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SPEED CONTROL IN QUADRUPEDAL LOCOMOTION: PRINCIPLES OF LIMB COORDINATION IN THE DOG

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Abstract. Long distance, overground locomotion in the dog was observed and analyzed using the two dimensional gait diagram method. Though the velocity of locomotion chosen by the animals over a 1,000 m course varied, a preferred speed generally emerged and was used during most of the experiment. This animal-specific preferred overground velocity was strongly correlated with the animal's limb lengths, and corresponded to the minimum observed swinging velocity of the limbs. Changes in the pattern of limb coordination during three-limb locomotion were also investigated. Depending upon which limb was restrained, dogs used trot-like or gallop-like gaits which exhibited the same temporal and spatial phase differences as were observed during normal locomotion. However, stride length and swing-stance durations were increased relative to those observed in four legged locomotion. Animals with an additional 2 kg weight trotted slowly, but no significant changes in limb movement parameters were found. Locomotion studies performed in darkness resulted in an immediate switch from asymmetrical (galloping) to symmetrical gaits (walking and trotting). These gaits allow for precise foot placement.

INTRODUCTION

During locomotion, an animal's limbs create a closed kinematic system which must perform three basic functions: (i) propulsion, (ii) support, and (iii) shock absorption (26). In order to successfully carry out these functions, interlimb coordination must provide a smooth velocity of locomotion with a high margin of active equilibrium. As observed by Muybridge (20) (and later formalized by Howell (16)), quadrupedal locomotion can be separated into two categories: (i) symmetrical and (ii) nonsymmetrical. Symmetrical gaits include walking, trotting and pacing, whereas different gallops would be classified as nonsymmetrical patterns of quadrupedal locomotion. Particular gaits in different species have been formally described by many investigators (9, 11, 15, 16, 20). However, many questions still remain unanswered. One of these is the relation between a given gait pattern and its range of velocities. Limited resources of metabolic energy force the animal to develop gaits that minimize energetic losses (e.g., 5, 7, 22). However, such activities as escape from predators or the capture of prey require extremely rapid movement that is not energetically conservative. Therefore, two general strategies of locomotion may be distinguished: (i) those which minimize energy consumption and (ii) those which maximize velocity. The choice of which strategy to use depends upon the behavioral context. Under most conditions, and especially during long distance locomotion, the animal relies on the first strategy. This principle, a sort of biological "conservation of energy" law, was anticipated by Marey (17) a century ago. The second strategy (maximizing of velocity) is, as was stated above, used either during hunting or escape from predators, where survival, and not energy conservation is the main consideration.

Energy cost per unit distance appears, then, to be one of the most important determinants of the parameters of limb movement and interlimb coordination (19). Alexander (5) calculated that running is energetically more efficient than walking. Based upon these calculations, Alexander predicted that work associated with limb displacement during the swing phase should be negligible in walking but significant at the faster gaits. However, Taylor et al. (22) experimentally demonstrated that the work done against the inertia of the limbs is not a very large factor in determining the metabolic cost of running. They measured the rate of oxygen consumption in cheetahs, gazelles, and goats while running on a treadmill. These animals are very similar in body weight and limb lengths, but differ slightly in the average distance between the center of mass and the pivot point for their respective limbs (i.e., the moment of inertia). The rate of oxygen consumption (which corresponds to the energetic cost of locomotion) at a given speed was observed to be the same for all animals. If work related to limb movement contributes strongly to total energy expenditure, then a preference for some optimum range of limb movement parameters should be observed.

In this study we wished to determine whether there was any preferred gait or range of speeds for long-distance locomotion in the dog, and if so, what were the corresponding optimum limb movement parameters (e.g., swing-stance duration, limb movement amplitude, etc.) for each gait. We were also interested in determining whether there were any constant relationships between these limb movement parameters and velocity of locomotion in different quadrupedal gaits.

METHOD

Ten mongrel dogs, of different sizes and weighing between 7 and 24 kg (Table I), were examined. The dogs were trained to move along an experimental platform 8 m long and 1 m wide. During each experiment, the animal was required to complete over 125 trials or runs, each trial consisting of uninterrupted locomotion along the full length of the pathway. Each trial was reinforced with 2 g of ground meat, so that the intertrial breaks were as short as possible. The gait and velocity of locomotion were not forced by the experimenters, but were decided solely by the animal.

TABLE I

Decomposition of gaits used by a given animal over a full experiment

Dog	Body weight (kg)	Hind-limb length*	Total number of run where the animal used		
			Walking	Trotting	Galloping
N1	19.6	0.39	32	111	136
N2	12.0	0.31	20	324	109
N3	14.4	0.29	35	452	60
N4	22.0	0.43	12	361	6
N5	15.0	0.28	26	286	48
N10	7.8	0.30	10	262	95
N12	13.5	0.34	10	310	0
N13	24.0	0.44	41	217	8
N15	19.0	0.34	12	290	0
N16	13.0	0.31	10	162	339

* Measured as the distance from the ground to the hip during a normal stance.

