

Lack of locomotor-cardiac coupling in trotting dogs

ADAM D. SIMMONS,¹ DAVID R. CARRIER,²
COLLEEN G. FARMER,¹ AND COLIN S. GREGERSEN²

¹*Department of Ecology and Evolutionary Biology, Brown University, Providence, Rhode Island 02912; and* ²*Department of Biology, University of Utah, Salt Lake City, Utah 84112*

Simmons, Adam D., David R. Carrier, Colleen G. Farmer, and Colin S. Gregersen. Lack of locomotor-cardiac coupling in trotting dogs. *Am. J. Physiol.* 273 (*Regulatory Integrative Comp. Physiol.* 42): R1352–R1360, 1997.—Coupling of locomotor and cardiac cycles has been suggested to facilitate effective arterial delivery and venous return during vigorous exercise. In an attempt to document locomotor-cardiac coupling, we ran five dogs on a motorized treadmill while monitoring heart activity with surface electrocardiogram electrodes and locomotor events with high-speed video and an accelerometer mounted on the dog's back. Analysis of the cardiac and locomotor frequencies revealed that heart rate was usually slightly greater than stride frequency. Hence the timing of the cardiac cycles varied with respect to the phase of the locomotor cycles, and therefore consistent coupling of the locomotor and cardiac cycles was not observed in any of the dogs. However, the period of the cardiac cycle sometimes varied in a rhythmic way that caused brief periods of transient coupling of the locomotor and cardiac cycles in three of the five dogs. These brief periods of coupling (5–20 heartbeats) occurred at approximately the same phase relationship in each of the three dogs. We hypothesize that the variation in cardiac period and the resulting transient coupling are a function of locomotor and ventilatory influences on venous return and/or ventricular ejection. Because venous return and ejection fraction are likely to vary in an unpredictable manner when animals run in a complex environment, we suggest that reflex control of heart rate will be important during locomotion and strict integer coupling of the locomotor and cardiac cycles is unlikely to evolve.

exercise; cardiac function; cardiac reflex; locomotion

THE CIRCULATORY SYSTEM plays a central role in aerobic exercise by linking the sites of gas exchange and energy storage with the mitochondria of working skeletal and cardiac muscle. Several lines of evidence suggest that the functional capacity of the cardiovascular system is the principal factor limiting the maximum rate of oxygen consumption during exercise in many or most mammals (7). The importance of cardiovascular function to respiration combined with potential mechanical limitations to arterial delivery and venous return during exercise has led several physiologists to suggest that coupling of the cardiac and locomotor cycles might improve locomotor stamina during vigorous exercise (2, 3, 5, 12, 13, 19–23).

Reports of coupling between the locomotor and cardiac cycles appear as early as the 1920s. Coleman (12, 13), while working at the zoological gardens of Regent's Park in London, described a matching of step rate and heart rate in people and a variety of animals including a lynx, a badger, and a serval. His observations of heart rate were taken by a variety of visual methods or by

feeling the radial pulse in the wrist. Consequently, although his results indicate a similarity in rates, they do not provide a direct demonstration of coupling.

Later, Aulie (2, 3) proposed a mechanical linkage between the locomotor and cardiac cycles during flapping flight in birds. He postulated that the increased thoracic pressure during contraction of a bird's pectoral muscles might push blood back into the heart. For the heart to work as efficiently as possible, one would expect it to contract when it is full of blood rather than when it is empty. Therefore, if the pectoral muscles functioned as a venous pump, the cardiac cycle of flying birds could be expected to be coupled with the wing stroke. Although Aulie's birds did not exhibit one-to-one coupling, he observed that heartbeats were less likely to occur during pectoral muscle activity than would be expected by pure chance. For much the same reason, the venous pump that results from skeletal muscle contractions, acting in conjunction with a series of one-way valves in the veins of the limbs of running animals, could also be expected to facilitate coupling of cardiac and locomotor rhythms.

A second type of venous pump, the respiratory pump, might also result in locomotor-cardiac coupling. In mammals, caudal displacement of the diaphragm helps produce inspiratory air flow by decreasing intrathoracic pressure. Simultaneously, the pressure in the abdomen increases. The net effect of these pressure changes is an increase in the pressure differential between the peripheral veins and the right atrium. Consequently, venous return is enhanced during inspiration. Because mammals and birds couple their breathing with their locomotor movements when they run (1, 5, 6, 8–10, 17, 28), it is not unreasonable to expect that coupling of the heart to the ventilatory and locomotor cycles would improve cardiac efficiency.

Kirby and collaborators (23) proposed a third possible reason to expect coupling. They noted that, during normal locomotion, intramuscular pressure rises to levels that often exceed peak systolic blood pressures. Therefore, locomotor activity is likely to periodically occlude blood flow through active muscles during each stride. To allow efficient transport, these investigators reasoned that the cardiac cycle should be timed to deliver blood through the locomotor muscles when they are relaxed rather than contracted. In their initial studies on humans walking, running, cycling (22, 23), and finger tapping (20), Kirby et al. found relationships between the rates of these activities and heart rate. However, their subsequent studies (21) showed that the relationship in tapping was not statistically significant. Furthermore, later studies during cycling (14) and hopping (19) showed neither a consistent phase relationship nor increased metabolic efficiency during episodes

when the locomotor and heart rates were matched. Work by Baudinette et al. (5) on wallabies hopping on a treadmill also found no correlation between locomotor and cardiac cycles. Thus, although there are several reasons to suspect that coupling might be advantageous, it remains an open question as to whether coupling occurs.

If coupling does enhance cardiovascular efficiency, we would expect it to be most important during vigorous exercise when metabolic demand is elevated. In an attempt to document locomotor-cardiac coupling in running mammals, we monitored heart activity and stride events in dogs as they trotted on a treadmill. If coupling exists, it is likely to be most apparent in species that have evolved high levels of locomotor endurance. As a family, canids are known to cover great distances while foraging.

MATERIALS AND METHODS

Experimental animals. Five dogs of mixed breed were used as subjects in this investigation. Their weights ranged from 17.6 to 30.0 kg, and their mean weight was 24.2 kg. They were purchased at ~1 yr of age from a USDA-licensed animal dealer. All five were easily trained to walk and run on a motorized treadmill and were comfortable trotting over a range of speeds.

