Rapid acceleration in dogs: ground forces and body posture dynamics

Rebecca M. Walter* and David R. Carrier

Biology Department, University of Utah, Salt Lake, UT 84112, USA

*Author for correspondence (e-mail: walter.rebecca.m@gmail.com)

SUMMARY

Because the ability to accelerate rapidly is crucial to the survival and reproductive fitness of most terrestrial animals, it is important to understand how the biomechanics of rapid acceleration differs from that of steady-state locomotion. Here we compare rapid acceleration with high-speed galloping in dogs to investigate the ways in which body and limb posture and ground forces are altered to produce effective acceleration. Seven dogs were videotaped at 250 Hz as they performed 'maximum effort' accelerations, starting in a standing position on a force plate and one and two strides before it. These dogs began accelerations by rapidly flexing their ankles and knees as they dropped into a crouch. The crouched posture was maintained in the first accelerating stride such that the ankle and knee were significantly more flexed than during steady high-speed galloping. The hindlimb was also significantly more retracted over the first stance period than during high-speed galloping. Ground forces differed from steady-state locomotion in that rapidly accelerating dogs supported only 43% of their body weight with the forelimbs, compared with 56–64% in steady-state locomotion. The hindlimbs applied greater peak accelerating forces than the forelimbs, but the forelimbs contributed significantly to the dogs' acceleration by producing 43% of the total propulsive impulse. Kinematically, rapid acceleration differs from steady-state galloping in that the limbs are more flexed and more retracted, while the back undergoes greater pitching movement. Ground reaction forces also differ significantly from steady-state galloping in that almost no decelerating forces are applied while propulsive force impulses are three to six times greater.

Key words: locomotion, acceleration, biomechanics, dogs, ground forces.

INTRODUCTION

Acceleration plays a critical role in predator–prey interactions that involve chases over short distances or frequent changes in direction. Success in interspecific and intraspecific competitions requiring charging and fighting may also be dependent on an animal's ability to accelerate rapidly. Although acceleration performance is important in many species, the biomechanics of acceleration in quadrupeds remain largely unknown.

Acceleration differs from steady-state running in that it requires net work to be done on the center of mass over each stride. During high-speed steady-state locomotion the muscles must rapidly and efficiently produce high forces and maintain high joint stiffness. By contrast, rapid acceleration appears to be more dependent on the ability of muscles to shorten rapidly and substantially while producing a large propulsive force. During rapid acceleration, turkeys and wallabies produce four or more times greater peak instantaneous power than when running at similar constant speeds (Roberts and Scales, 2002; McGowan et al., 2005). These species increase the positive work done in each stride by producing propulsive forces at the hip and ankle joints over a larger angle of joint extension (Roberts and Scales, 2004; McGowan et al., 2005). Studies on human sprint performance have found that maximum speed is correlated with leg stiffness as well as muscle strength and power, whereas acceleration is only correlated with muscle strength and power (Chelly and Denis, 2001; Bret et al., 2002). During acceleration, human sprinters begin the stance phase with their leg joints more flexed than when running at a constant speed, and these joints undergo greater net extension during stance (Jacobs and van Ingen Schenau, 1992; Jacobs et al., 1993; Kuitunen et al., 2002).

Ground forces during rapid acceleration in bipeds differ from those during running at constant speed in that they are mainly if not entirely propulsive. In the most rapid accelerations, turkeys are able to eliminate braking forces entirely (Roberts and Scales, 2002). Although not entirely eliminated, braking forces are also greatly reduced in the first stance phases for human sprinters (Cavagna et al., 1971; Mero, 1988).

Accelerating animals must also contend with the challenge of maintaining balance along the pitch axis. To avoid a net pitching moment, their net ground reaction force vector over each stride must be directed through the center of mass. Whereas in steady-state locomotion this requires directing the net ground reaction force vector vertically, in acceleration it must be directed forward, which may make avoiding net pitching moments more difficult. It may also be beneficial to minimize the pitching that occurs within each stride, as pitching requires the input of mechanical energy. Bipeds such as humans and some bipedal running lizards do not avoid a net head-end up pitch in the first strides of rapid accelerations and instead begin the most rapid accelerations quadrupedally or with a more head-end down posture and gradually tilt upright (Aerts et al., 2003; Mero et al., 1983).

Based on studies of rapidly accelerating bipeds (Roberts and Scales, 2004; McGowan et al., 2005; Jacobs and van Ingen Schenau, 1992; Jacobs et al., 1993) we expected that the hindlimb joints of quadrupeds would extend over greater angular excursions during rapid acceleration than during high-speed galloping and that braking forces would be absent or minimal. As an excessively head-end up pitch angle would compromise the ability of quadrupeds to apply propulsive forces with their forelimbs, we anticipated that they would modify their posture and ground forces to minimize pitching moments and to maximize potential forelimb stance time. Instantaneous pitching moments may be reduced by lowering the center of mass, beginning acceleration with a head-end down posture, and holding the limbs at more retracted

angles (Roberts and Scales, 2004; McGowan et al., 2005; Lee et al., 1999). We also expected that dogs would reduce the net pitching moment that they produced in each stride of acceleration by applying a greater proportion of the vertical forces with their hindlimbs (Lee et al., 1999).

In this study, we examined how dogs altered their limb and body postures during the initial strides to achieve the net ground reaction force vectors necessary for rapid acceleration. We started by analyzing the ground reaction forces applied by the fore- and hindlimbs during the initial pushoff and first two strides of acceleration to determine how and where in the stride cycle propulsive forces were applied. Next, we compared these ground reaction forces, along with the hindlimb joint, hindlimb and back angles over the first stride, to those recorded from dogs during steady-speed galloping. Finally, we examined how the ground reaction forces and modifications in body posture that we recorded in accelerating dogs compared with those previously observed in accelerating bipeds.

MATERIALS AND METHODS
Subjects and equipment
Seven 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. The average mass of the subjects was 26.6±9.7 kg.

The equipment and procedure used were similar to those previously described for a study of galloping in dogs (Walter and Carrier, 2007). A 0.6 m×0.4 m Kistler 9281B SN force plate mounted flush with a 40 m carpeted runway recorded vertical and fore–aft forces at 500 Hz. Approximately 3.5 m of the runway including and surrounding the force platform was covered with sandpaper to improve traction over the first strides. Trials were videotaped at 250 Hz with a NAC HSV-500 camera positioned perpendicular to the runway. Average velocity over the first 2 m of each acceleration was measured using laser sensors (Keyence LV-H41) positioned at the approximate starting location for each trial and 2 m from the start. A reflective band wrapped around the thorax of each dog activated the sensors as the dogs passed. A National Instruments (Austin, TX, USA) 6034 A/D board was used to import data from the laser sensors and force plate into the computer where it was analyzed with Labview software.

Procedure
In this analysis, the forelimb pushoff was defined as the forces and kinematics of the forelimbs from the start of the acceleration until they were first lifted off the ground (Fig. 1A,B). This was followed by the hindlimb pushoff, which consisted of the vertical and propulsive force impulse applied by the hindlimbs before they were

lifted off the ground and the associated kinematics (Fig. 1C–E, Fig. 3). The first stride consisted of initial steps that dogs usually took with the forelimbs during the hindlimb pushoff and first hindlimb flight phase (Fig. 1D–G) as well as the first hindlimb stance phase (Fig. 1H,I). Stride two consisted of the next fore- (Fig. 1J,K) and hindlimb (Fig. 1L,M) stance periods.

As only one force platform was available, separate trials were required to measure each step. For trials measuring the forces applied in the initial fore- or hindlimb pushoff, dogs started from a standing position with either both fore- or both hindlimbs on the force platform. An experimenter positioned the dog by holding its collar prior to the start of each trial. The subject was released and encouraged to accelerate maximally along the runway by allowing it to chase either a tennis ball or an experimenter running with a hotdog. Trials in which video recordings showed the dog pulling on the collar prior to release were not used for analysis. Dogs that were more than 10% slower than previous subjects, or did not appear, based on visual inspection of the videos, to accelerate with maximum effort were not used in this study.