The experimental platform was made from soft conductive wire mesh. The ends of the mesh were connected to an 80 mV dc power supply so that the voltage drop along the mesh platform was linear. The time of foot contact, as well as its position on the platform (for all four limbs), could therefore be measured using specially designed contact electrodes. The electrodes were fixed to the pad of the third digit of each foot. Stance phase was recorded as a square pulse whose amplitude was proportional to the distance along the runway (i.e., the voltage at that point) and its width depended on the stance duration (T_{st}). The interval between successive pulses (the base line) indicates swing (T_{sw}). The difference between the amplitudes of two successive pulses for a particular limb determines stride length (L). Such a sequence of pulses recorded simultaneously for all four legs creates a two-dimensional gait diagram (2-D diagram). Using such measurements the following parameters could then be computed (defined below): (i) step length (l); (ii) mean velocity of locomotion during a trial (v); (iii) and (iv) temporal- and spatial- phase differences between limb movements; (v) limb velocity during swing phase (vs); (vi) duty factor (df). The 2-D gait diagram method has been described in detail in our previous papers (2, 3). In these experiments parameters of locomotion were determined from the diagrams which allowed us to calculate stride length with accuracy better than ±10% whereas an error of the temporal limb movement parameters never exceeded ±5%.

Stride length is simply the distance covered by the limb between successive footfalls. The step length is the amplitude of limb movement if the limb pivot point (or joint) were stationary and is given by the following relationship:

$$l = L - v\,(T_{sw} + T_{ds}), \tag{1.1}$$

where: T_{ds} is the double support time duration.

For symmetrical gaits where at least one foot is always on the ground, stride length is equal or greater to twice the step length ($L \geqslant 2l$).

Temporal phase difference (during steady-state locomotion) may be defined as the time interval between the centers of the pulses (stance phase) for two limbs during successive steps (ΔT) divided by the stride cycle (the sum of successive stance and swing epochs, $T = T_{st} + T_{sw}$).

$$\varphi t = \Delta T/T, \tag{1.2}$$

Similarly, to describe spatial limb coordination, we define the term spatial phase difference (φs) as the distance (Δl) between support points of a particular pair of limbs (e.g., the difference in amplitude for adjacent pulses for RF and RH) divided by a stride length (L) of one of the limbs (e.g., the difference in amplitude for successive pulses for RF alone).

$$\varphi s = \Delta l/L. \tag{1.3}$$

Duty factor is defined as the fraction of the stride cycle for which a foot was on the ground:

$$df = T_{st}/(T_{st} + T_{sw}). \tag{1.4}$$

Using 2-D diagrams, it is also possible to calculate velocity of locomotion. Total mean velocity of the animal during a run can be calculated either by dividing distance (8 m) by the duration time of the trial or, more precisely, by multiplying mean stride length by stride frequency, i.e.:

$$v = LF, \tag{1.5}$$

where:

$$F = l/(T_{st} + T_{sw}) = l/T. \tag{1.6}$$

Limb velocity during swing phase was calculated using the following equation:

$$vs = l/T_{sw} \tag{1.7}$$

For more information regarding the above presented definitions, see reference (2-4).

In order to further enhance our understanding of the control of interlimb coordination, we also examined the effects produced by several constraints. For example, we examined three-limb locomotion. This was obtained by restraining one of the animal's limb in the flexed position so that it could not be used to support the body. We also studied the result of attaching a 2 kg weight to the dog's trunk, as well as locomotion in the dark.

RESULTS

Locomotion speeds for examined dogs ranged between 0.5 and 5 m/s and included such typical gaits as walking, trotting and transverse galloping. Four of the animals also, on occasion, exhibited rotatory gallop. Upon reviewing the entire sequence of trials, it was possible to distinguish three characteristic periods of locomotor activity. The first, a period of intensified activity, was only observed during the first 5-30 trials. During this period, the subjects ran at high speeds, usually preferring gallop or the fastest trot. At the end of this period of intensified activity, gallop-trot and trot-gallop transitions were observed. During the next 80-100 trials, velocity of locomotion decreased and stabilized, so that the animals trotted at an almost constant speed. During this second period, preferred velocities ranged between 1.8 and 2.7 m/s, depending upon dog size (especially limb length). Finally, during the third period of extinguishing locomotor activity, the tired and satiated subjects began to slow down, usually to a walk. The session ended when the animal broke off the performance of the task.

Decomposition of gaits used by a given animal over a full experiment is given in Table I. The specific details within each period shall now be discussed.

The initiation of gait

During each experimental session, many types of gait initiation were observed, but only a few occurred frequently. One characteristic common to all gait initiations was that the relationships between swing and stance phases differed from those of steady state. Moreover, during the initial period of acceleration, limb movement frequencies could vary drastically, so that it was impossible to describe interlimb coordination with the same parameters (e.g., phase difference) used to describe locomotion at a constant speed.

The structure of gait initiation depended upon the final steady state gait pattern. During the initiation of walking (Fig. 1*A*), the animal typically leaned forward while simultaneously taking a short step with one of its forelimbs. For most of the animals examined, one of the forelimbs was favored in taking this initial step. However, depending upon animal posture, gait could be, on occasion, initiated by the hind limb. After the initial step by the forelimb, the diagonal hindlimb was lifted and the animal immediately fell into the typical footfall pattern of walking.