Data collection. To monitor the timing of the heartbeat, we recorded an electrocardiogram (ECG) signal with surface electrodes instrumented to an AC amplifier (P511, Grass Instruments, West Warwick, RI). Sites for the electrodes were shaved. Each electrode was held in place by a belt of masking tape wrapped around the trunk, and a generous dollop of electrode gel provided the electrical connection to the subject. One electrode was positioned on the dorsal midline just caudal to the tips of the scapulae, and another was placed on the skin over the middle of the sternum. A third electrode served as a ground and was positioned on the dorsal midline in the lumbar region. Leads from the electrodes traveled in a shielded cable to a high-impedance probe (F-HIP511G, Grass Instruments) that was taped to the side of the treadmill. The ECG signal was amplified 500 or 1,000 times, filtered below 10 Hz and above 300 Hz, and recorded on a Macintosh computer at 500 samples/s with the use of an Acknowledge data acquisition board and software (Biopac Systems, Goleta, CA).

To monitor stride frequency, we recorded the vertical accelerations of the trunk with an accelerometer (model 104, Omega, Stamford, CT) that was attached to the dog's back. To correlate the signal from the accelerometer with the phases of limb support, we recorded the trials with a high-speed video system (Peak Performance Technologies, Englewood, CO) at 120 fields/s. The accelerometer and video recordings were synchronized with a circuit that triggered the beginning of data acquisition and simultaneously illuminated a light-emitting diode in the view of the video camera.

Experimental protocol and analysis. Recordings were made from the dogs while they ran at a range of trotting speeds. Specifically, we started each subject running at its slowest trotting speed, just above the speed of the walk-to-trot transition. The dog was run at this speed for 3 min before the beginning of recording to provide a warm up and to allow the dog to approach steady state. We then recorded cardiac and locomotor cycles for 3 min. The speed of the treadmill was then increased by 0.2–0.7 m/s (depending on the dog). The dog was given a 1-min acclimation period at the new speed,

and then data were recorded for 3 min. Data were collected in this way for four to five speeds that covered the entire range of trotting speeds for the dog. Immediately after the 3-min recording period at the highest speed, the treadmill was slowed to the lowest speed, and the full protocol was repeated twice so that 9 min of data were collected at each speed. Thus each dog was run for a total of 51 or 63 min. In three of the dogs, this hour-long protocol was repeated on 2 or 3 different days.

We analyzed the raw recordings to determine the phase relationship between heartbeats and stride. We used Igor software (WaveMetrics, Lake Oswego, OR) to determine timing of the peak of the R wave in the ECG signal and the timing of the zero crossing of the accelerometer signal. These times were then used to calculate the phase angle (0–360°) at which each heartbeat began in the locomotor cycle. We defined the beginning of the heart cycle as the timing of the peak in the R wave. We also identified the timing of the peak of the T wave for each cardiac cycle. This allowed us to determine the duration of the systole (time from R wave to T wave) and the duration of diastole (time from T wave to R wave). This made it possible to sort out whether variation in cardiac cycle duration during locomotion was due to changes in systole, diastole, or both.

Test of the hypothesis of coupling. Because each heartbeat can be assumed to influence the timing of the heartbeat that follows it, individual heartbeat times cannot be assumed to be independent for purposes of statistical analysis. We therefore designed and carried out a series of randomization tests (25) that exploit the independence of individual runs (trials) performed by each dog. On the null hypothesis that there is no coupling between the cardiac cycle and the locomotor cycle, cardiac cycles from different runs that are at different running speeds and separated in time by minutes can certainly be assumed to be independent of each other, even if individual heartbeats within a given run are not.

We divided the stride cycle into 24 bins and assigned the cardiac cycles from each run to bins on the basis of their start times. On the null hypothesis, there should be no tendency for cardiac cycles to occur disproportionately at any particular point in the cycle, so we expect them to be distributed evenly (on average) over the 24 bins. We therefore used the goodness-of-fit χ^2 statistic $\chi^2 = \sum(O - E)^2/E$ as our measure of association between the locomotor and cardiac cycles [here O is the observed number of cardiac cycles in a given bin, and E is the expected (average) number (total/24)]. A sample in which the cardiac cycles were uniformly distributed among the bins (i.e., no coupling of cardiac cycle to stride) would give a χ^2 value near zero, whereas a sample in which all of the cardiac cycles occurred in one bin (i.e., highly coupled) would produce a very large value of χ^2 . We calculated this statistic for the pooled data from all runs of each dog individually and for the pooled data from all five dogs together.

These observed values of χ^2 cannot be tested for significance by comparison to the χ^2 distribution because we cannot assume that individual heartbeats are temporally independent of each other. So to generate the sampling distribution of χ^2 under an appropriately conservative null hypothesis, we added a random phase shift to the entire sequence of heartbeats from each run and repeated the χ^2 calculation. Within each simulated run, the sequence of heartbeats remains exactly the same as in the actual data, but the relationship to the stride cycle is randomized. On the null hypothesis, this should have no effect on the average value of χ^2 . But if there really is a tendency for heartbeats to occur at particular points in the stride cycle, then the randomization process will distribute heartbeats more evenly over bins than in the

original data, thereby reducing the calculated χ^2 in most cases. For each test, we performed 1,000 such randomizations and interpreted the proportion of randomized χ^2 values that were greater than the observed value of χ^2 as an apparent level of statistical significance. Tests were carried out for all of the recorded runs of each dog separately and then for all of the runs from all of the dogs together.

RESULTS

Initial attempts to record an ECG from surface electrodes placed on the lateral body wall just caudal to the forelimb resulted in very noisy signals during locomotion. Often the QRS waves were not distinguishable from the noise. Fortunately, the technique of placing the electrodes on the dorsal and ventral mid-lines produced clean and repeatable signals in which the QRS and T waves were clearly visible (Fig. 1).