The same basic procedure was used to collect recordings from the first two accelerating strides. For these trials, subjects started with their fore- or hindlimbs one or two stride lengths in front of the force plate. Trials for each dog were recorded on multiple days. On each recording day, dogs performed trials until their velocity decreased as a result of fatigue or boredom. After the completion of each recording session the dogs were weighed on the force plate. Each dog performed at least twenty trials initiated at each starting location. In many cases, more trials were required in order to achieve a sufficient number for analysis. For each dog, the five trials for each step with the fastest 2 m velocity that met all necessary requirements (described below) were used for analysis.

Analysis
Trials were accepted for analysis if they met the following criteria: (1) velocity over the first 2 m was within 12% of the maximum measured for that dog; (2) the limb or limbs on which forces were analyzed landed fully on the force plate; and (3) they were the only feet on the plate for at least 95% of its stance period. Optimally, trials in which both fore- and hindlimbs contacted the plate simultaneously would have been excluded from analysis, as the role of the individual limbs is obscured during this period of overlap. Some dogs, however, nearly always exhibited simultaneous ground contact of the lead forefoot and the hindfeet in the first stride. Because these feet are also placed very close together, trials without any overlap could not be achieved for all dogs, and trials with minimal overlap (less than 5% of stance) were used for analysis when necessary.

The following parameters were measured for each trial analyzed: velocity, contact time, mean and maximum vertical and fore–aft

Table 1. Description of the subjects

Subject	Breed*	Mass (kg)	Standing % fore support[†]	Mean 2 m velocity (m s^{-1})
A	Labrador retriever	33.1	62.3%	3.7±0.12
B	Labrador retriever	25.2	NA	3.4±0.17
C	Pit bull/Labrador retriever	23.3	66.5%	3.7±0.08
D	Hound/mixed breed	34.2	NA	3.5±0.10
E	Hound/mxed breed	28.5	61.4%	3.6±0.14
F	Labrador retriever	34.7	65.4%	3.7±0.10
G	Shih tzu	7.0	60.9%	3.6±0.11
Average		26.6±9.7	63.3±2.5%	3.6±0.12

*Many of dogs were adopted from a local pound and so all breeds are approximations based on the subjects' appearance.
[†]Standing % fore support refers to the percentage of the dog's body weight that was supported by the forelimbs when the dog stood at rest. It indicates the fore–aft position of each dog's center of mass. It was not measured for dogs B and D.
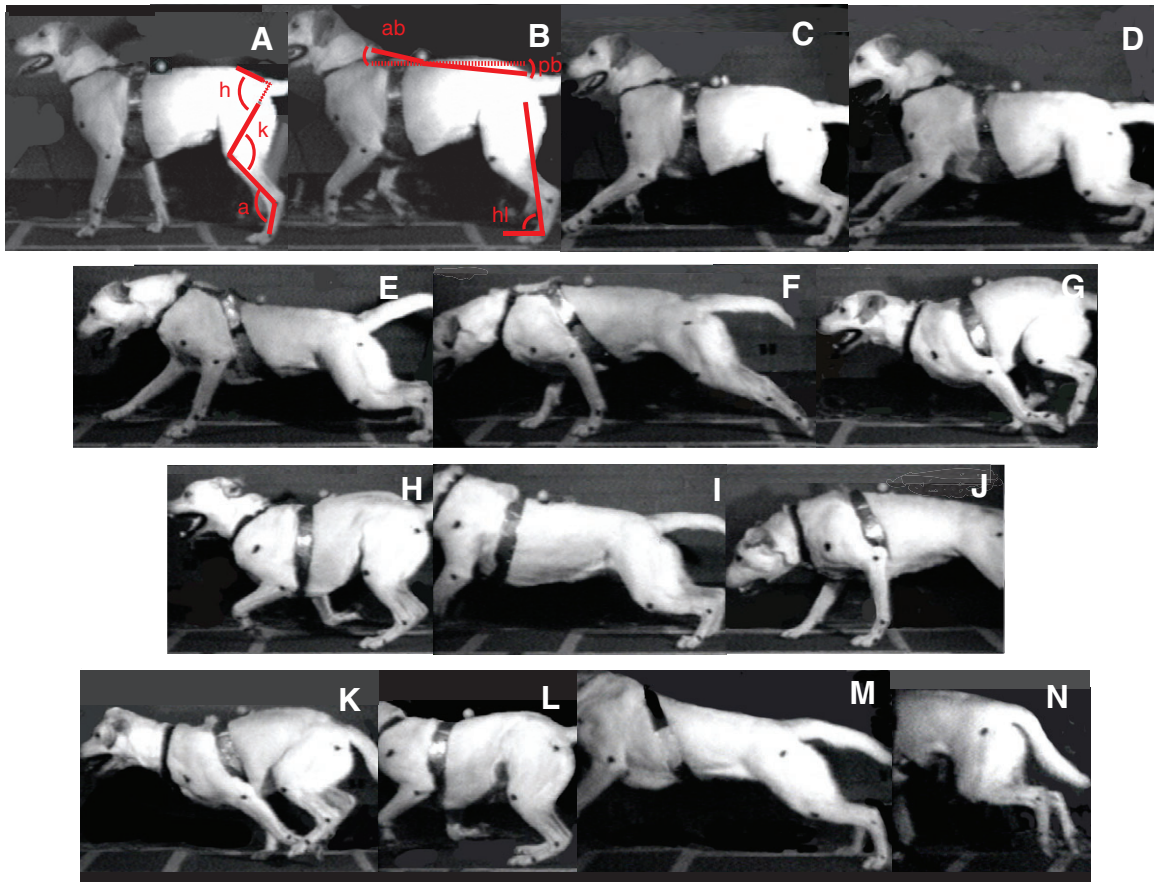
Fig. 1. Photo series of dog A starting from a standing position and taking the first two strides of a 'maximum effort' acceleration taken at 80 ms intervals. Photos are taken from a composite of four trials as the camera's field of view was not large enough to encompass the entire two strides. The hindlimb joint and back angles measured are indicated in the first two frames: a, ankle; k, knee; h, hip; ab, anterior back; pb, posterior back; hl, hindlimb. See Materials and methods section for a full description of angle measurements.

forces, force impulses, and force vector angles. Contact time was taken as the period over which dogs applied forces greater than or equal to 4% body weight to the plate.

Kinematic measurements

To compare the limb and back angles over stance with those used in a high-speed gallop, kinematic measurements were made on five of the dogs over the first hindlimb step of acceleration (Table 1; dogs A–E). In addition, video recordings from a previous study were used to make similar kinematic measurements on the same five dogs during the lead and trailing hindlimb stance phases in high speed galloping (Walter and Carrier, 2007). For two of these dogs (dogs B,E), it was not possible to analyze the kinematics of the lead hindlimb in the gallop as it was always facing away from the camera. All angles were averaged over three trials for each dog, with the following exceptions in galloping: for the trailing hindlimb (dog A, 1 trial; D, 2 trials) and for the lead hindlimb (dog C, 1 trial).

The hindlimb joint angles over the course of the first stance were measured by marking and digitizing centers of joint rotation for the hip, knee, ankle and metatarsal phalangeal (toe) joints (Fig. 1A). To measure the back angles, a reflective ball was taped to the back over the last thoracic vertebra. The anterior back angle was measured as the angle made by the base of the neck and the reflective ball with the horizontal, whereas the posterior back angle was the angle between a line connecting the reflective ball

and the base of the tail and the horizontal (Fig. 1B). Positive back angles represent a head-end up pitch and negative back angles represent a head-end down pitch. The hindlimb angle was the angle made by a line connecting the hip and toe with the horizontal (Fig. 1B) such that larger angles indicate a more protracted limb and smaller angles indicate a more retracted limb. For angular velocity, joint flexion is shown as negative and joint extension is positive. Kinematic data for the gallop were digitized from videos made during a previous study on galloping dogs (Walter and Carrier, 2007). Velocity and acceleration over the first hindlimb step were calculated by taking the first and second derivatives of position of the reflective ball on the back (approximate center of mass) using a moving regression (Lanczos, 1956). The first step was chosen for analysis because dogs applied the largest peak propulsive forces in this step.