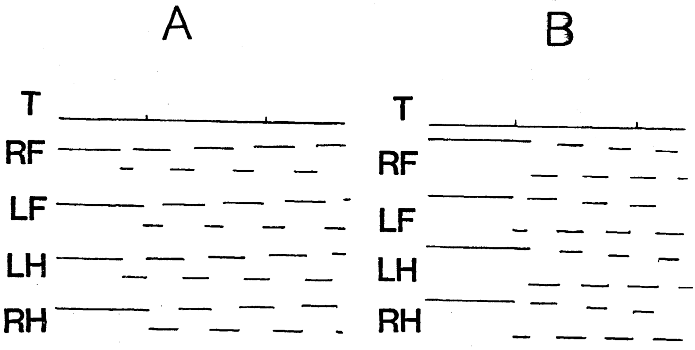

Fig. 1. A typical 2-D gait diagram of (A) walk initiation and (B) trot initiation (observed in dog N2). Tics in top trace of each diagram indicate one second interval. Subsequent traces show the sequence of swing (low level) and stances (high level) phases of the individual limbs: RF, right forelimb; LF, left forelimb; LH, left hindlimb; RH, right hindlimb.

During the initiation of trotting, the very first short step was performed by one pair of diagonal limb (e.g., LF and RH in Fig. 1*B*). The animal then fell immediately into the typical footfall pattern of trotting. Occasionally, a dog started walking and then, after a couple of strides, the walk-trot transition appeared.

Walk

This is a stereotypical gait used by dogs at the lowest velocities of locomotion. A typical 2-D gait diagram of a walking dog is shown in Fig. 2. Walking (between 0.5 and 1.5 m/s) was usually observed in tired or satiated dogs. The range of observed walking velocities depended primarily upon the animal's size. Smaller (shorter limbed) animals walked at lower velocities than did the larger ones. During steady state (constant velocity) walking, there were no significant differences in swing-stance durations for limbs of the same girdle. However, such differences did exist between hind and forelimbs. Generally, stance phase in the forelimbs was significantly longer then that in the hindlimbs. Whereas, forelimb swing phase was shorter than that in the hindlimbs, so that the total stride cycle for all limbs was the same. An increase in walking velocity caused a decrease in both swing and stance durations. Stride frequency mainly increased as a result of stance duration shortening. At the same time, significant increases in step and stride lengths was observed (Fig. 3). The same pattern of changes in these parameters were manifested in all experimental subjects.

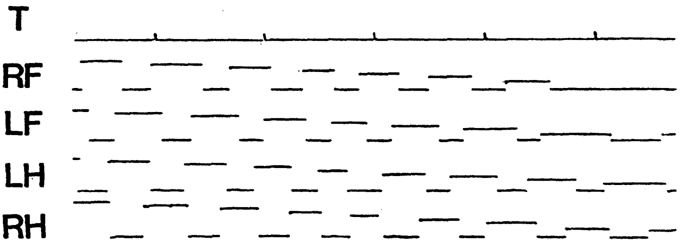

Fig. 2. A typical 2-D gait diagram of steady-state walking (observed in dog N13). Same notation as in Fig. 1.

Phase differences between unilateral and diagonal limbs during walking, as calculated from gait diagrams, did not vary significantly over the entire range of speeds and were independent of the animal's size. These phase differences were 0.3 and 0.2 for diagonal and unilateral pairs of legs respectively. However, a phase difference of 0.3 between right and left limbs was occasionally observed during walking ("diagonal walk"). Typical phase differences observed for walking are given in Table II. Spatial footfall patterns may be completely characterized by spatial phase differences. A comparison of both temporal and spatial phase differences during walking (0.76 m/s) in a typical dog is given in Table III. For this animal, spatial phase differences between unilateral legs ranged about a mean of 0.01, which means that the hindlimb were placed 6 mm in front of a support point of the unilateral forelimb.

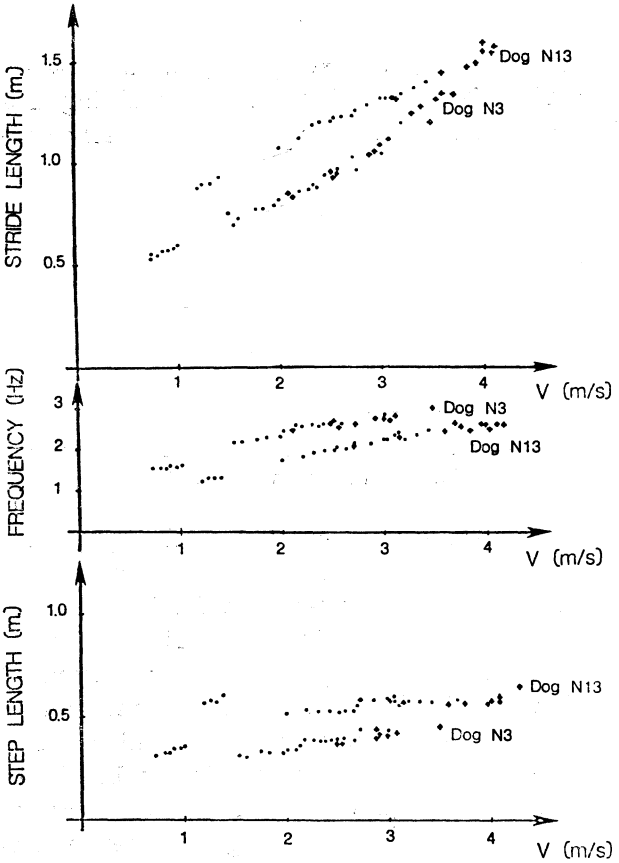

Fig. 3. Stride length (L), stride frequency (F) and step length (l) as a function of speed of locomotion (v) for two different size dogs (N3 and N13). Parameters for symmetrical gaits (walking and trotting) are marked by points while those for galloping are marked by crosses.