In all of the recordings, the period of the cardiac and locomotor cycles differed, with the heart beating slightly faster than the locomotor cycle (Fig. 2). This small difference in frequency was observed in all five dogs and was maintained over the full range of trotting speeds. The frequencies did not differ by an integral amount; hence the cardiac cycle drifted with respect to the phase of the locomotor cycle. This was true in all five dogs and at all speeds that were studied. Consequently, none of the dogs exhibited phase locking of the locomotor and cardiac cycles (Figs. 3 and 4). If coupling were to occur at one cardiac cycle per stride, the vast majority of heartbeats would occur over a single narrow range of phase angles in Figs. 3 and 4. Similarly, if there were coupling at two cardiac cycles per stride there would be two peaks of phase angle in which most of the heartbeats occurred. However, heartbeats occurred at all phases of the locomotor cycle.

Results of the randomization test clearly indicate that tight coupling does not occur in these dogs (Table 1). If the heartbeats were uniformly distributed among the 24 bins of the stride cycle, the randomization test would give a value near zero. If, however, all of the heartbeats had occurred in a single bin, which would

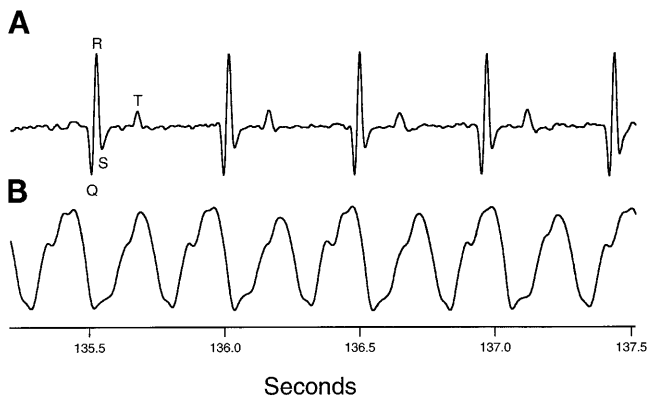


Fig. 1. Sample electrocardiogram (ECG) (A) and accelerometer signal (B) from dog trotting at 2.2 m/s. QRS and T waves are marked in the first cardiac cycle shown. In accelerometer trace, each peak represents vertical acceleration that occurs during 1 step. Consequently, 2 peaks represent 1 locomotor cycle. Notice that length of cardiac cycle is slightly less than length of locomotor cycle.

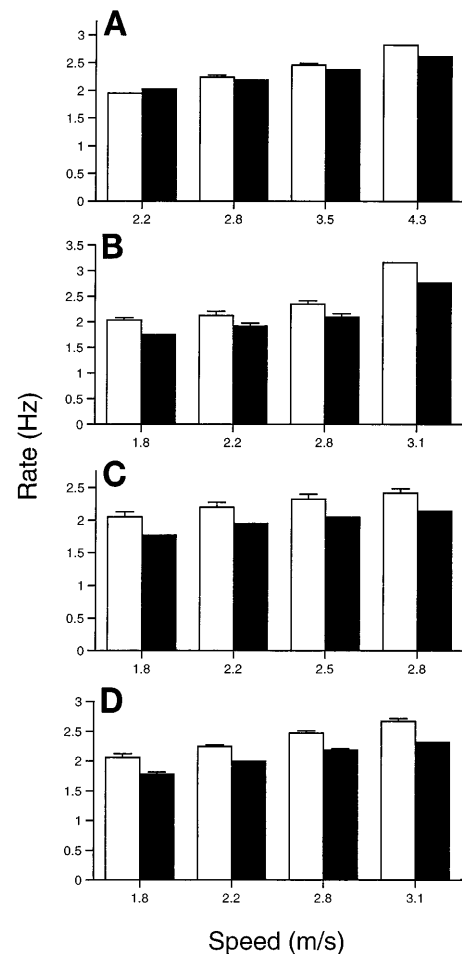


Fig. 2. Histogram comparing frequency of the heart cycle (open bars) to frequency of locomotor cycle (solid bars) over a range of speeds in 4 dogs (A–D) during trotting. Each bar represents mean and SD of mean frequencies from 5–9 1-min samples.

have indicated very strong coupling, the test statistic would have been $>80,000$ in every case. The largest χ^2 value observed was 171, which was 0.14% of the value that would have occurred if there had been tight coupling.

Although none of the dogs exhibited tight coupling of the locomotor and cardiac cycles, in three of the five dogs we observed a tendency toward slightly more heartbeats at ~ 80 – 120 and 260 – 300° of the locomotor cycle (Figs. 3 and 4). This weak relationship was found to be statistically significant in three of the five dogs (Table 1 and Fig. 4). A significant effect was also found when the test was performed on all of the data from all five dogs (Table 1). This pattern was most apparent at intermediate speeds and during the 3-min recording periods early in the recording session. The pattern was rarely observed late in the recording sessions. We also observed the pattern in one dog when we continuously varied the belt speed of the treadmill from 2.0 to 3.5 m/s (Fig. 3). The timing was such that the QRS waves were slightly more likely to occur just as the diagonal forelimbs and hindlimbs were touching down to begin the support phase of a step in the trotting cycle. Conversely, the QRS waves were slightly less likely to