Statistics

Angles and angular velocities were compared between step one and the lead and trailing hindlimb of the gallop using ANOVA from Statview. Selected force parameters (noted in Results) were compared using Student's t-tests in Microsoft Excel.

RESULTS

All dogs used a half-bound during the first strides of acceleration, such that trailing and lead forelimbs began and ended their stance

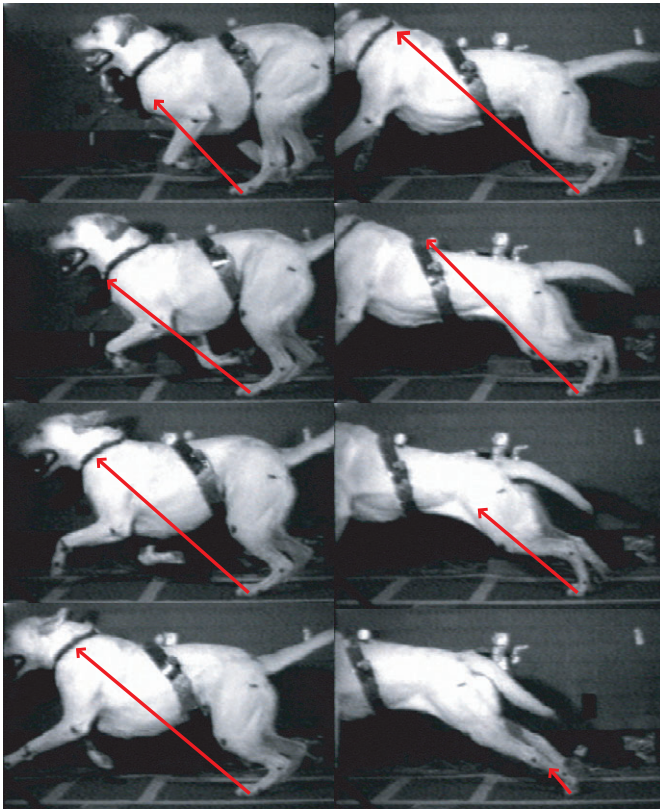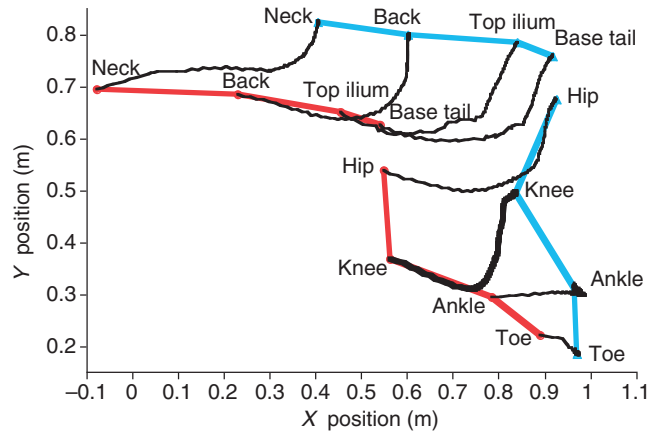Fig. 3. Position of the neck, back, top of the ilium, base of the tail, hip, knee, ankle and toe tracked over the course of the hindlimb pushoff for a representative trial by dog A. The dog progresses from right to left during the pushoff. The posture of the back and hindlimb at the start of the pushoff and at toe-off are shown in blue and orange, respectively. Joint positions over time are shown with back lines. Note the extreme (38%) drop in knee height (heavy black line) that occurred as dogs dropped to a crouched posture. This vertical drop of the hindquarters preceded forward acceleration in nearly all trials.

Fig. 2. Photo series of dog A taken at 24 ms intervals over the first hindlimb stance period. Orange lines show the instantaneous ground reaction force vectors for the left hindlimb. (Here we assumed that the right and left hindlimbs applied equal forces throughout the step.)

phases sequentially whereas the hindlimbs began and ended stance simultaneously (Figs 1 and 2). Average velocity over the first 2 m, calculated from the time between activation of photosensors, 0 m and 2 m from the start, was $3.6\pm0.12\,\mathrm{m\,s^{-1}}$ (N=7; Table 1). Average velocity and acceleration over the first hindlimb stance phase, calculated from position data, were $3.5\pm0.3\,\mathrm{m\,s^{-1}}$ and $14.3\pm1.0\,\mathrm{m\,s^{-1}}$ (N=5), respectively.

Initial acceleration

Dogs began accelerations either by lifting both forelimbs and dropping the body into a crouched posture or by stepping forward with one or both forelimbs as they lowered themselves into a crouched posture (Fig. 1A–D, Fig. 3). In the first case, the forelimbs did not apply a forward impulse before being lifted and the vertical forces they applied simply dropped to zero without a prior rise. After attaining a crouched posture, dogs proceeded with the hindlimb

Table 2. Hindlimb joint, hindlimb, and back angles as shown in Fig. 1

	Ankle			Knee			Hip		
	TD	TOff	Min	TD	TOff	Min	TD	TOff	Min
Step 1	119±1.6*	154±3.3*	81±4.0*,†	107±4.3*	124±3.3*,†	90±4.0*,†	75±4.5*	123±3.5*	75±4.5*
Gallop lead	147±5.3*	158±3.1	96±8.8*	146±3.3*	147±3.4†	123±4.6†	66±2.9†	115±5.9*	66±3.2†
Gallop trail	140±3.8*	161±2.4*	97±3.8†	139±2.9*	140±3.6*	110±4.4*	81±6.4*,†	130±4.2*	80±6.0*,†

	Hindlimb		
	TD	TOff	Mean
Step 1	110±2.6*,†	43±1.5*,†	76±1.0*
Gallop lead	121±1.7*	53±3.1*	87±1.7*
Gallop trail	120±1.5†	49±1.2†	83±0.9*

	Anterior back (thorax)				Posterior back			
	TD	TOff	Max	Min	TD	TOff	Max	Min
Step 1	−14±1.4*	6±3.9*,†	14±1.4*,†	−14±1.4*	10±2.7*	14±1.6*	15±1.7*	8.6±2.2*
Gallop lead	14±3.4*	16±4.4*	21±4.1*	13±3.8*	11±1.6*	3±2.5*	11±1.6*,†	2±2.1*,†
Gallop trail	3±2.8*	19±3.2†	20±3.2†	2±2.8*	14±2.4*	10±3.2*	16±2.7†	10±2.4†

TD, touchdown; Toff, take off; Min, maximum flexion or minimum joint angle during stance. For back angles Max and Min are the maximum and minimum pitch angles respectively.

