dogs' velocity changed by less than 10% over the 5 m encompassing the force plate, the fore-aft impulse averaged over all trials was slightly, but significantly, positive at 3.8±1.9 BW ms. Thus, in the trials analyzed, there was a net tendency for the dogs to accelerate slightly as they ran over the force plate. The mean vertical impulse was 80.5±3.2 BW ms, so the net fore-aft impulse was very small in comparison.

Lead vs trailing forelimb

The lead forelimb had a 5% longer stance period than the trailing forelimb (*P*=0.03). The average mean and maximum vertical forces for the trailing forelimb were 5% greater than

Table 2. *Contact times and ground reaction forces*

	Lead fore	Trail fore	Lead hind	Trail hind
Contact time (ms)	74.5±4.6*	70.8±5.0*	71.5±3.2	74.3±4.0
Forces (BW)				
Mean vertical	1.25±0.07	1.31±0.08	0.99±0.07*	0.94±0.07*
Peak vertical	2.12±0.10	2.23±0.13	1.64±0.11*	1.47±0.09*
Peak accelerating	0.44±0.04[†]	0.49±0.04[†]	0.46±0.07[†]	0.38±0.05[†]
Peak decelerating	–1.02±0.10	–1.00±0.11	–0.62±0.05	–0.57±0.03
Peak lateral	0.22±0.04	0.20±0.04	0.12±0.03	0.16±0.03
Peak medial	–0.11±0.03	–0.11±0.04	–0.12±0.03	–0.11±0.04
Impulses (BW ms)				
Vertical[‡]	91.7±3.0	91.8±4.0	70.0±4.2	68.6±3.8
Accelerating	10.8±0.90[†]	12.3±0.75[†]	13.0±2.22*	10.7±1.85*
Decelerating[‡]	–11.0±0.43*	–9.80±0.79*	–5.41±0.70	–5.43±0.78
Lateral	3.81±0.80	3.88±1.17	1.87±0.83	4.36±1.23
Medial	–1.2±0.44	–1.77±0.90	–1.37±1.24	–2.18±1.49

Significant difference between leading and trailing limbs with *$P<0.05$, [†]$P<0.01$. [‡] indicates a significant difference between total forelimb and total hindlimb impulses ($P<0.01$). BW, body weights.

those of the lead forelimb, but the difference was not significant ($P=0.08$ and $P=0.10$, respectively) (Table 2; Figs 2, 3). Because the lead forelimb had a greater contact time but a lower vertical force, both forelimbs had equal vertical impulses (Fig. 4). In the fore-aft direction, the trailing forelimb had a 12% greater peak accelerating force and a 14% greater accelerating force impulse, whereas the lead forelimb had an 11% greater decelerating force impulse (Table 2).

Mediolateral force curves for all dogs showed a similar pattern for the first half of stance (Fig. 2) and did not differ between leading and trailing limbs. The forelimbs applied laterally directed forces for about the first 20% of ground contact then switched to medially directed forces and showed a medial force peak ~20–25% into the contact phase. Then, at ~30% of ground contact, forces returned to the lateral direction until at least midstance. From midstance to takeoff, mediolateral force patterns differed greatly between dogs, however each individual dog applied similar forces in all trials. Peak medial and lateral forces were similar in magnitude and were 7% and 34% as large as peak vertical and accelerating forces, respectively (Table 2; Fig. 3).

Lead vs trailing hindlimb

The trailing hindlimb tended to have a 4% longer stance period than the lead ($P=0.06$), while the lead hindlimb exerted 10% greater peak vertical forces and 5% greater mean vertical forces than those of the trailing hindlimb ($P=0.03$ for both) (Table 2; Figs 2, 3). Both the peak accelerating force and the net accelerating force impulse were roughly 18% greater in the lead hindlimb (Fig. 4). Mediolateral force curves for the leading and trailing hindlimbs were similar in appearance and showed the same general pattern for five of the six dogs (Fig. 2). For these dogs, mediolateral forces hovered around zero during the first third of stance and then medial forces were applied for the remainder of stance. Mediolateral forces in the

sixth dog were equally small but were laterally directed over the entire stance. Net mediolateral forces were not significantly different from zero for either of the hindlimbs, and the two hindlimbs did not differ for one another in any of the measured mediolateral force parameters (Table 2).