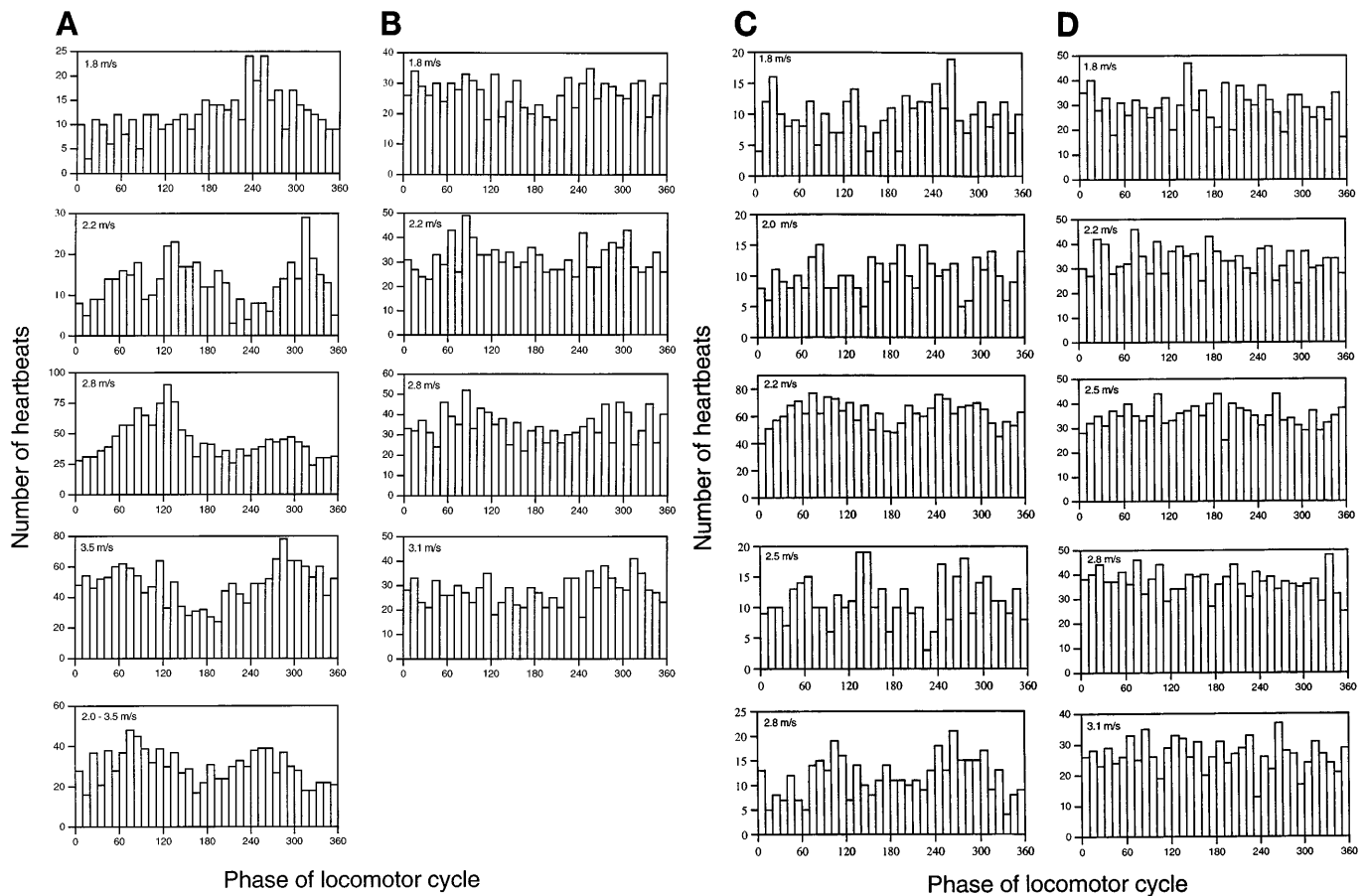


Fig. 3. Histograms from 4 dogs (A–D) showing number of heartbeats that began in different phase angles of locomotor cycle. In each case, locomotor cycle begins (zero phase angle) at end of support by right hindlimb. Running speed (m/s) is listed in top left corner of each graph. Bottom graph from A shows data from 2 3-min trials in which we varied speed of treadmill continuously from 2.0 to 3.5 m/s. Although heartbeats begin at all phases of locomotor cycle, in 3 of the dogs shown here, there are speeds in which a few more heartbeats were found to occur at phase angles of 60–120 and 260–320°: A at all speeds, B at 2.2 and 2.8 m/s, and C at 2.2 m/s.

occur right before the limbs were about to come off the ground, leading into the flight phase.

To gain a better understanding of what this pattern of slightly more heartbeats occurring at the beginning of the support phase might mean, we compared the period of each cardiac cycle to the phase of the locomotor cycle in which it occurred (Fig. 5). Because more heartbeats occurred at ~100 and 280° of the locomotor cycle, we expected those heartbeats to be of shorter duration. However, the phase of the locomotor cycle that had the most heartbeats also tended to have cardiac cycles of slightly longer duration. Examination of variation in the duration of systole and diastole showed that changes in the period of the cardiac cycles were entirely due to changes in the length of diastole (Fig. 6). The duration of diastole increased as the period of the cardiac cycle increased, but the length of systole remained constant. This was further illustrated by plotting diastole duration against the phase of the locomotor cycle in which the heartbeat occurred (Fig. 7). Thus the two phases in the locomotor cycle that tend to have a few more heartbeats have cardiac cycles of longer duration because of a longer diastole.

The correlation of the longest heartbeats also being the most frequent was a function of the heart rate normally being faster than the stride rate. Because the heart cycle was of shorter duration than the stride cycle, the cardiac cycle drifted in time relative to the stride cycle, and it appeared to drift through the stride cycle. Those heartbeats that were of longer duration were closer in length to the duration of the stride cycle, and so the drift through the stride cycle was slowed. If these longer heartbeats were very close to the length of the stride cycle, the two functions appeared to become coupled for a brief period of time. This resulted in a greater number of heartbeats occurring at any phase angle of the stride in which there was a tendency for the heartbeats to be of slightly longer duration. The heartbeats that occurred at the beginning of the support phase tended to be longer than heartbeats that occurred at other times in the stride, and this greater length caused the cardiac and locomotor cycles to become transiently coupled. Transient coupling slowed the drift of the heart cycle through the stride cycle and resulted in a few more heartbeats occurring at the beginning of the support phase.