*,†Same symbols denote significant differences between angles at P<0.05. For the comparisons between the trailing hindlimb of the gallop and step one of acceleration N=5; for comparisons involving the lead hindlimb of the gallop N=3; and for trunk angles N=4.
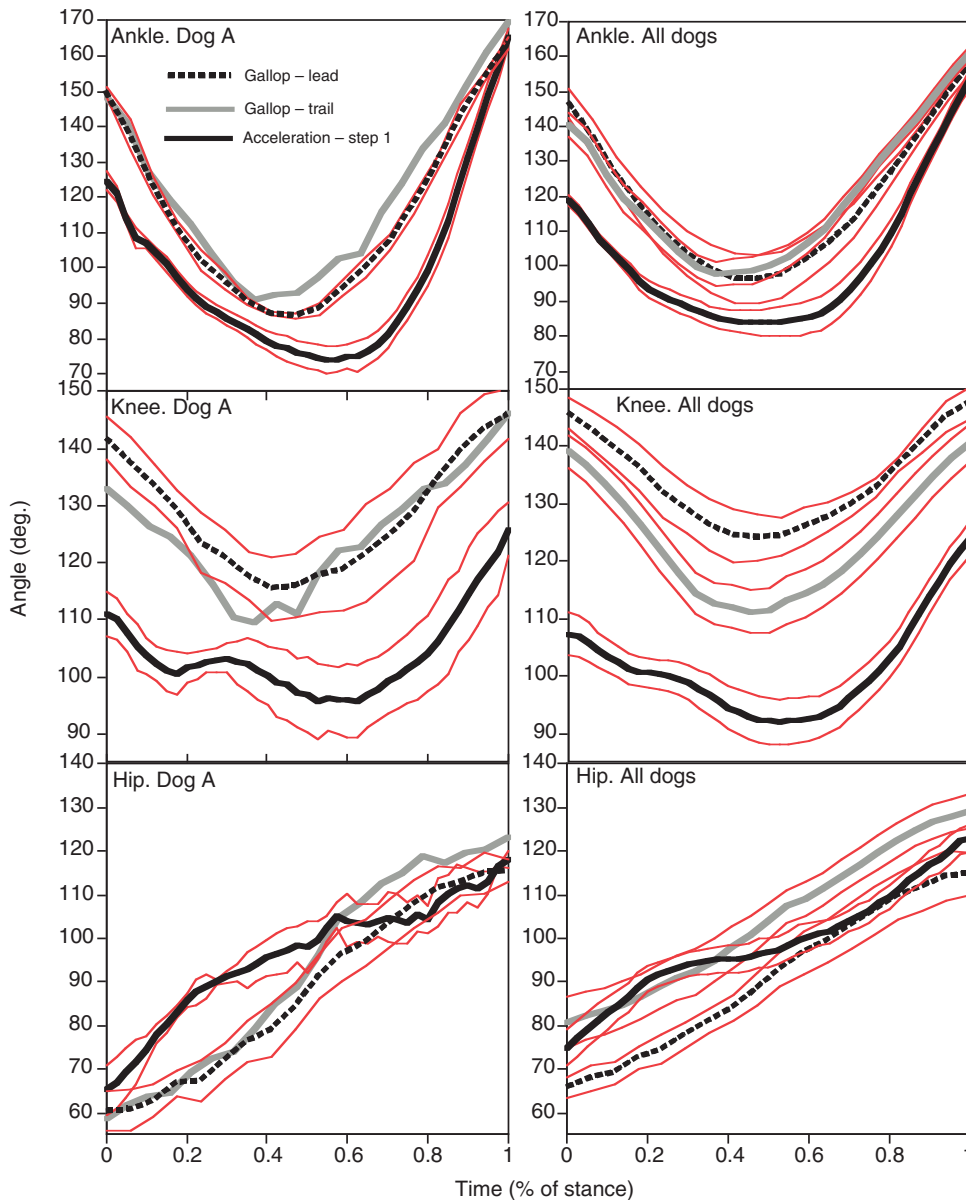
Fig. 4. Mean angles for the hindlimb of dog A and the average angles of dogs A–E plotted over the course of stance. For step 1 and the trailing hindlimb $N=5$ dogs, and for the lead hindlimb $N=3$ dogs. Angles measured are depicted in Fig. 1 with smaller angles indicating more flexed joints. The mean angles are plotted with thick lines as follows: acceleration (black), lead hind gallop (dotted) and trailing hind gallop (gray). Thin orange lines show positive and negative standard deviations for dog A and standard errors for the average of all dogs.

pushoff in which strong vertical and propulsive forces were applied by the hindlimbs (Fig. 1D–F). During most of this hindlimb pushoff, the forelimbs for the first step were already on the ground and dogs angled their upper bodies sharply head-end up and then head-end down as they vaulted over the forelimbs (Fig. 1D–G).

Hindlimb joint angles and angular velocity compared between step 1 and galloping

The ankle and knee flexed during the first 40% of stance and extended during the last 40% of stance in both galloping and acceleration, whereas their average angular velocity over the middle 20% of stance was very low (Figs 4 and 5). Overall, the knee and ankle were more flexed during the first step of acceleration than during galloping (Table 2, Fig. 4). At the end of stance, the ankle was fully extended during both galloping and acceleration. By contrast, the knee remained about 20 deg. more flexed at takeoff in acceleration than in galloping (Table 2, Fig. 4). Both flexion and extension occurred more rapidly in the gallop, especially in the knee, for which angular velocity of flexion was

five times greater in the gallop during the first 20% of stance than in acceleration (Fig. 5).

In contrast to the knee and ankle, the hip experienced extension throughout the entire stance period in both the gallop and acceleration. In acceleration, however, the rate of hip extension was greatest at the beginning and end of stance, whereas in the gallop it was greatest during midstance (Fig. 5). The mean hindlimb angle was significantly more retracted in the first step of acceleration than in the gallop. The hindlimb was also more retracted at touchdown and takeoff during the first step (Table 2).

Joint angles compared between lead and trailing hindlimbs in galloping

At the onset of stance, the lead hindlimb had a more flexed hip and a more extended knee and ankle than trailing hindlimb (Table 2). In fact, the hip of the trailing hindlimb remained more extended throughout the entire stance while the trailing hind knee remained more flexed. By contrast, the ankle angles at maximum flexion and at takeoff did not differ significantly between the two hindlimbs.
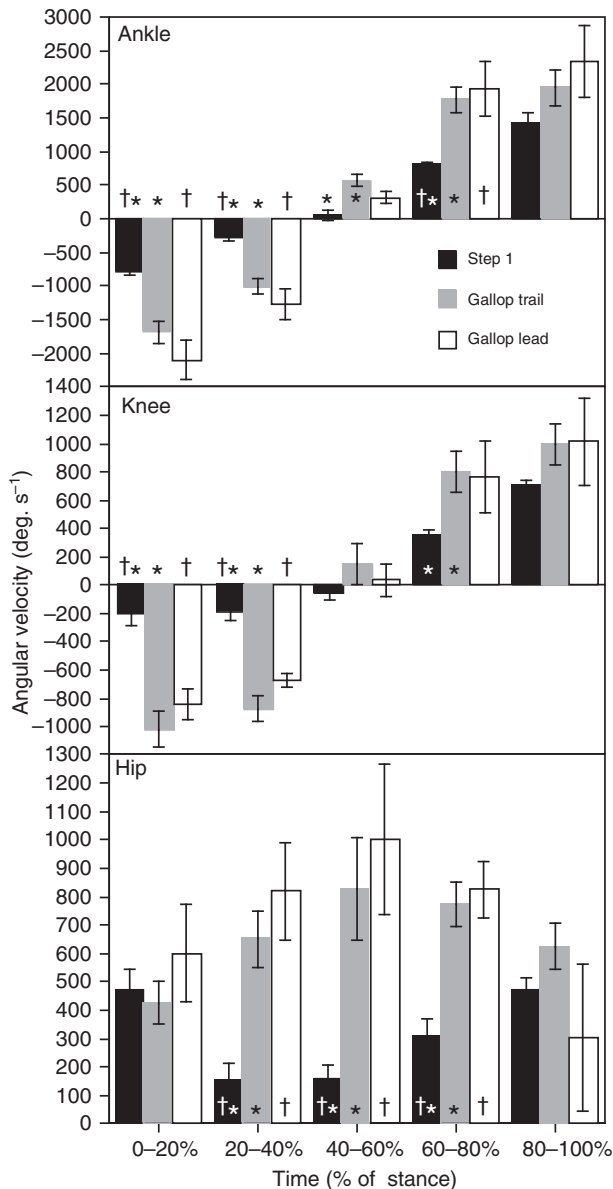
Fig. 5. Angular velocity for hindlimb angles in degrees per second averaged over each of five sections of stance. Step one, black bars; lead hindlimb for the gallop, white bars; trailing hindlimb for the gallop, grey bars. Error bars show the standard errors for five dogs for step one and the trailing hindlimb and three dogs for the lead hindlimb. The same symbols above bars denote significant differences between limbs or steps for each section of stance.