Forelimbs vs hindlimbs

The total vertical impulse for both forelimbs was 32% greater than that for both hindlimbs. The decelerating impulse was 92% greater in the forelimbs than in the hindlimbs, while the total accelerating impulses for the fore- and hindlimbs were similar. The net fore-aft impulse was accelerating in the hindlimbs and did not differ significantly from zero in the forelimbs (Table 2).

Discussion
Lead vs trailing forelimb

Mean and peak vertical forces were about 5% greater in the trailing forelimb than in the lead. Although this difference in forces was not significant, it is likely that with more subjects a significant difference would be obtained. Nevertheless, the two forelimbs did not differ in the total vertical impulses that they applied because the lead forelimb applied forces over a 5% longer stance period. These results indicate that both forelimbs of galloping dogs contribute more or less equally to the support of body weight. Both peak accelerating forces and accelerating impulses were greater for the trailing forelimb whereas decelerating impulses were greater for the lead forelimb. This pattern was also found in a previous study on galloping dogs (Bryant et al., 1987).

Differences in ground forces between the leading and trailing forelimbs of cantering and galloping horses show the same trends as in dogs but are of greater magnitudes. During cantering at slow speeds (4.4–5.6 m s^{-1}), peak vertical forces
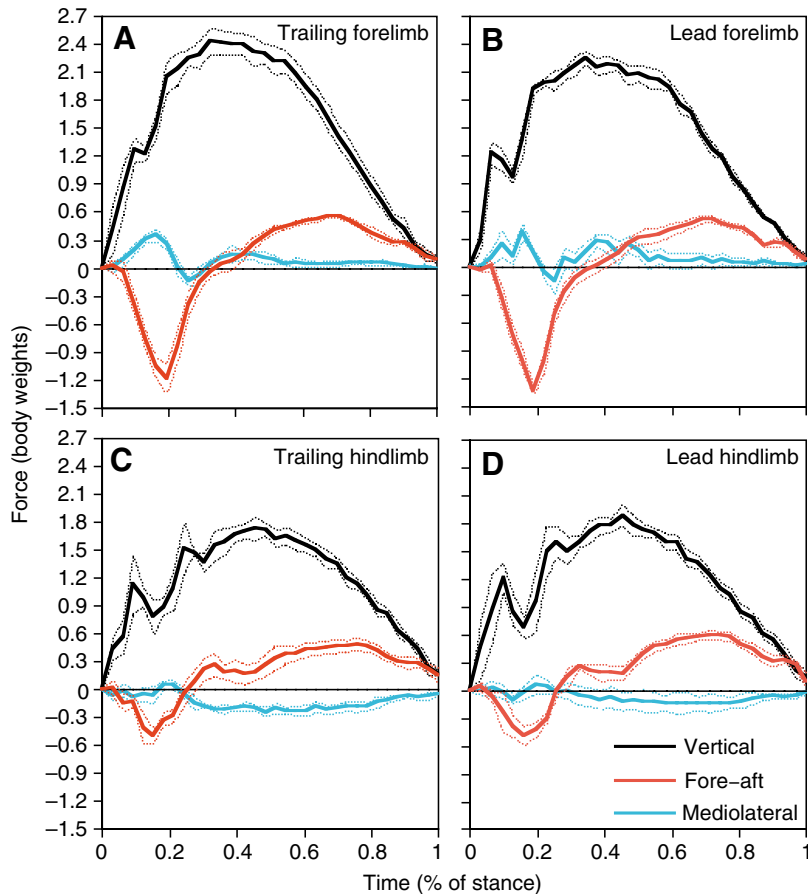
Fig. 2. Ground reaction force curves for Dog F plotted in body weights over the course of stance for each limb: (A) trailing forelimb, (B) lead forelimb, (C) trailing hindlimb, (D) lead hindlimb. Solid and broken lines represent the mean of the five trials from each limb and s.e.m., respectively. Lateral forces are plotted as positive values and medial forces are plotted as negative values.