Stride length and stride frequency increased linearly as the velocity of walking was increased (Fig. 3). This increase in frequency appeared to be primarily due to a decrease in the duration of the stance phase. Duty factor in the walking dog ranged between 0.59-0.68.

TABLE II

Means of observed temporal phase differences during walking. RF, right forelimb; LF, left forelimb; LH, left hindlimb; RH, right hindlimb

Dog	Phase difference between the given pair of limbs						Speed range (m/s)
	RF/LF	RH/LH	RF/LH	RH/LF	RF/RH	LF/LH	
N1	0.50	0.51	0.30	0.32	0.21	0.19	0.7–1.1
N2	0.49	0.51	0.32	0.31	0.19	0.20	0.6–0.9
N3	0.51	0.48	0.28	0.27	0.24	0.21	0.5–0.9
N4	0.52	0.51	0.29	0.31	0.21	0.20	0.5–1.1
N5	0.50	0.51	0.32	0.30	0.19	0.22	0.5–0.9
N10	0.50	0.50	0.32	0.30	0.20	0.19	0.8–1.1
N12	0.48	0.49	0.29	0.32	0.19	0.19	0.6–0.8
N13	0.51	0.50	0.32	0.32	0.18	0.18	1.0–1.5
N15	0.50	0.50	0.30	0.30	0.21	0.20	0.6–0.9
N16	0.48	0.51	0.29	0.30	0.21	0.19	0.9–1.2

TABLE III

An example of the temporal φt, and spatial φs, phase difference observed during walking ($v = 0.76$ m/s, $L = 0.61$m) in dog N15 (for 14 strides)

Limb pair	φt (mean±SD)	φs (mean±SD)
RF/LF	0.50±0.01	0.49±0.06
RH/LH	0.50±0.01	0.51±0.07
RF/LH	0.30±0.02	0.50±0.06
LF/RH	0.30±0.02	0.51±0.08
RF/RH	0.21±0.01	−0.01±0.08
LF/LH	0.20±0.01	−0.01±0.07

Trot

In every dog examined, trotting always appeared at speeds ranging between 1.2 and 3.1 m/s. Though a very wide range of trotting velocities was observed, a given animal preferred a specific speed during long-distance locomotion. This speed was highly correlated with the dog's hind limb length ($r = 0.83$, $p < 0.05$). As with walking, all limb movement parameters were highly correlated with speed of locomotion (upper part of Table IV). Only the temporal phase differences between legs were invariant with the velocity. These phase differences during trotting are presented in Table V. Temporal phase differences between fore and be-

TABLE IV

Mean correlation coefficient *r*, between several kinematic parameters for trotting and galloping (sample size: 8 dogs, 100 trials). V, locomotion velocity; ST, stance duration; SW, swing duration; L, stride length

r	V−ST	V−SW	V−L	ST−SW	ST−L	SW−L
Trot	−0.94	−0.92	0.94	0.63	−0.89	0.76
Gallop	−0.86	0.02	0.93	−0.21	−0.76	−0.13

TABLE V

An example of the temporal φt, and spatial φs, difference observed during trotting (2.3 m/s) in dog N3 (size sample: 46 strides)

Limb pair	φt (mean±SD)	φs (mean±SD)
RF/LF	0.50±0.02	0.47±0.06
RH/LH	0.47±0.03	0.53±0.06
RF/LH	0.05±0.03	0.51±0.05
LF/RH	0.00±0.02	0.58±0.10
RF/RH	0.50±0.03	−0.10±0.02
LF/LH	0.54±0.02	−0.09±0.03

tween hind limbs were the same, and equal to the spatial phase differences observed for those same limb pairings. However, phase differences between unilateral limbs were significantly different from those between diagonal limbs. In addition, for those limb pairings, temporal and spatial differences were quite different. As was the case for walking, unilateral spatial phase differences in trotting were very small (0.01 or less) but consistently smaller than those observed during walking.

The step length during trotting was smaller than that observed in the walking dog (4.8 cm in the smallest dog N5, and about 11.2 cm in the dog N13, Fig. 3). An increase in trotting velocity resulted in an increase in stride length and stride frequencies. On the other hand, step length was nearly constant over the entire range of speeds (Fig. 3). The relative velocity of the limb during swing phase was estimated using equation 1.5. The results of these calculations are shown in Fig. 4. Relative limb velocity attained its minimum for those speeds of locomotion corresponding to moderate trot, and increased either for walking or faster trotting. One interesting observation is that the swinging velocity was smaller in the hindlimbs than in the forelimbs.