Back angles compared between acceleration and galloping

During the first step of acceleration, the pitch angle of the anterior back was much lower at the beginning of hindlimb stance (i.e. dogs backs were angled head-end down) than during high-speed galloping (Figs 2 and 6, Table 2). The torso then rotated head-end up through a greater angular excursion during the initial phases of hindlimb stance, such that by the end of hindlimb stance the pitch angle of the anterior back was only slightly lower in the first step than in the high-speed gallop. The lower back tended to pitch head-end up during stance in acceleration, whereas it leveled out or became more horizontal during hindlimb stance in the gallop (Fig. 6).

Ground reaction forces

Figures 7 and 8 show the footfall sequences and ground forces applied for dogs A and G, a 33.1 kg Labrador retriever and a 7 kg Shih tzu, respectively. The Shih tzu applied relatively greater forces with the forelimbs and its step sequence occurred over a shorter time scale. In other aspects, however, such as the timing of the footfalls relative to one another and the shapes of the force curves, the two traces are remarkably similar considering the large differences in size and shape of the two dogs.

Maximum vertical forces applied by the forelimbs in the first and second strides were only about 30% and 42%, respectively of those applied during the gallop (Table 3, Fig. 7). Although the contact times of the forelimbs during acceleration were longer than for galloping, their vertical impulses were still lower because of the greater effect of the low mean vertical forces. Their propulsive impulses in the first and second strides were about 70 and 50% as large as their vertical impulses. Nevertheless, the peak accelerating forces were not significantly different from those applied by the forelimbs in the high-speed gallop (Table 3, Figs 7 and 8). No braking forces were applied with the forelimbs during the first two accelerating strides.

Both mean and maximum vertical forces applied by the hindlimbs increased as dogs progressed from the initial pushoff into the gallop (Table 3, Figs 7 and 8). This increase in vertical force, however, was paralleled by a proportionately greater decrease in contact time with increased velocity such that the vertical impulse decreased with progressive steps. By contrast, mean and maximum propulsive forces applied by the hindlimbs decreased as dogs progressed into the gallop, with the exception that both were greater in the first step than in the initial hindlimb pushoff. Three of the dogs had no braking forces in the first two accelerating strides and the braking forces applied by the other four dogs were negligible, having peak values of only 1% and 2% of body weight for the first and second strides, respectively. In fact, the hindlimbs' net ground reaction force vector maintained a strikingly similar propulsive orientation throughout stance (Table 3, Fig. 2).

DISCUSSION
Postural changes during maximum acceleration

Dogs began accelerations by flexing the knee and ankle joints to drop into a crouched posture (Figs 1 and 3). This crouching could enhance storage of strain energy by pre-stretching extensor muscles and tendons in the hindlimbs and thereby increase the propulsive work done during pushoff. Muscles produce greater force and do more work when exposed to a rapid pre-stretch prior to contraction due to potentiation of the contractile tissue and to the contribution of stretch reflexes (Cavagna et al., 1968; Dietz et al., 1979; Heglund and Cavagna, 1985). Stretching the tendons also stores elastic strain energy that could be released later in the pushoff to increase the positive work done.

In the pushoff and first strides the ground force was greatest at the end of the stance period when the angular velocities of the hindlimb joints were greatest (Figs 5, 7 and 8). The ability of muscles to produce force, however, decreases with increased contraction velocity (Fenn and Marsh, 1935). One possibility is that the extensor muscles produced lower forces than they were capable of at the beginning of stance. It seems more probable that a low mechanical advantage at the beginning of stance caused much of the force applied by the ankle extensors to stretch in series tendons rather then immediately extending the ankle (Roberts and Marsh, 2003). This would have stored elastic strain energy that could have been released at the end of stance as a power amplification mechanism. Although the mechanical advantage at the ankle joint was not
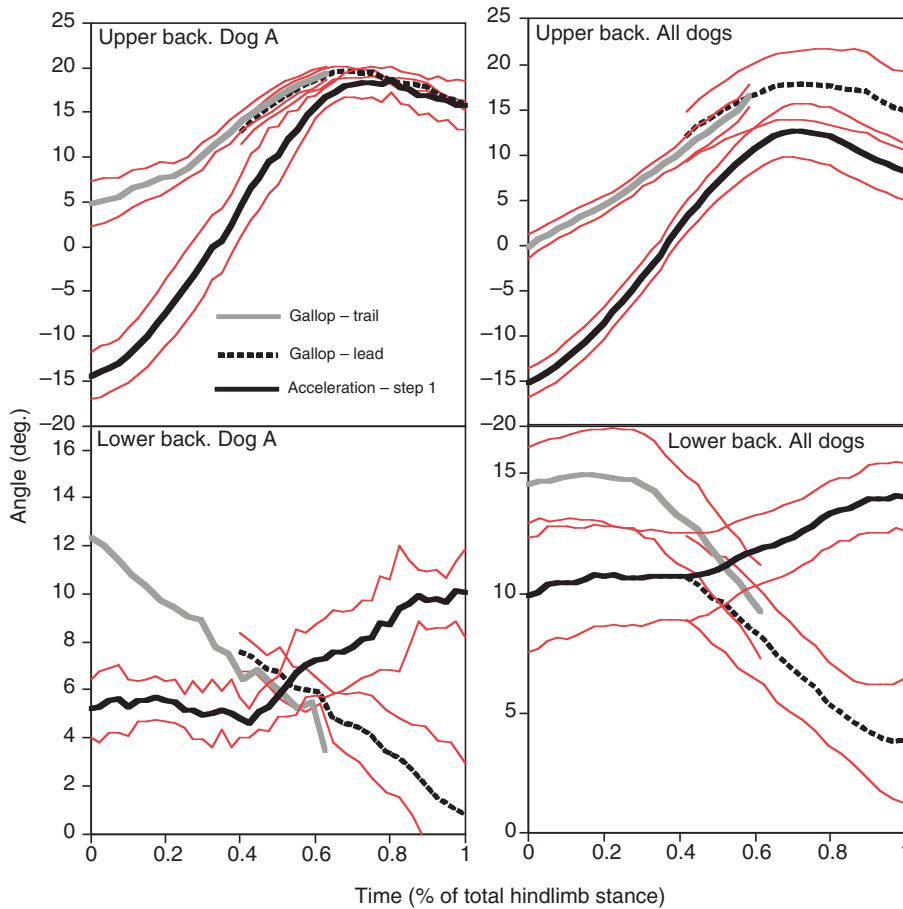
Fig. 6. Mean back angles from dog A and the average back angles from dogs A–E plotted over total hindlimb stance. For the gallop, time=0 at the beginning of trailing hindlimb stance and time=1 at the end of lead hindlimb stance. Lines are colored as in Fig. 3.

measured in this study, changes in mechanical advantage during stance in galloping and jumping dogs would facilitate such elastic storage (Carrier et al., 1998; Gregerson and Carrier, 2004). Use of tendons for power amplification at the ankle joint has been demonstrated in jumping frogs and humans and is also likely to occur in accelerating turkeys (Roberts and Marsh, 2003; Kurokawa et al., 2003; Roberts and Scales, 2002). These tendons increase the positive work done by muscles by decoupling their contraction velocities from joint extension velocities and allowing them to

operate at a better position on the force–velocity curve (Fenn and Marsh, 1935; Roberts and Marsh, 2003). This allows greater force to be produced in the later part of stance when joints are extending more rapidly (Roberts and Marsh, 2003).