are 25% greater in the trailing forelimb of horses, whereas at higher galloping speeds ($12\ \mathrm{m\ s^{-1}}$) peak vertical forces are predicted to be only 19% greater for the trailing forelimb based on the maximum metacarpophalangeal joint angles (Merkens et al., 1993; McGuigan and Wilson, 2003). Horses galloping at high speed also have a longer stance period on the lead forelimb (Deuel and Lawrence, 1986). During slow cantering, horses apply four times greater peak accelerating forces with their trailing forelimbs than with their leading forelimbs (Merkens et al., 1993), which is also much greater than the 12% difference observed in dogs. Differences between dogs galloping at high speed and cantering horses could be due to interspecific differences in body morphology, or they could represent inherent differences between the two gaits. The canter is used by horses at moderate speeds and differs from the high-speed gallop in that the contact phases of the lead forelimb and trailing hindlimb overlap entirely (Merkens et al., 1993; Hildebrand, 1977). Even at high speeds, the transverse gallop of horses differs from the rotary gallop of dogs in that right and left hindlimb ground contacts occur in the same order as forelimb contact. Further, horses galloping at high speeds do not exhibit a flight phase between the stance phases of the lead hindlimb and trailing forelimb. Unfortunately, the ground forces for the transverse gallop of horses or for other animals galloping at high speeds have not been reported.

Whereas one might expect the two forelimbs to act together,

first decelerating and then accelerating the body, in both dogs and horses the trailing forelimb applies a greater accelerating impulse while the lead forelimb applies a greater braking impulse (Bryant et al., 1987; Merkens et al., 1993). This difference in fore-aft impulses may be explained by the vertical position of the center of mass during each limb's stance. The center of mass is relatively high when the trailing forelimb lands, low when the trailing forelimb pushes off and the lead forelimb lands, and high again when the lead forelimb pushes off (D. Bramble, personal communication) (Cavagna et al., 1977). Thus, the lead forelimb must touchdown either at a more protracted angle than the trailing (i.e. further in front of the shoulder) or with a more crouched limb posture whereas the trailing forelimb must be more retracted (i.e. further behind the shoulder) or extended at takeoff. In fact, results from dalmatians show that the trailing forearm was significantly more retracted at takeoff whereas the lead forearm tended to be more protracted on landing, although this trend was not significant (Alexander et al., 1980). Thus, the vertical oscillations of the center of mass during the gallop likely constrain the trailing forelimb to spend a greater proportion of stance with the ground contact caudal to the limb's fulcrum, whereas the lead forelimb must spend a greater portion of stance with its ground contact cranial to the limb's fulcrum. Because the primary retractor muscles of a dog's forelimb show little or no activity associated with stance phase during a
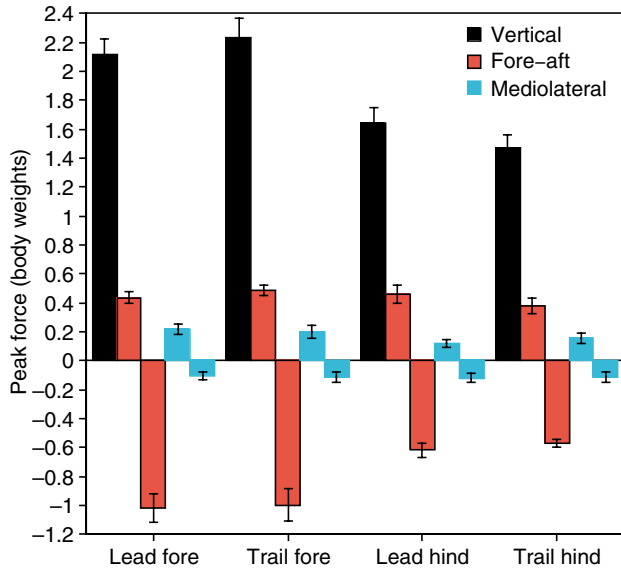
Fig. 3. Peak ground reaction forces applied by each limb in body weights ± s.e.m. (*N*=6 dogs).

Fig. 4. Force impulses exerted on each limb in body weight milliseconds ± s.e.m. (*N*=6 dogs).

steady-state gallop (D.R.C., unpublished data), the forelimbs appear to act as elastic struts rather than as levers actively propelling the dog. As such, the angles of the limbs are a main determinant of the polarity of their fore-aft forces, such that retracted forelimbs tend to apply propulsive forces while protracted forelimbs apply braking forces. Thus, the trailing forelimb, which lands in a more retracted position and spends a greater portion of its stance time with the ground contact point caudal to the limb's fulcrum, exerts a lower braking impulse and a greater accelerating impulse than the lead forelimb.