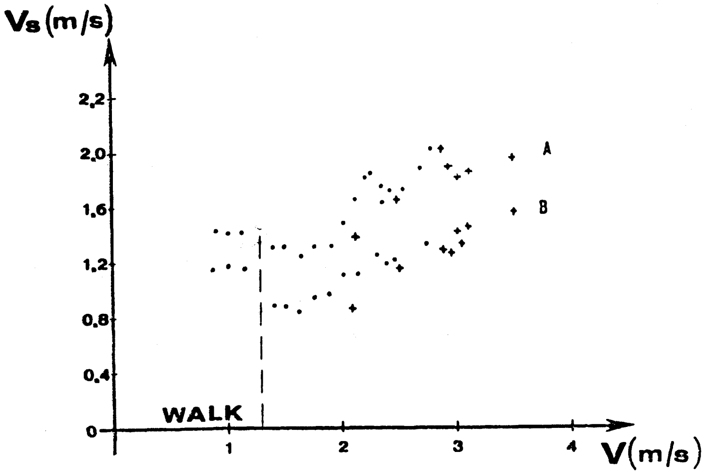

Fig. 4. The dependence of mean swing velocity (vs) on the overground velocity of locomotion (v) for (A) the forelimb and (B) the hindlimb. Same notation as in Fig. 3.

Transitions between walk and trot

In our study, each animal had its own characteristic range of walking and trotting velocities. Although for most animals, the velocity of locomotion uniquely determined which of these two gaits was used, the velocity ranges of trot and walk could occasionally overlap (see, e.g., the effects of a carried weight).

Walk-trot transition was observed at velocities between 0.8 and 1.2 m/s. All recorded transitions had the same characteristic pattern. Such a pattern involved a shortening of the step length in all four limbs, starting with the hindlimb. (In Fig. 5, the changes mentioned above may be recognized as a shortening of the corresponding swing phases). As a result of these changes, over the course of a single stride, the diagonal

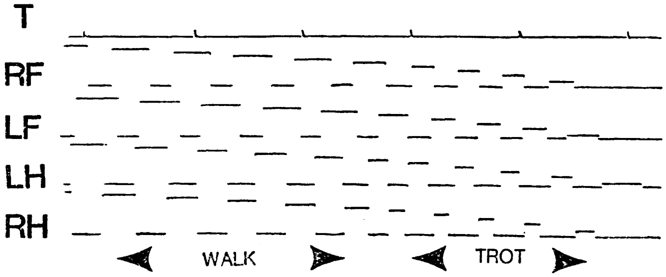

Fig. 5. A typical 2-D gait diagram of walk-trot transition (observed in dog N1). Same notation as in Fig. 1.

phase difference decreased (from 0.3 to 0.0), with a concomitant increase in the unilateral phase difference (from 0.2 to 0.5; see Fig. 6*A*). The transition was always characterized by a shortening of step length and an increase in stride frequencies.

A significant reduction in trotting velocity usually resulted in a gait transition from trotting to walking. Similarly, as was the case for the walk-trot transition, the trot-walk transition started abruptly with momentary increase in all hindlimb amplitudes. (In Fig. 7, these changes in step length correspond to the lengthening of the appropriate swing phase). Although all later steps were shorter then this initial, transitional one, the step lengths made by all the limbs (where the animal is now

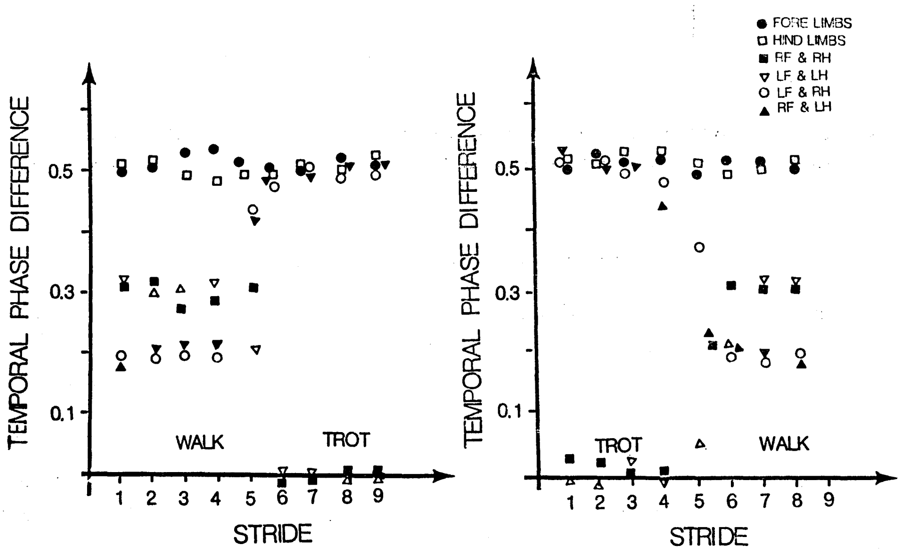

Fig. 6. Temporal phase difference changes (φt) as a function of successive step cycles observed during A) walk-trot and B) trot-walk transitions between the indicated pair of limbs.