In addition to stretching limb muscles and tendons, adopting a crouched posture could be advantageous in that it brings the pelvic and pectoral girdles closer to the ground. This would allow animals to extend their limbs farther posteriorly relative to their trunks while maintaining ground contact, increasing the distance over which their

Table 3. Mean ground force measurements for acceleration and galloping

		Stance time (ms)	Maximum forces (BW)		Mean forces (BW)		Force impulses (BW ms^{-1})		Mean force vector angle (deg.)
			Vertical	Propulsive	Vertical	Propulsive	Vertical	Propulsive	
Hindlimb	Pushoff	285±16	0.69±0.02	0.55±0.04	0.44±0.02	0.34±0.03	125.7±8.1	93.3±6.8	54±2.0
	Step 1	160±11	0.92±0.03	0.65±0.05	0.60±0.02	0.41±0.03	96.2±6.5	63.4±3.8	57±1.8
	Step 2	133±11	1.01±0.04	0.57±0.03	0.64±0.02	0.34±0.03	85.2±6.6	43.2±2.6	63±1.8
	Gallop lead*	71.5±3.2	1.64±0.11	0.46±0.07	0.99±0.07		70.0±4.2	13.0±2.22	
	Gallop trail*	74.3±4.0	1.47±0.09	0.38±0.05	0.94±0.07		68.6±3.8	10.7±1.85	
Forelimb	Step 1 trail (N=4)	255±21	0.60±0.07	0.41±0.04	0.33±0.04	0.23±0.02	80.1±12.0	57.3±7.6	54±2.0
	Step 1 lead	174±15	0.63±0.08	0.45±0.04	0.37±0.05	0.27±0.02	62.5±6.6	42.1±4.3	55±2.0
	Step 2 trail (N=5)	124±13	0.95±0.08	0.47±0.03	0.53±0.04	0.27±0.02	64.4±4.4	32.8±2.4	60±1.4
	Step 2 lead	117±8.3	0.86±0.08	0.43±0.03	0.51±0.04	0.27±0.02	58.7±4.8	31.2±1.9	59±1.4
	Gallop lead*	74.5±4.6	2.12±0.10	0.44±0.04	1.25±0.07		91.7±3.0	10.8±0.90	
	Gallop trail*	70.8±5.0	2.23±0.13	0.49±0.04	1.31±0.08		91.8±4.0	12.3±0.75	

Stance times are in milliseconds, forces are in body weights (BW), and impulses are in body weight per milliseconds (BW ms^{-1}). The mean force vector angle was calculated by averaging the instantaneous force vector angles over the stance period. *Values for galloping are taken from a previous study (Walter and Carrier, 2007), and are means and standard errors for six dogs, five of which were also used in this study. Other values are means and standard errors for seven dogs unless otherwise noted.
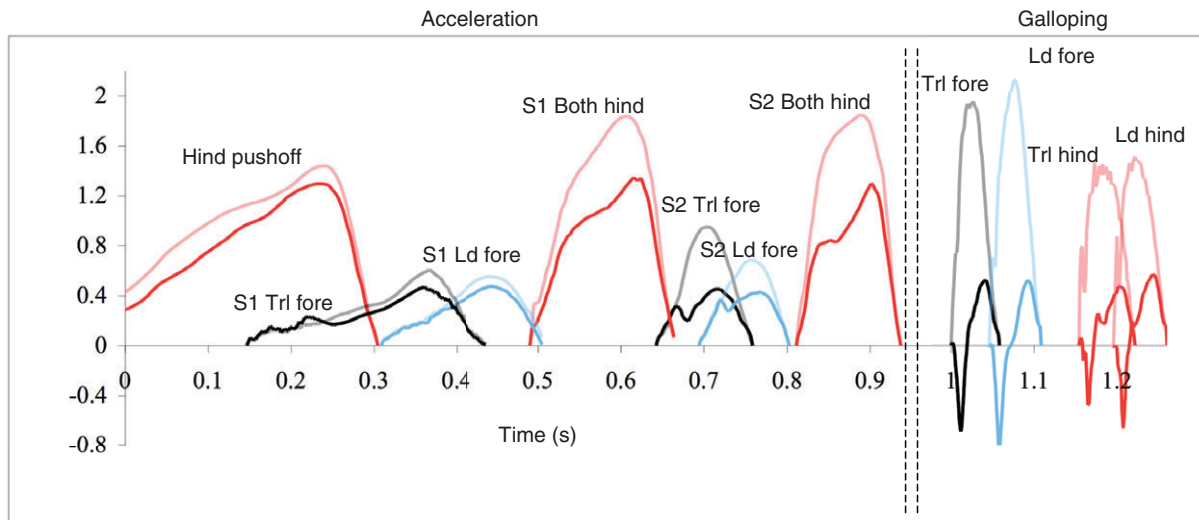
Fig. 7. Ground reaction forces plotted over time for the hindlimb pushoff, first two strides, and the full-speed gallop from dog A. Note the large increase in vertical forces and the decrease in stance period that occur as dogs progress from the first strides into the gallop. Heavy lines show propulsive forces and light lines show vertical forces. Lines show the means and standard deviations from five trials unless otherwise indicated. For step 1 there was only one trial from this dog for the trailing forelimb and only four trials for the lead forelimb. Lines are colored as follows: orange, both hindlimbs combined (acceleration), lead and trailing hindlimb (galloping); black, trailing forelimb; light blue, lead forelimb. S1 and S2, strides 1 and 2; Ld, lead; Trl, trailing.

body could travel while their limbs applied propulsive ground reaction forces and the propulsive work done (Biewener, 1983). This increase in the distance traveled by the center of mass during ground contact would also increase the contact time and thereby increase the propulsive impulse. Additionally, as the moment arm for applying a purely propulsive force is approximately the vertical distance of the joint to the ground, crouching increases the mechanical advantage for applying propulsive forces by shortening the muscles' out-levers. Because accelerating dogs are simultaneously applying vertical forces, this would not always decrease the net moment arm at the hip and ankle. It would however, decrease the net moment arm at the knee throughout acceleration (Fig. 2). Smith and Savage (Smith and Savage, 1956) discuss how this decrease in the horizontal force out-lever would allow a fossorial mammal to dig more forcefully, however, it could also enable a crouched mammal to produce a greater propulsive thrust in acceleration.

Dogs maintained a crouched posture over the first strides of acceleration. Their ankles and knees were more flexed than during constant speed galloping (Table 2, Figs 1–4). Whereas, the ankle extended fully at the end of the first stance period, the knee remained about 20 deg. more flexed than in a gallop. This is a surprising result given that, (1) the knee is an important joint in positive work production in galloping and jumping, (2) dogs fully extend the knee at takeoff during these activities, and (3) unlike in bipeds, in dogs the moment at the knee joint at the end of stance is positive in acceleration such that knee extension produces positive work (Fig. 2) (Alexander, 1974; Gregersen et al., 1998; Gregersen and Carrier, 2004; Jacobs and Van Ingen Schenau, 1992; Jacobs et al., 1996; McGowan et al., 2005; Roberts and Scales, 2004). It is possible that the forward facing orientation of the knee restricts the amount of knee extension possible while a low center of mass is maintained. During acceleration, maintaining a low center of mass at the end of hindlimb stance could facilitate the simultaneous touchdown of the forelimbs and the onset of their propulsive force production.