Lead vs trailing hindlimb

Both galloping horses (Deuel and Lawrence, 1986) and dogs tended to have a slightly longer stance period on the trailing hindlimb, although in dogs this difference was not significant. Forces in the hindlimbs were opposite to those in the forelimbs, with the lead hindlimb exerting greater vertical and 18% greater accelerating forces. A similar trend toward greater accelerating forces in the lead hindlimb of galloping dogs was found by Bryant and colleagues (Bryant et al., 1987). Cantering horses also apply greater vertical forces with the lead hindlimb, however their hindlimb fore-aft forces are opposite to those of dogs, with the trailing hindlimb applying a much greater accelerating impulse (Merkens et al., 1993). Because the center of mass is higher at touchdown and lower at takeoff (Cavagna et al., 1977; Minetti et al., 1999), an elastic strut model in which the limbs are not actively retracted or extended during stance (as described above for the forelimbs) predicts that both dogs and horses should apply greater accelerating forces with the trailing hindlimb. This suggests that the hindlimbs of cantering horses act in a more strutlike fashion whereas galloping dogs may use more muscular power in retracting or extending their hindlimbs. Hindlimb ground forces are also likely to differ
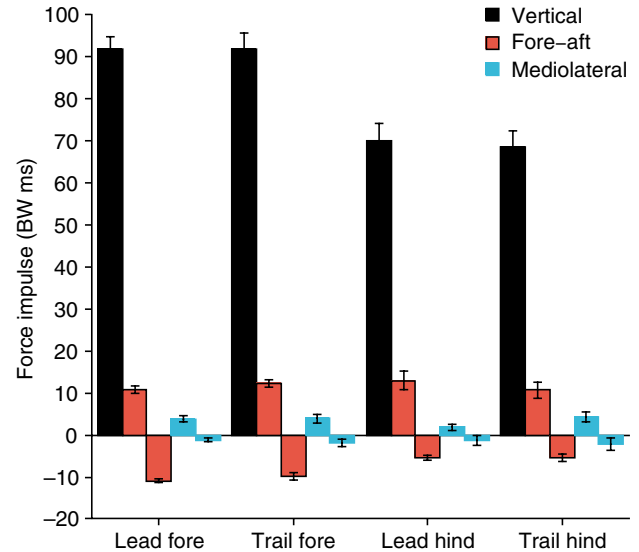
between dogs and horses because sagittal bending tends to decrease with increasing body size and is generally greater in carnivores than ungulates (Gambaryan, 1974). Much of the back extension that occurs was observed during hindlimb stance. This back extension simultaneously increases center of mass height and applies strong propulsive forces, which is inconsistent with a simple strut model. In fact, mechanical energy traces for galloping dogs show large increases in both kinetic and potential energy during the ground contact period of the lead hindlimb (Cavagna et al., 1977), demonstrating that the hindlimbs of galloping dogs cannot be acting as elastic struts as do the forelimbs.

Whereas active extension and retraction can explain why the net fore-aft impulse of the lead hindlimb is so strongly propulsive, it does not explain why the accelerating impulse of the trailing hindlimb is so small. In fact, the accelerating impulse of the trailing hindlimb is smaller than that of either forelimb. There is likely a limitation in how effective propulsive forces from the trailing hindlimb can be during the period that the lead hindfoot is in front of the hip joint. Because the lead hindlimb may be limited in its ability to apply propulsive forces during this period, greater accelerating forces from the trailing hindlimb might simply lead to greater braking forces in the lead hindlimb.

Mediolateral forces

Initially upon ground contact, both forelimbs applied laterally directed ground forces followed by a relatively large medially directed ground force peak and then further lateral forces until midstance. After midstance, mediolateral forces varied in their polarity among dogs but were consistent through the five trials for each dog. In five of the dogs, mediolateral forces in both hindlimbs fluctuated about zero during the first

third of stance and then medial forces were applied for the remainder of stance. Because of these changes in polarity, net mediolateral impulses were not significantly different from zero for any of the limbs (Fig. 2; Table 2). Laterally directed forces could result from feet placed lateral to the midline applying a net force vector directly through the center of mass. Alternatively, if the feet were placed on or near the midline, abductor muscles in the shoulders or hips could exert lateral forces to prevent the limb from collapsing. Feet positioned near the midline could also apply medial forces if the net force vector passed through the shoulder girdle or hip joint. Because the mediolateral positions of the feet during force application were not recorded, the yaw and roll moments produced by the mediolateral forces cannot be determined from these data. Mediolateral forces were quite small, with peaks only 7% and 34% as large as peak vertical and accelerating forces, respectively. The mediolateral forces recorded from cantering horses were highly variable and were less than 5% and 20% as large as fore-aft forces and vertical forces, respectively (Merkens et al., 1993; Biewener, 1998).