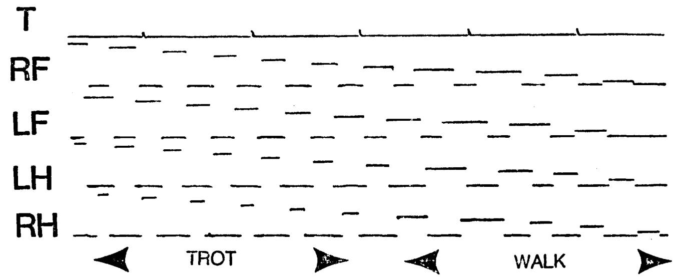

Fig. 7. A. typical 2-D gait diagram of trot-walk transition (observed in dog Nl). Denotations as in Fig. 1.

walking) are larger (i.e., have a higher duty factor) than those during trotting. (Step length during walking is, in general, greater than that in trotting). As a result of these step length changes, the intergirdle phase differences changed. For example, the unilateral phase difference dropped from 0.5 (during trotting) to 0.2 (during walking). The diagonal phase difference simultaneously increased from 0.0 to 0.3. These changes in phase differences during a typical trot-walk transition are shown in Fig. 6*B*.

Gallop

Eight of examined dogs routinely used the most common of all gallops, the transverse gallop (see 2) for a detailed description of galloping in the dog). Only in four animals was the rotatory gallop occasionally observed. The results of our statistical analysis of galloping are presented in Table IV. Unlike the symmetrical gaits, transverse galloping exhibited no correlations between swing and stance durations, between velocity of locomotion and swing duration, or between swing duration and stride length. Galloping was characterized by a greater step length than that observed for trotting. An increase in the velocity of locomotion during galloping resulted in an increase in both stride length and step length, but had no effect on stride frequency (Fig. 3).

Three-limb locomotion

In a few experiments, we restrained one of the dog's limbs in a flexed position, so that it was not able to use that limb for body support. Under these conditions, we were therefore able to record 2-D diagrams of three limb locomotion. This movement restraint caused a modification in the interlimb coordination pattern and limb movement parameters. These changes were studied in 5 animals running along the experimental pathway at different speeds. Observed changes from normal movement in the parameters of the three unrestrained limbs depended upon whether a fore or hind limb was restrained. Dogs with one restrained forelimb trotted and galloped over the same range of speeds as was observed for normal locomotion. The most common trot-like pattern is shown in Fig. 8. For this gait, the hindlimbs performed alternate movements and only one pair of diagonal legs moved in phase (0.0 temporal phase difference). The means for interlimb phase differences were not different from those for normal locomotion. However, the corresponding standard deviations for three limb locomotion were much greater than those for normal locomotion (Table VI). Significant changes in limb duty factors were also observed.

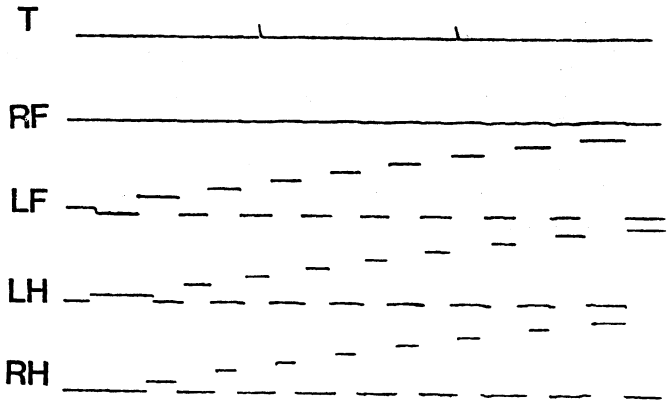

Fig. 8. A typical trot-like 2-D gait diagram observed in dog N3 during three-limb locomotion (RF restrained). Denotations as in Fig. 1.

TABLE VI

An example of observed the temporal phase differences during three-limb locomotion at a trot-like gait (2.6 m/s) in dog N3 ($n = 10$ trias)

Limb pair	Temporal phase difference (mean±SD)		
	Normal locomotion	3-limb trot RF restrained	3-limb trot RH restrained
RF/LF	0.51±0.02	–	0.48±0.06
RH/LH	0.49±0.03	0.51±0.07	–
RF/LH	0.02±0.03	–	0.04±0.05
LF/RH	0.04±0.03	0.03±0.05	–
RF/RH	0.47±0.03	–	–
LF/LH	0.53±0.03	0.51±0.06	0.49±0.07

In the forelimb, stance duration and step length increased while swing duration decreased. For example, in dog N3, during three legged locomotion without the right forelimb, we observed a 15% increase in forelimb (LF) stance phase duration for a locomotion velocity of 2.5 m/s. This increase was much more pronounced at lower speeds, but almost disappeared at speeds above 2.9 m/s. This increase was the result of a lengthened step. The stride frequency for all three limbs was unchanged from normal locomotion due to an appropriate shortening of the swing phase duration. Likewise, the hindlimbs parameters exhibited no significant changes.