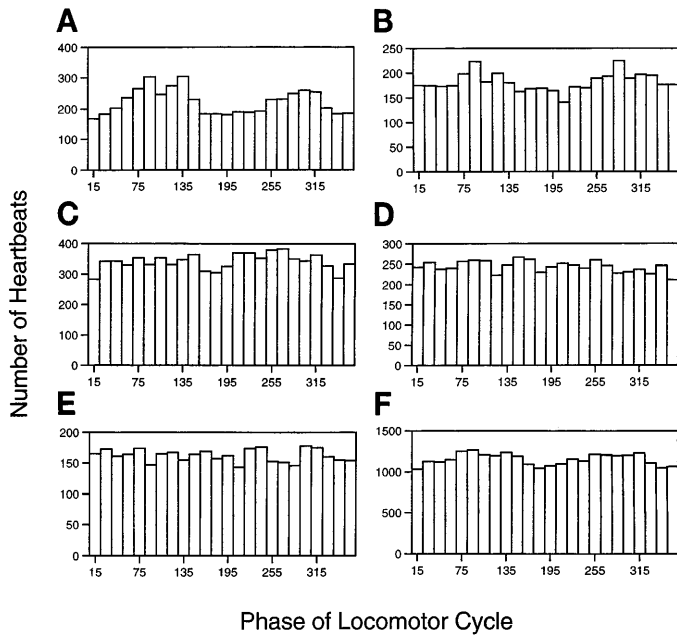


Fig. 4. Histograms for all analyzed trials from each of 5 dogs (A–E) showing number of heartbeats that began in different phase angles of locomotor cycle. In these graphs, all running speeds are lumped together. In each case, locomotor cycle begins (zero phase angle) at end of support by right hindlimb. F shows data from all trials from A–E: 65 trials and 27,603 heartbeats inclusive.

Figure 8 compares the timing of systole and diastole with the vertical acceleration of the dog’s trunk to illustrate the phase relationship of the locomotor cycle in which heartbeats are most likely to occur (Fig. 8A) and the phase relationship in which heartbeats are least likely to occur (Fig. 8B). Several points warrant mention. First, the cardiac cycles that occurred during the phase of the locomotor cycle that had more heartbeats had periods that were approximately the same length as that of the locomotor cycle. When this occurred, the two cycles were “transiently coupled” for periods of 5–20 cycles. Second, the timing of systole in these heartbeats coincided with the support phase and the peak vertical accelerations, whereas diastole began at the beginning of the suspension phase and ended a step and one-half later at the start of the next support phase. In contrast, during the phase of the locomotor cycle in which heartbeats were least likely to occur, the

Table 1. χ^2 Values for observed relationship between timing of cardiac cycle relative to locomotor cycle and for randomization test

| Dog | Runs | Heartbeats | χ^2 Observed | Randomization Test | | |
|----------|------|------------|-------------------|--------------------|---------------|-------------|
| | | | | df | Mean χ^2 | P |
| A | 10 | 5,335 | 170.82 | 9 | 75.6 | 0.011 |
| B | 11 | 4,364 | 42.51 | 10 | 21.1 | 0.003 |
| C | 21 | 8,187 | 47.34 | 20 | 26.9 | 0.015 |
| D | 14 | 5,829 | 18.51 | 13 | 17.2 | 0.373 |
| E | 9 | 3,888 | 14.60 | 8 | 21.0 | 0.830 |
| All dogs | 65 | 27,603 | 98.37 | 64 | 32.2 | $\ll 0.001$ |

df, degrees of freedom. Phase of cardiac cycles was shifted by a random amount in each recorded trial in randomization test. Dog letters correspond to same letters on Figs. 2–5 and 7.

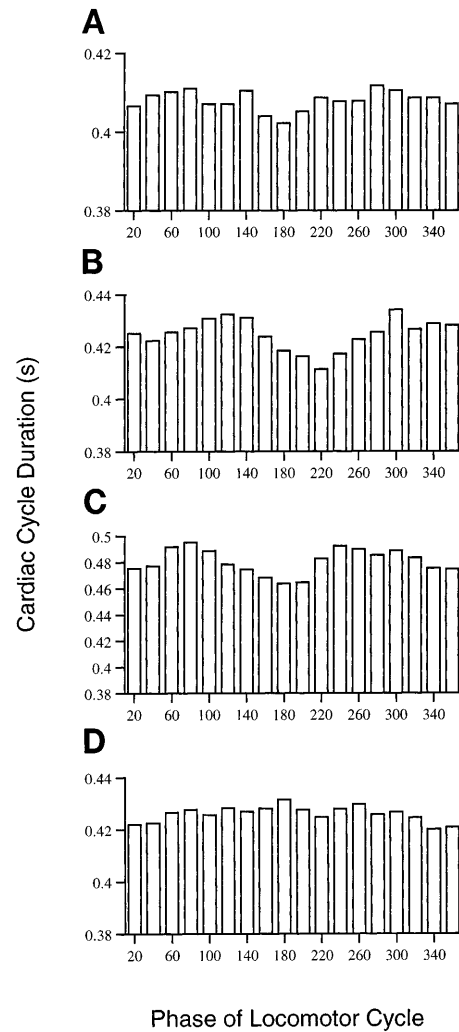


Fig. 5. Histograms plotting average length of cardiac cycles that occurred at different phase angles of locomotor cycle. Data are from speeds at which 3 of the dogs exhibited a few more heartbeats at phase angles of 60–120 and 260–320°. Sample sizes: A, 1,755 heartbeats; B, 738 heartbeats; C, 1,122 heartbeats; D, 840 heartbeats.

periods of the cardiac cycles were of shorter duration than the locomotor cycles. This resulted in rapid drift of the cardiac cycle through the locomotor cycle. Systole during these heartbeats coincided with the suspension phase and the lowest accelerations, and diastole began early in the support phase and ended less than a step later at the start of the next support phase.

Changes in the length of the cardiac cycle as a result of variation in the length of diastole were readily apparent in our dogs during rest. Figure 9 plots an ECG signal relative to a recording of inspiratory and expiratory airflow in a resting dog. The heart cycle slowed down during each expiration and then increased in frequency during each inspiration. The longest cardiac periods during expiration were approximately twice as long as the shortest cardiac periods during inspiration. This variation resulted from changes in the length of diastole.