Implications of force differences between lead and trailing limbs

Although ground forces differed between lead and trailing limbs, and four of the six dogs had preferred lead limbs ($P<0.01$), it seems unlikely that natural selection would favor significant musculoskeletal asymmetries in the limbs of mammals. Galloping in the natural environment requires mammals to turn and to adapt their gait to varying terrain, which would severely limit the usefulness of favoring one limb over another. The skeletal asymmetries observed in horses are more likely due to selection and remodeling for the turn direction of racetracks (Pearce et al., 2005; Watson et al., 2003; Hanson and Markel, 1994). Switching leads could help gallopers delay muscle fatigue by alternating the forces each limb must produce. Force differences between lead and trailing limbs also seem to play a role in turning. In turns, gallopers prefer to use the inside forelimb as the lead limb (Hildebrand, 1977). This is advantageous because in a rotary gallop the trailing forelimb and lead hindlimb, both of which apply greater accelerating forces than their contralateral limbs, are placed on the outside of the turn.

Forelimbs vs hindlimbs

Although the net duty factor for the forelimbs was the same as that for the hindlimbs, the forelimbs supported 57% of body weight whereas the hindlimbs supported only 43%. This vertical force distribution between the fore- and hindlimbs is similar to that found in dogs trotting at constant speed, where the forelimbs supported 64% and 56% of body weight in labradors and greyhounds, respectively (Lee et al., 1999), and to that found in dogs galloping at 7.5 m s^{-1} while accelerating slightly, where the forelimbs supported 56–59% of body weight (Bryant et al., 1987). Cantering horses similarly support 56% of the body weight with the forelimbs despite an equal duty factor in the fore- and hindlimbs (Merkens et al., 1993).

The accelerating impulse did not differ between both fore- and both hindlimbs whereas the decelerating impulse was much greater for the forelimbs. Thus, the hindlimbs of galloping dogs did show net fore-aft impulses that were more accelerating than those of the forelimbs, as expected based on their location relative to the center of mass. However, this difference was not achieved by the hindlimbs applying greater accelerating impulses but by their applying smaller decelerating impulses. Whereas the net fore-aft forces of the forelimbs were not significantly different from zero, this result is most likely due to the slight net acceleration that occurred in the trials. Without this net acceleration, the net fore-aft impulse of the forelimbs would likely have been negative while that of the hindlimbs would have been less accelerating. Bryant and colleagues (Bryant et al., 1987) similarly found that galloping dogs applied only slightly greater accelerating impulses with the hindlimbs than with the forelimbs but much greater decelerating impulses with the forelimbs.

Why gallop?

Both the lead forelimb and the trailing hindlimb exerted lower peak forces than their contralateral limbs. They also had longer ground contact periods, which suggests that unless these limbs rotate over a greater angle, or their joints extend through greater angles, their muscles are contracting at a lower velocity. This combination of lower ground forces and lower contraction velocity in the lead forelimb and trailing hindlimb would suggest that the muscles of these limbs produce less power than those of their contralateral limbs. Intuition might suggest that if maximum running speed were limited by the force or power produced by limb muscles, dogs and horses might achieve higher speeds using a bounding gait that would allow all limbs to produce maximum power. Alternatively, the increased power that an animal produced by bounding might be offset by a decrease in efficiency.

The collisional loss model proposed by Ruina and colleagues (Ruina et al., 2005) contends that the main energetic cost of locomotion is overcoming the kinetic energy lost upon foot impact with the ground. Comparing the limbs of a runner to the spokes on a rimless wheel, it suggests that more spokes would make for a rounder, more efficient wheel, as less energy would be lost in the collision of the spokes with the ground. Thus, the gallop, where each limb acts as an independent spoke, would be more efficient than the bound, where paired limbs combine to form a single spoke, or the half-bound (Ruina et al., 2005).