At higher speeds, it was also possible to observe a three legged

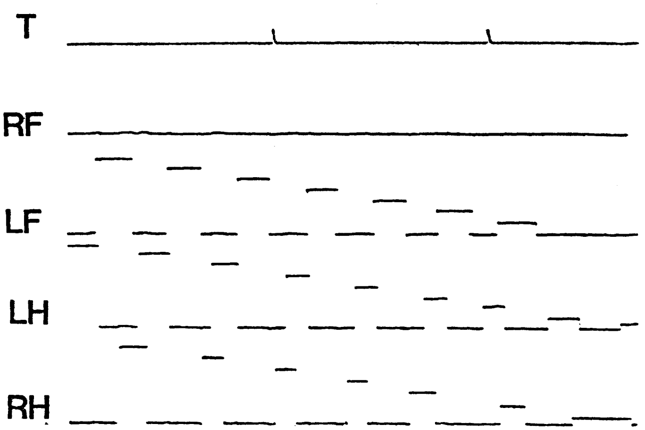

Fig. 9. A typical gallop-like 2-D gait diagram observed in dog N3 during three-limb locomotion (RF restrained). Denotations as in Fig. 1.

gallop-like pattern (Fig. 9). During normal transverse galloping, the animal would initially land on a single hindlimb. This would be followed by the simultaneous planting of the opposite hindlimb and its diagonal forelimb. Finally the animal would plant and lift off from the remaining forelimb (diagonal to the initially planted hindlimb). For example, a typical galloping sequence might be (i) RH, (ii) LH and RF and (iii) LF.

In the case of three limb locomotion when a forelimb is restrained, no significant differences from normal locomotion were observed. The corresponding galloping sequence for the example given above would be (i) RH, (ii) LH and (iii) LF (where RF is restrained). The temporal phase differences between the hindlimbs and between the pair of unilateral (left) limbs would be the same as those observed for normal locomotion. In addition, all parameters characterizing a single limb were unchanged.

The situation was quite different, however, when a hindlimb was restrained. Under these circumstances, the dogs never galloped, with the fastest gait observed corresponding to a normal trot (Fig. 10). For a normal trot, the temporal phase differences between forelimbs and between diagonal pairs were 0.5 and 0.0 respectively. Both these parameters exhibited larger standard deviations than those for a normal gait (Table VI). Observed differences in stride cycle subcomponents depended upon the speed of locomotion. Generally, these changes were more significant for the slower velocities. For example, at a speed of 2.1 m/s (trotting), dog N5 exhibited an increase in stance duration and duty factor for all three limbs over those observed during normal trotting. However, at a speed of 2.8 m/s, there were no significant changes in these parameters.

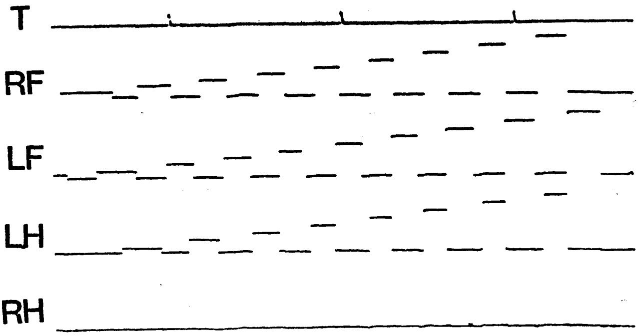

Fig. 10. A typical 2-D gait diagram observed in dog N1 during three-limb locomotion (RH restrained). Denotations as in Fig. 1.

Locomotion with additional weight

The effects of an additional weight on the kinematic parameters of the limb were studied in seven dogs. A two kilogram weight was placed on the dog's back near its overall center of mass. Tested animals weighed between 7.5 and 24 kg, so the added weight comprised 8-27% of their body weight. These animals moved much more slowly, preferring a slow trot or moderate walk. Under these conditions, the typical numerical footfall formula for a very slow trot (2-4-2-4) was observed. Temporal phase differences, stance and swing durations, and stride and step lengths were not significantly different from those observed in normal locomotion.

Locomotion in darkness

We also examined the effects on locomotion due to limited visual information. During the course of these experiments, the lights were randomly turned off so that the animals moved in complete darkness. Although the dogs were familiar with the environment, they always slowed down. If they were in the middle of a gallop, they would immediately switch to one of the slower symmetrical gaits (trot or walk).