DISCUSSION

Lack of coupling in trotting dogs. If coupling between the cardiac and locomotor cycles existed, contraction of the heart would be restricted to one or more phases of the locomotor cycle, presumably phases that maximized efficient gas transport. We found no evidence of a consistent temporal correlation between cardiac cycle and stride. In our recordings, the cardiac cycle was almost always shorter than the locomotor cycle. Hence the ECG signal drifted in time relative to the stride. This was true for all five dogs throughout the full range of speeds in the trot. Thus, under the conditions of this study, the locomotor and cardiac cycles were not phase locked. This finding is consistent with a number of studies that have looked for but not observed locomotor-cardiac coupling (2, 3, 5, 14, 19, 21). If coupling is an important phenomenon, it should occur consistently, and it would likely be most apparent when dogs run at a steady pace in uncomplicated terrain, as was the case in this study. However, because running speed was controlled by us, it is possible that the dogs did not run at a speed that was conducive to coupling, as might be the case when they run in the natural world. We believe this is unlikely because we monitored four or five

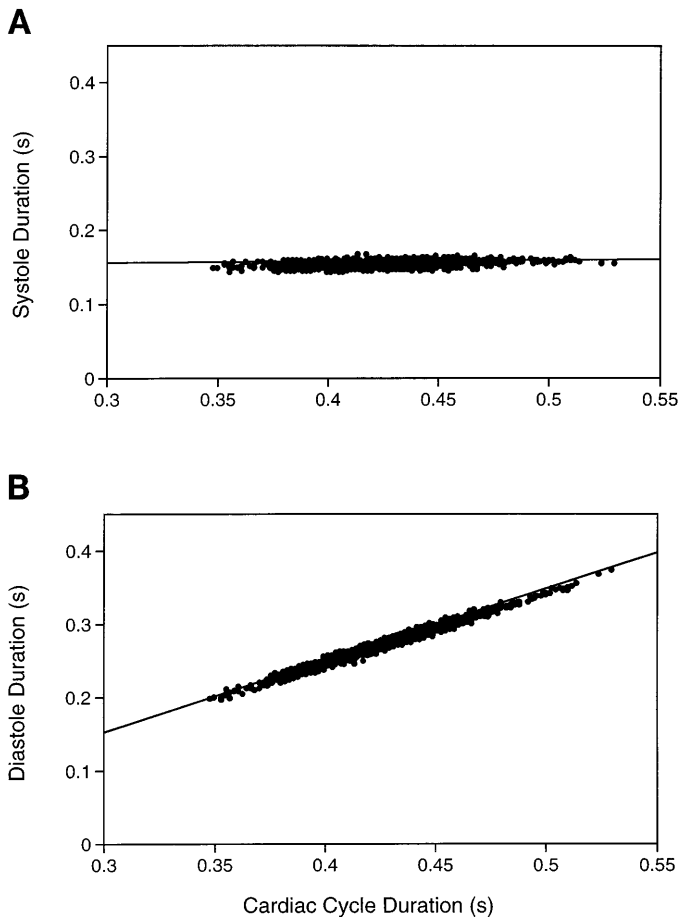


Fig. 6. Graphs of systole (A) and diastole duration (B) vs. heartbeat duration for 1,262 heartbeats from a dog trotting at 2.8 m/s. Least-squared regression to the power equation yielded $y = 0.018x + 0.151$ ($r^2 = 0.038$) for systole duration and $y = 0.980x - 0.141$ ($r^2 = 0.988$) for diastole.

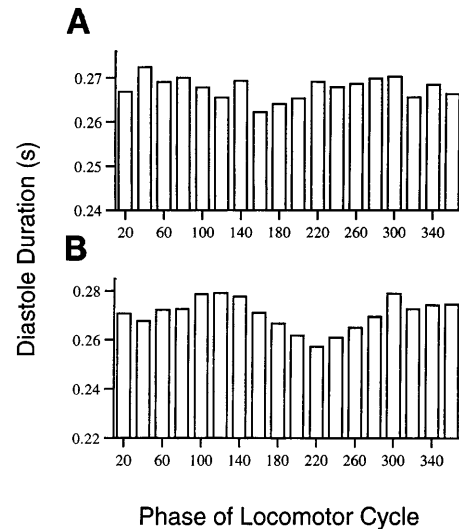


Fig. 7. Histograms plotting average length of diastole vs. phase angle at which heartbeats began. Data are presented for 2 dogs. Running speeds were 3.5 (A) and 2.8 (B) m/s. Sample sizes were 1,755 (A) and 738 (B) heartbeats.

speeds for each subject within their trotting range, and we checked each of these speeds three times over the course of an hour of running, during which time the level of exertion was constantly increasing. Additionally, in three of the dogs, the entire protocol was repeated two or three times on different days. Consequently, this study indicates that the locomotor and cardiac cycles are not tightly coupled in trotting dogs.

Influence of stride and/or ventilation on the cardiac cycle during trotting. Although our results indicate that trotting dogs do not couple their heart cycle with their stride, the cardiac cycle was at times influenced by some aspect of locomotion or possibly by ventilation that was coupled to the stride. In three of the five dogs, there was a repeatable and statistically significant trend in which a few more heartbeats coincided with the beginning of the support phase of the locomotor cycle. The period of these cardiac cycles was slightly longer as a result of a longer diastole, and this resulted in brief periods in which the heart became transiently coupled to the stride. Because diastole was what changed in a regular way relative to the phase of the locomotor cycle, we suspect that the observed pattern was a function of stride-related variation in the time it takes to fill the heart with blood [within limits, changes in the duration of diastole reflect changes in the rate of ventricular filling (27)]. At rest, the length of diastole was strongly influenced by lung ventilation (Fig. 9). Inspiration facilitates venous return to the right side of the heart (15) while decreasing stroke volume from the left side of the heart (18), and, in our dogs at rest, inspiration was associated with cardiac cycles that were as much as 50% shorter than those during expiration. Such changes in heart rate are thought to be mediated through stretch receptors in and around the heart that elicit an increase in heart rate through the