The gallop may also increase efficiency because less vertical motion of the center of mass is required to achieve the same stride length. In a gallop, the distance traveled during the support phases is based on the summed angular excursions of all four limbs (minus half the angular excursion that occurs during the phases of forelimb and hindlimb double contact). In a bound, because the contact period of contralateral limbs overlaps completely, the distance covered during the support phases is based only on the angular excursion of one fore- and one hindlimb, and is less than in a gallop. To achieve the same

stride length, a bounding animal must spend a greater portion of the stride in suspension phases, which requires a greater vertical displacement of the center of mass. For example, when hybrid deer bound, the pitch angle of their back undergoes a greater excursion than when they gallop, suggesting a more vertically oriented flight phase trajectory and a greater vertical displacement of the center of mass (Lingle, 1992). Because kinetic and potential energy fluctuations are in phase during a bounding gait, this greater fluctuation in center of mass height equates to a greater fluctuation in the mechanical energy over the stride (Heglund et al., 1982). This means that more mechanical work is required for each stride of a bound. If all of the energy required to elevate the center of mass could be stored elastically and released during each stride, then this increase in mechanical work might be irrelevant. However, previous studies on running, galloping and hopping mammals have shown energetic recoveries of only 20–40% through elastic storage (Biewener, 1998). Thus, more muscular work is likely required to lift the center of mass in a bounding stride than in a galloping stride of equal length. In fact, it is likely that a combination of greater collisional energy losses and greater fluctuation in center of mass height makes the bound less efficient than the gallop.

Large mammals can probably achieve higher velocities by galloping than by bounding because galloping is more energetically efficient, even though one limb of each pair is unable to operate at full power as it could in a bound. Based on this, mammals could be expected to switch to a half-bound or bound during sharp turns and rapid accelerations and decelerations when power production is more important than efficiency. If increased efficiency is the primary advantage of the gallop over other gaits involving sagittal bending of the trunk, there are several possible explanations for why many small mammals use the bound or half-bound. First, their locomotor behaviors often include more accelerations and sharp turns than larger mammals. This could increase the importance of power production relative to efficiency. Second, because their limb muscles are more powerful relative to their body mass (Alexander et al., 1981), their speed could be reduced more by limiting the force and power production of the lead forelimb and trailing hindlimb. Third, the crouched posture and muscle tendon properties of smaller animals may decrease their ability to save energy through either kinetic/potential energy transfer between fore- and hindlimbs or elastic storage within the trunk and limbs, as large mammals are able to achieve in the gallop. This could decrease the difference in energetic efficiency between galloping and bounding. Thus, the use of the bound or half-bound by small mammals and by large mammals during accelerations and decelerations is consistent with the hypothesis that the gallop is preferred due to increased efficiency.

Conclusion

Galloping dogs apply greater accelerating forces with their trailing forelimbs and greater decelerating forces with their lead

forelimbs. As the trailing forelimb spends a greater portion of the stance phase in a retracted position and the lead forelimb spends a greater portion protracted (Alexander et al., 1980), this force difference would be expected if the forelimbs were to behave as elastic struts rather than being actively extended or retracted during stance. The two forelimbs exert equal vertical impulses over the stride, however the trailing forelimb tends to exert higher mean and peak vertical forces whereas the lead forelimb exerts forces over a longer time interval. Forces in the hindlimbs are the opposite, with the lead hindlimb applying greater vertical and accelerating forces than the trailing hindlimb. The trailing hindlimb may be unable to apply greater accelerating forces without incurring greater decelerating forces from the lead hindlimb. Furthermore, back extension likely contributes more to the accelerating forces during lead hindlimb contact. Although the accelerating impulse is not significantly different between the fore- and hindlimbs, the forelimbs do net deceleration overall because they apply a greater decelerating impulse whereas the hindlimbs do net acceleration.

In the gallop, the lead forelimb and trailing hindlimb are constrained in their ground force production. The gallop is likely preferred over the bound and half-bound, which may allow more of the limb muscles to operate at full power, because it is a more efficient gait. For mammals rapidly accelerating or decelerating and for small mammals running at constant speed, the importance of power relative to efficiency may be greater, making the bound or half-bound more advantageous. During turns, quadrupeds make use of the force differences between lead and trailing limbs by positioning the trailing forelimb and the lead hindlimb, both of which apply greater accelerating forces than their paired limb, on the outside of the turn.

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