In addition to adopting a more crouched posture, accelerating dogs also underwent greater pitching of the trunk (Table 2; Figs 1,

2 and 6). They began the first hindlimb step with the anterior portion of their trunks pitched sharply head-end down. Their trunks then pitched head-end up through an angular excursion of about 28 deg., so as to finish stance at a similar angle as in the high-speed gallop. Beginning hindlimb stance with the anterior back pitched downward could simply be a mechanism of compensating for the head-end up rotation caused by the ground reaction force of the hindlimbs, which is directed in front of the center mass during the first part of stance (Fig. 2). It could, however, provide additional benefits such as raising the hind end and increasing the vertical clearance for the hindlimbs. This would allow them to be brought further forward under the body prior to the onset of stance, and could thereby increase stride length. The head-end down pitch at the beginning of hindlimb stance would also lower the center of mass and could help bring the ground force vector closer to it.
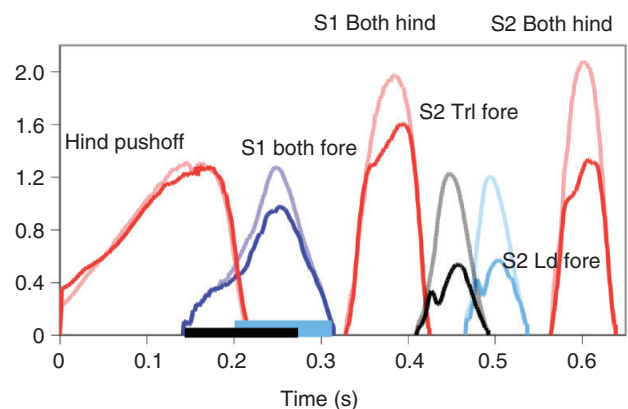

Fig. 8. Ground reaction forces plotted over time for the hindlimb pushoff and first two strides from dog G. Line widths and colors are the same as for Fig. 7. It was not possible to obtain a separate force record for the trailing forelimb in the first stride for this dog, so the forces of the two forelimbs are combined in the trace. Black and light blue bars beneath the force curve show the stance times for the trailing and lead forelimbs of the first stride, respectively. S1 and S2, strides 1 and 2; Ld, lead; Trl, trailing.

To the extent that muscle power limits how rapidly dogs can accelerate, it would seem optimal for dogs maximize the proportion of their muscular work that is transferred into linear kinetic energy. To this end, pitching of the torso would seem to be wasted motion. Although the torso of a galloping horse only pitches through a 19 deg. angular excursion during the stride cycle, the fluctuation in internal mechanical energy resulting from this pitching was measured to be about 1000 J, which was 10% as large as the total fluctuation in external mechanical energy over the stride (Pfau et al., 2006). The muscular work required for pitching is proportional to the angular displacement, which was 38% greater when dogs accelerated than when they galloped at steady state. In galloping horses, the muscular work expended in this pitching may be reduced through conversions between potential energy and rotational kinetic energy (Pfau et al., 2006). Accelerating dogs may also convert part of their rotational kinetic energy into potential energy or linear kinetic energy. In absence of such an energy exchange, the muscular work expended in pitching would seem to detract from the work available for linear acceleration. However, the location of dogs' centers of mass relative to their limbs may make pitching unavoidable during rapid acceleration, limiting how effective they can be in converting muscle force into linear acceleration.

Vertical forces

Dogs applied much lower vertical forces during the first strides of 'maximum' acceleration than when galloping at high speed. This resulted in greater duty factors during acceleration such that the support phases of the two hindlimbs overlapped almost entirely and there was also some overlap between hindlimb and forelimb support (Figs 7 and 8). By contrast, during high-speed galloping (Walter and Carrier, 2007), both fore and hindlimb support were succeeded by flight phases, and the average overlap in support between the two hindlimbs was only about 20% of the total hindlimb stance time (Fig. 7). Duty factors during acceleration were also greater than those for dogs trotting or pacing steady-state at similar speeds (Maes et al., 2008). Similarly, human sprinters had greater duty factors during acceleration than sprinters running steady-state at similar speeds (Johnson and Buckley, 2001; Weyand et al., 2000). Whereas top speed in human sprinters is strongly correlated with the mean vertical force they apply during contact, lower vertical forces may be optimal during the acceleration phase (Weyand et al., 2000; Hunter et al., 2005). In acceleration, longer flight phases may be disadvantageous because propulsive ground forces cannot be applied during these periods. In fact, the optimal flight phase duration during acceleration may be the minimum amount of time required to reposition the limbs (Hunter et al., 2005).

Propulsive forces

The hindlimbs played a greater role in acceleration than the forelimbs, as has been described previously (Table 3, Figs 7 and 8) (e.g. Bryant et al., 1987). The forelimbs did, however, make a significant contribution to the accelerating impulse during the first strides, providing 43% of the total propulsive impulse in the first and second strides. Despite this contribution, maximum propulsive forces applied by the forelimbs in the first accelerating strides did not differ significantly from those applied by the forelimbs in the high-speed gallop (Walter and Carrier, 2007). The forelimbs produced no decelerating forces in the first strides and braking forces in the hindlimbs were either completely absent or miniscule. Similarly, turkeys produced little or no braking forces during rapid accelerations (Roberts and Scales, 2002). By contrast, human sprinters applied braking forces up to 0.44 body weight in the first

step out of the blocks, which decreased their forward velocity by 4.8%. This braking force is applied despite their centers of mass being ahead of the ground contact point at foot touchdown (Mero, 1988). Such a braking force, oriented behind the center of mass, would induce a head-end down pitching moment, which may be necessary in order for humans to maintain their forward angled body posture during acceleration. Accelerating humans may also be limited by the internal work necessary to reposition the legs for the next stride. Because of the short flight phases during acceleration there may be less time to reposition the limbs than in high-speed running. If humans were unable to reposition the leg and begin swinging it backward to match ground speed prior to touchdown, the inertia of the limbs would cause a braking force upon ground contact. As quadrupeds, dogs may have more time to reposition their limbs while still applying propulsive forces. In addition, the legs of dogs and turkeys have relatively lower inertia than those of humans and would require less power to rapidly reposition.

Mass distribution and balance

To avoid net pitching of the torso during locomotion, a quadruped's net ground reaction force vector must pass through its center of mass. Whereas in steady state locomotion the average force vector over the course of a stride is directed vertically, in acceleration it is directed forward. Thus, to avoid a pitching moment during acceleration quadrupeds must shift the origin of the ground force vector posteriorly. Lee et al. (Lee et al., 1999) proposed two methods by which this shift could be accomplished. First, quadrupeds could alter the fore- to hindlimb force distribution ratio such that a greater proportion of the vertical force is applied by the hindlimbs. Second, they could use a more retracted limb posture such that the origin for both fore- and hindlimb forces would be further back (Lee et al., 1999).

During small accelerations, trotting dogs used primarily the first method, decreasing the proportion of the total vertical force applied by the forelimbs (Lee et al., 1999). During these accelerations, the dogs applied only about 50% of the total vertical force with the forelimbs, whereas when standing still and galloping or trotting at steady-state dogs support between 56 and 65% their body weight with their forelimbs as a result of the relatively anterior position of the center of mass (Lee et al., 1999; Lee et al., 2004; Bryant et al., 1987; Walter and Carrier, 2007). By contrast, during the first two strides of 'maximum effort' accelerations, the deviation from steady-state load distribution was more extreme with the dogs supporting only 43% of their body weight with their forelimbs (Table 3).

Lee et al. (Lee et al., 1999) derived the following formula to determine the shift in vertical force distribution required to balance out the head-end up pitching moment incurred by a given net accelerating force:

$$R - R_0 = A_y D ,$$

where $R–R_0$ is the change in vertical force distribution from steady-state, A_y is the mean body weight normalized propulsive force and D is the ratio of center of mass height to trunk length. Based on this formula, Lee et al. (Lee et al., 1999) determined that the head-end down pitching moment induced by the shift in vertical force distribution during acceleration in trotting dogs was sufficient to account for the head-end up pitching caused by the acceleration. The dogs in the study of Lee et al. (Lee et al., 1999) applied accelerating forces ranging from about –0.18 to 0.16 body weights and had differences in fore–hind load ($R–R_0$) from stead-state between –0.1 and 0.12. By contrast, dogs in this study applied mean

accelerating forces of about 0.3 body weights with each foot, whereas the difference in fore–hind load from steady state was only 0.14. If we assumed that our dogs had a similar value for $D \approx 0.7$, as did the greyhounds and Labradors studied by Lee et al. (Lee et al., 1999), a change in vertical force distribution of 0.21 would have been required to balance out the head-end up pitch incurred by the accelerating forces. Thus, for our dogs to balance out the entire head-end up pitching moment by altering the vertical force ratio, they would have had to apply 64% of the total vertical force with the hindlimbs, rather than only 57%. Such a distribution of vertical forces would probably limit the ability of the forelimbs to apply propulsive forces.