DISCUSSION

Commands controlling muscle activities during locomotion arise as a result of the integration of central and peripheral inputs. This allows all limb movement parameters to adapt to changing environmental conditions at every stride. During steady-state locomotion on the experimental platform, the kinematic parameters of the limbs are quite constant. When a velocity is not forced by a moving treadmill, dogs tended to trot with a constant and specific speed during long distance locomotion. This speed (which always resulted in a trot) ranged between 1.8 to 2.7 m/s and depended upon the size of the dog. For a given animal, this preferred speed was constant and repeatable from session to session. This speed was highly correlated with the animal's hindlimb length and corresponded to the minimum observed swinging velocity of the limb. As has been proposed for bipeds, the stride frequencies chosen by trotting dogs at these preferred velocities may correspond to the natural resonant frequencies of their swinging limbs (13). These frequencies would result in minimum energy expenditure while swinging the limbs. Although Taylor et al. (22) observed that the rate of oxygen consumption for a given speed was nearly the same for animals with different limb shapes (i.e., moments of inertia), our results imply that the work done in swinging its limbs is still a factor that the animal seriously considers in attempting to minimize the metabolic cost of locomotion. Based upon the observations by Arshavsky et al. (6) in the dog and Wetzel et al. (24, 25) in the cat, Alexander (5) assumed that the amplitude of a swinging limb is constant over all speeds of locomotion and predicted that the work performed by a swinging limb increased as the speed of locomotion increased. However, our results indicate that the amplitude of limb movement changes according to the gait used. For walking and galloping, step length is much larger than that observed for trotting. Presumably, the distance between the shoulder and pelvis, coupled with the fact that the fore and hindlimbs move out of phase (0.5 temporal phase difference), limits step length. For the faster trots where a flight phase is observed (all four limbs are off the ground), step length definitely lengthens and becomes an active factor determining the velocity of locomotion.

An interesting observation is that, for symmetrical gaits (i.e., walking and trotting), the hind paw is usually placed in front or at the exact point where the unilateral fore paw had been in the previous stride. (The data of Gambaryan (9) and Gray (11), confirm this). Our 2-D method allowed us to quantitatively study this phenomenon by the measurement of spatial phase differences. Our results confirmed that a 0.0 spatial phase difference between unilateral limbs is a characteristic feature of walking and trotting. This has functional significance. As mentioned above, one of the most important ends of successful locomotion is sustaining a high margin of dynamic stability. Under many circumstances, visual input is very important in the placement of the forelimbs (for references see 12, p. 1224). This is especially apparent during locomotion over very rough terrain. However, the placement of the hindlimbs cannot be controlled visually, so that under conditions of uncertain terrain, one way to guarantee stability is to place the hindlimb at a point which has already been tested and determined as safe. Such a point would be where the unilateral forelimb was placed in the previous step. Under these conditions, then, walking and trotting are potentially more stable gaits. As might be expected, they were the preferred gaits during locomotion in the dark.

All propulsion (the primary determinant of locomotion speed and direction) and support (the primary determinant of stability) may only be performed by the limbs during the stance phase. Stance phase duration decreases approximately hyperbolically as the velocity of locomotion increases (e.g., 1, 6, 12, 21). This represents an interesting challenge to limb control: all limb movement parameters, as well as the pattern of interlimb coordination, must adapt to a change in speed. It is commonly accepted that the structure of quadrupedal locomotion is based on diagonal support (3, 8, 15). Diagonal support is relatively stable for high speeds where the center body mass is moving forward at a sufficiently rapid velocity. However, at slower velocities, such a support strategy is unstable, so that the locomotor pattern must change in such a way as to improve the longitudinal stability margin. According to McGhee and Frank (18, see also 16), a slow gait will be stable if, during successive strides, the center of gravity is always within or on the closed figure formed by the points of contact of all feet on the ground. Two feet on the ground may only define a straight line, so that any equilibrium points are unstable. However, three feet on the ground may form a triangle (where all equilibrium points within the interior are stable). The animal therefore attempts to always maintain three feet on the ground while moving at these slower speeds. Such a stable gait can be obtained if the temporal phase differences between unilateral limbs are 0.25 and the duty factors are all 0.75. These values are characteristic of observed normal walking. Duty factor can be increased by increasing stance phase duration relative to total stride cycle duration. Such an increase may, in turn, be generated by increasing step length. However, during trotting, high duty factors cannot be obtained since step length increases are limited by shoulder to hip distances and a 0.5 temporal phase difference between fore- and hindlimbs (10). The transition from trotting to walking results in a decrease in the unilateral temporal phase difference from 0.5 to 0.2. This allows the animal to lengthen its step. All these changes are completed within a single stride (3, 23).

In the walking or slowly trotting animal, an increase in the speed of locomotion is generally the result of an increase in stride frequency and, therefore, a decrease in total stride cycle time (4). However, this results in a decrease in stance duration and, therefore, the total time the animal's foot is in contact with the ground. This reduces the total time the foot may generate propulsive force. In an attempt to avoid any reduction in absolute stance duration, the animal attains faster overground locomotion speeds during fast trotting and galloping by increasing its step length (and not stride frequency) (see also 14). This is accomplished by increasing swing duration (for gallop, by the addition of a flight phase) with a resultant decrease in the duty factor (3).

When an additional weight was added to the back of our experimental animals, no significant changes were observed in any of the kinematic parameters at the speeds examined. Since no change was observed in stance duration, compensation to this added weight was possibly due to an increase in the total force generated by each foot. Similar results were obtained for dogs running on the treadmill (21).

Each gait could be uniquely characterized and distinguished by its kinematic parameters. These kinematic parameters reflect the primary objective of each gait, and within each gait, increases in speed are accomplished by modifying different sets of parameters. For example, during walking, where maintaining three point stability is the primary goal, the animal attempts to maintain a high duty factor, and increases overground speed of locomotion by appropriately increasing stride length and frequency. Similar cases can be made for the other gaits. Control of locomotion, then, within each gait is qualitatively different and a single, common strategy for speed increase would be insufficient.

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