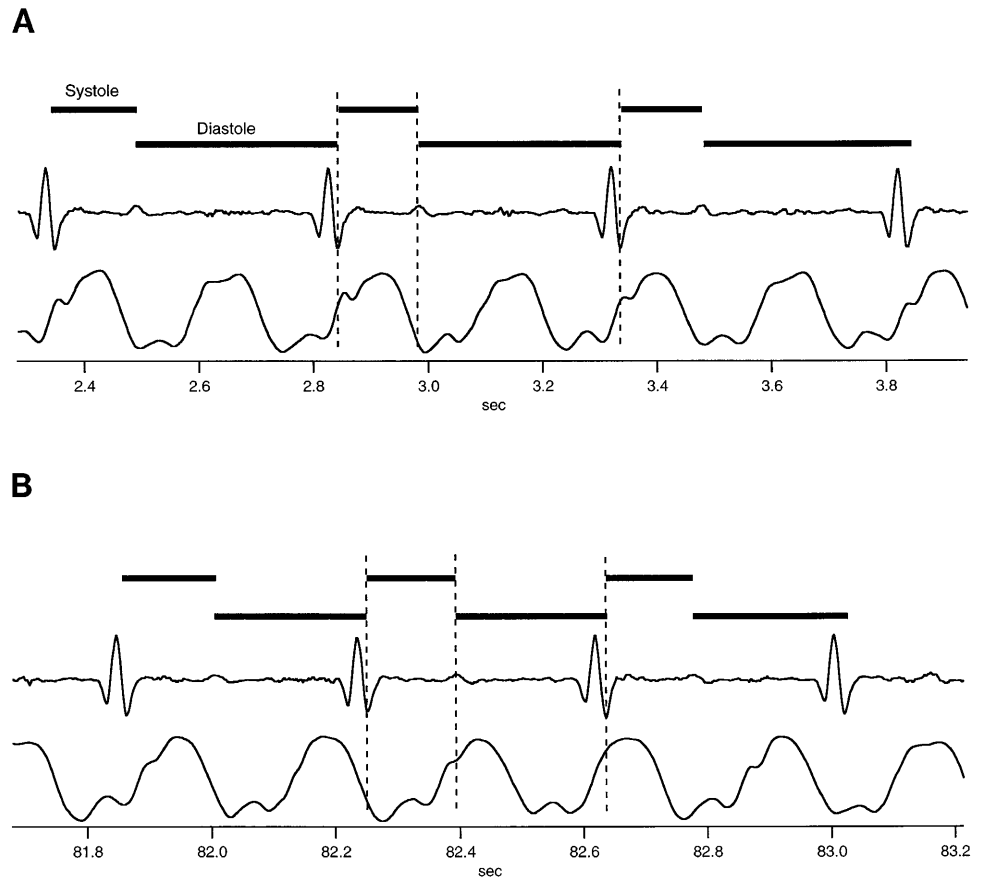


Fig. 8. Timing and duration of systole and diastole plotted relative to ECG signal and vertical acceleration of trunk for heartbeats that occur most frequently and are the longest (A) and for heartbeats that occur least frequently and are the shortest (B). In accelerometer trace (bottom), each large peak, lasting slightly less than 0.2 s, represents time in which feet are in contact with ground during a single step. Thus the most frequent heartbeats occur at beginning of support phase.

Bainbridge and baroreceptor reflexes (4, 16). Consequently, both ventilation coupled to the locomotor cycle and locomotor forces that influence vascular dynamics could possibly lead to phases of the stride in which the atria fill relatively rapidly because of increases in venous return. This would cause stretch reflex-mediated increases in heart rate that could be expected to result in the observed relationship between cardiac cycle duration and phase of the locomotor cycle.

Although the observed variation in diastole during trotting appears to result from a locomotor influence,

sorting out whether this modulation of cardiac function results from changes in preload or afterload is difficult. Preload, or the rate of ventricular filling, could possibly be affected by the locomotor cycle in at least two ways. First, pressure applied to veins by contracting skeletal muscles, in combination with one-way venous valves, acts to pump blood toward the heart. These oscillating skeletal muscle pumps presumably produce variations in the rate of venous return that would be expected to correlate with the specific phases of the locomotor cycle. Second, locomotor- and/or respiratory-induced changes

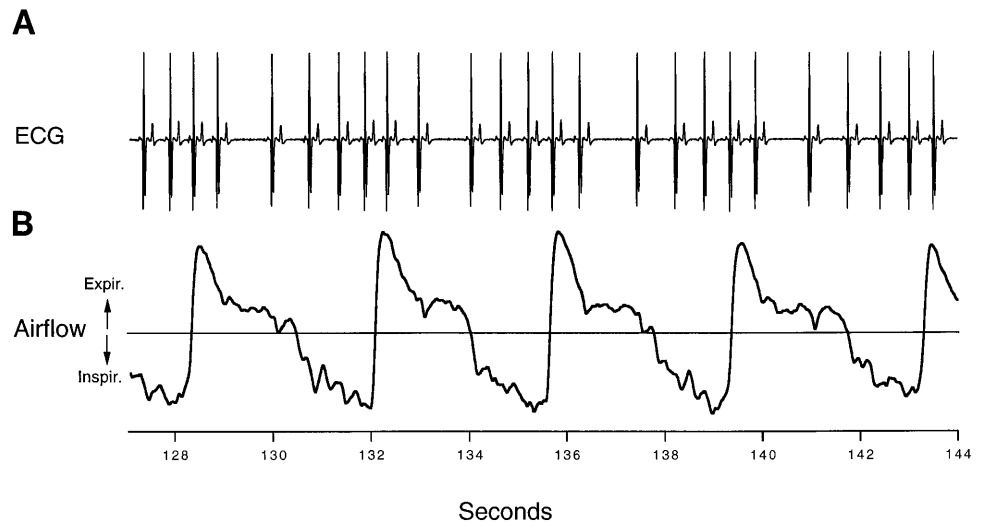


Fig. 9. Relationship between period of cardiac cycle and phase of lung ventilation in a resting dog. A: ECG. B: lung ventilation recorded at nares with mask-mounted screen pneumotach. Expiration (Expir) occurred when trace was above baseline, and inspiration (Inspir) occurred when trace was below baseline. Notice that shortest cardiac cycles occur during inspiration and that variation in cycle time is primarily because of differences in length of diastole (time from T wave to R wave).

in thoracic and abdominal pressures may vary the rate of venous return. However, changes in thoracic pressure can independently influence both ventricular filling and emptying (24). Consequently, this mechanism could either vary the rate of venous return and filling of the heart or vary the degree to which the ventricles empty (ejection fraction) and therefore the time required to fill the heart during the next cardiac cycle.