Thus it appears that dogs did not compensate entirely for the head-end up pitching moment with a fore- to hindlimb shift in vertical force distribution. This would suggest that either they used another method of balancing out the pitching moment, such as using more retracted limb angles, or they incurred greater pitching moments. Our measurements of hindlimb angles show that dogs did use a more retracted limb posture during acceleration than during high speed galloping (Table 2). Furthermore, they applied peak vertical forces later in the stance period when the limbs were more retracted, as do accelerating humans and turkeys (Roberts and Scales, 2002; Cavanga et al., 1971) (Fig. 7). This would have further increased the effective limb retraction angle for force application. Despite their rearward shift in vertical force distribution and use of more retracted limb angles, dogs' torsos pitched through greater angular excursions during acceleration than during high-speed galloping (Fig. 6). Increased pitching of the torso may be unavoidable if dogs are to maximize the propulsive forces they produce.

Conclusions

Whereas it is inherent that the fore–aft forces applied during acceleration must differ from those in constant speed galloping, we found that accelerating dogs also differed from dogs running at constant speed in their body postures and the vertical forces they applied. Accelerating dogs used more crouched and more retracted limb postures. Using a more crouched limb posture during acceleration could help direct a forward angled ground reaction force vector through the center of mass. It would also increase the mechanical advantage for the application of propulsive forces by bringing limb girdles closer to the ground and the joints more in line with the ground force vector. Using a more retracted limb posture would help dogs better align the propulsive ground reaction force vector with the limb axis and with the center of mass.

The dogs' torsos underwent greater pitching motion during acceleration. This increased pitching may be unavoidable if dogs are to maximize the propulsive impulses they apply. Mean and maximum vertical forces were lower during acceleration, causing duty factors to be greater. This would be advantageous in that propulsive forces can only be applied during contact phases. Accelerating dogs applied a greater portion of the vertical forces with the hindlimbs, thereby reducing the head-end up pitching moment incurred by the application of net propulsive forces.

REFERENCES

Aerts, P., Van Damme, R., D'Août, K. and Van Hooydonck, B. (2003). Bipedalism in lizards: whole-body modeling reveals a possible spandrel. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **358**, 1525-1533.

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

Biewener, A. A. (1983). Allometry of quadrupedal locomotion: the scaling of duty factor, bone curvature, and limb orientation to body size. *J. Exp. Biol.* **105**, 147-171.

Bret, C., Rahmani, A., Dufour, A. B., Messonnier, L. and Lacour, J. R. (2002). Leg strength and stiffness as ability factors in 100m sprint running. *J. Sport Med. Phys. Fitness.* **42**, 274-281.

Bryant, J. D., Bennett, M. B. and Alexander, R. M. (1987). Forces exerted on the ground by galloping dogs (*Canis familiaris*). *J. Zool. Lond.* **213**, 193-203.

Carrier, D. R., Gregersen, C. S. and Silverton, N. A. (1998). Dynamic gearing in running dogs. *J. Exp. Biol.* **201**, 3185-3195.

Cavagna, G. A., Dusman, B. and Margaria, R. (1968). Positive work done by a previously stretched muscle. *J. Appl. Physiol.* **24**, 21-32.

Cavagna, G. A., Komarek, L. and Mazzoleni, S. (1971). The mechanics of sprint running. *J. Physiol.* **217**, 709-721.

Chelly, S. M. and Denis, C. (2001). Leg power and hopping stiffness: relationship with sprint running performance. *Med. Sci. Sports Exerc.* **33**, 326-333.

Dietz, V., Schmidtbleicher, S. and Noth, J. (1979). Neuronal mechanisms of human locomotion. *J. Neurophysiol.* **42**, 1212-1222.

Fenn, W. O. and Marsh, B. S. (1935). Muscular force at different speeds of shortening. *J. Physiol.* **85**, 277-297.

Gregerson, C. S. and Carrier, D. R. (2004). Gear ratios at the limb joints of jumping dogs. *J. Biomech.* **37**, 1011-1018.

Gregerson, C. S., Silverton, N. A. and Carrier, D. R. (1998). External work and the potential for elastic storage at the limb joints of running dogs. *J. Exp. Biol.* **201**, 3197-3210.

Heglund, N. C. and Cavagna, G. A. (1985). Efficiency of vertebrate locomotor muscles. *J. Exp. Biol.* **115**, 283-292.

Hunter, J. P., Marshall, R. N. and McNair, P. J. (2005). Relationship between ground reaction force impulse and kinematics of sprint-running acceleration. *J. Appl. Biomech.* **21**, 31-43.

Jacobs, R. and van Ingen Schenau, G. J. (1992). Intermuscular coordination in a sprint push-off. *J. Biomech.* **25**, 953-965.

Jacobs, R., Bobbert, M. F. and van Ingen Schenau, G. J. (1993). Function of mono- and biarticular muscles in running. *Med. Sci. Sport Exer.* **25**, 1163-1173.

Jacobs, R., Maarten, F. B. and van Ingen Schenau, G. J. (1996). Mechanical output from individual extensor muscles during explosive leg extensions: the role of biarticular muscles. *J. Biomech.* **29**, 513-523.

Johnson, M. D. and Buckley, J. G. (2001). Muscle power patterns in the mid-acceleration phase of sprinting. *J. Sport Sci.* **19**, 263-272.

Kuitunen, S., Paavo, K. V. and Kyröläinen, H. (2002). Knee and ankle joint stiffness in sprint running. *Med. Sci. Sports Exerc.* **34**, 166-173.

Kurokawa, S., Fukunaga, T., Nagano, A. and Fukashiro, S. (2003). Interaction between fascicles and tendonous structures during counter movement jumping investigated *in vivo*. *J. Physiol.* **95**, 2306-2314.

Lanczos, C. (1956). *Applied Analysis*. London: Isaac Pitman and Sons.

Lee, D. V., Bertram, J. E. 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.

Maes, L. D., Herbin, M., Hackert, R., Bels, V. and Abourachid, A. (2008). Steady locomotion in dogs: temporal and associated spatial coordination patterns and the effect of speed. *J. Exp. Biol.* **211**, 138-149.

McGowan, C. P., Baudinette, R. V. and Biewener, A. A. (2005). Joint work and power associated with acceleration and deceleration in tammar wallabies (*Macropus eugenii*). *J. Exp. Biol.* **208**, 41-53.

Mero, A. (1988). Force-time characteristics and running velocity of male sprinters during the acceleration phase of sprinting. *Res. Q. Exerc. Sport* **59**, 94-98.

Mero, A., Luhtanen, P. and Komi, P. V. (1983). A biomechanical study of the sprint start. *Scand. J. Sport. Sci.* **5**, 20-28.

Pfau, T., Witte, T. and Wilson, A. M. (2006). Center of mass movement and mechanical energy fluctuation during gallop locomotion in the Thoroughbred racehorse. *J. Exp. Biol.* **209**, 3742-3757.

Roberts, T. J. and Marsh, R. L. (2003). Probing the limits to muscle-powered accelerations: lessons from jumping bullfrogs. *J. Exp. Biol.* **206**, 2567-2580.

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

Roberts, T. J. and Scales, J. A. (2004). Adjusting muscle function to demand: joint work during acceleration in wild turkeys. *J. Exp. Biol.* **207**, 4165-4174.

Smith, J. M. and Savage, R. J. G. (1956). Some locomotory adaptations in mammals. *Zool. J. Linn. Soc. Lond.* **42**, 603-622.

Walter, R. M. and Carrier, D. R. (2007). Ground forces applied by galloping dogs. *J. Exp. Biol.* **210**, 208-216.

Weyand, P. G., Sternlight, D. B., Belizzi, M. J. and Wright, S. (2000). Faster top running speeds are achieved with greater ground forces not more rapid leg movements. *J. Appl. Physiol.* **89**, 1991-1999.