In those cardiac cycles of the shortest duration, diastole began early in the support phase of a step (Fig. 8B). These diastoles began during the phase of the locomotor cycle when there was peak loading of the skeletal muscles responsible for support. Thus these relatively short diastoles could potentially have been a result of enhanced venous return from the skeletal muscle pumps. Additionally, the short diastoles also corresponded to peak inspiratory airflow (9, 11) and therefore could possibly reflect enhanced venous return resulting from subatmospheric intrathoracic pressures aspirating blood to the heart from the vena cava. These mechanisms are not mutually exclusive, and both could play a role in enhancing venous return and thereby decreasing the duration of the cardiac cycle.

On the other hand, the cardiac cycles with the longest diastoles may either be a consequence of reduced venous return or greater ejection fraction, requiring a longer time for filling during the next cardiac cycle. Emptying of the heart could be facilitated by increased contractility of the heart or decreased afterload. In our dogs, systole of the cardiac cycles of longest duration began early in support and therefore completely overlapped the time in a step when thoracic pressure would have been elevated (Fig. 8). Elevation in thoracic pressure during locomotion can have a significant effect on vascular dynamics; for example, during galloping in horses thoracic pressures undergo transient elevations of 20 mmHg during each stride (26). Such elevations in thoracic pressures are known to reduce afterload and facilitate blood flow to the extremities (reviewed in Ref. 18). Consequently, the longer cardiac cycles observed in the dogs may possibly have been a consequence of a greater ejection fraction, which necessitated a longer period of filling during the next cardiac cycle and led to a longer diastole.

The question remains as to whether the pattern of longer cardiac cycles occurring at the beginning of limb support and the resulting transient coupling is of any functional significance. It is possible that this pattern reflects homeostatic reflexes of the heart that do not confer any improved energetic efficiency in blood transport during locomotion. Alternatively, if the increased thoracic pressure during support aids pumping of blood to the periphery, then the longer cardiac cycles that are associated with the beginning of support may represent an energetically advantageous way of pumping blood. Simultaneous recordings of the cardiac cycle (ECG) and cardiac output in trotting dogs may help resolve this question.

This influence of locomotion on the cardiac cycle (i.e., longer cardiac cycles at the beginning of limb support) was observed relatively rarely. It was most apparent at

the beginning of the exercise protocol. The absence of an interaction that occurs all the time may be due to variation in the physiological state of the running dogs. If the interaction is a function of venous return, then factors such as blood volume, blood viscosity, and sympathetic stimulation, which are important determinants of venous return, may play a role in whether the interaction occurs. For example, the heart is sensitive to changes in right atrial pressures over a discrete range; if factors such as a high blood volume or high sympathetic stimulation to the veins elevate the pre-load beyond this range, then the heart might be insensitive to changes in venous return caused by variation in the respiratory or locomotor pumps, and the interaction would be less apparent.

Would strict locomotor-cardiac coupling be advantageous? As outlined above, there are a number of reasons why locomotor-cardiac coupling might enhance the efficiency of blood delivery, and there are several reports of coupling in the literature. Consequently, the absence of consistent coupling in trotting dogs came as a surprise. However, one factor that may make strict coupling between the cardiac and locomotor systems impractical, and perhaps even disadvantageous, is the variation in venous return from the skeletal muscle pumps and respiratory pump that can be expected to occur on a stride-by-stride basis when animals run in the natural world. If the amount of blood returning to the heart varies from stride to stride, then a strict coupling of locomotor and cardiac cycles would result in variable stroke volumes and possibly ineffective pumping by the heart.

Venous return during locomotion can be expected to vary because animals move through a complex, three-dimensional landscape. Running animals are constantly forced to change direction and speed, avoid obstacles, and adjust to the angle of the terrain. Their speed and direction of travel are also influenced by conspecifics, predators, and prey. Thus, in a natural setting, stride rate, intramuscular pressures in each limb, and locomotor influences on thoracic pressure are all likely to vary with each step. Under these circumstances, venous return from the skeletal muscle and respiratory pumps and ejection fraction from the ventricles will likely be as variable as the strides the animals take. Effective cardiovascular function during periods when external variables are strongly influencing vascular dynamics may require that the cardiac pump follow the lead of the skeletal muscle and respiratory pumps. For example, it would likely be advantageous for heart rate to respond if venous return suddenly slowed or increased. Such a change in the cardiac cycle would be accomplished through the reflexes that control the rate and contractility of the heart (stretch of the sinus node, Bainbridge reflex, baroreceptor reflex, and Frank-Starling reflex). These reflexes enable modulation of both heart rate and stroke volume so that the cardiac pump maintains homeostasis. Hence the reflex capacity to vary heart rate and stroke volume may enable the cardiac pump to compensate for fluctuations in the circulation of blood caused by locomotion. We

suspect that this more subtle and complex coupling of cardiac function to the locomotor system is likely to be more effective in the production of efficient circulation than would be possible with a strict entrainment of the cardiac and locomotor cycles.

Perspectives

The results of this investigation suggest that dogs do not phase lock their locomotor and cardiac cycles during trotting. We hypothesize that variation in venous return and ventricular ejection during running in a three-dimensional, complex environment may make strict locomotor-cardiac coupling impractical. Although there does not appear to be tight coupling, the locomotor and/or ventilatory cycles appear to influence the cardiac cycle. Our data showed a repeatable pattern of cardiac cycles of longer duration occurring at the beginning of the support phase of a step rather than at other times in the step cycle. Because the length of diastole is what varies relative to the phase of the step cycle, we believe that this pattern is a function of the time required to fill the heart. It is unclear whether the pattern reflects variation in the rate of venous return or if it reflects greater emptying of the ventricles in the previous cardiac cycle. In either case, these data suggest that stretch receptors in and around the heart are modulating heart rate on a beat-by-beat basis. Variations in venous return and ejection fractions that are likely to result from running in a complex environment may make the reflexes that control the rate and contractility of the heart more important to homeostasis during locomotion than during rest.

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Address for reprint requests: D. R. Carrier, Dept. of Biology, 201 Biology Bldg., Univ. of Utah, Salt Lake City, UT 84112.

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