Running and Breathing in Mammals

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Summary. Mechanical constraints appear to require that locomotion and breathing be synchronized in running mammals. Phase locking of limb and respiratory frequency has now been recorded during treadmill running in jackrabbits and during locomotion on solid ground in dogs, horses, and humans. Quadrupedal species normally synchronize the locomotor and respiratory cycles at a constant ratio of 1:1 (strides per breath) in both the trot and gallop. Human runners differ from quadrupeds in that while running they employ several phase-locked patterns (4:1, 3:1, 2:1, 1:1, 5:2, and 3:2), although a 2:1 coupling ratio appears to be favored. Even though the evolution of bipedal gait has reduced the mechanical constraints on respiration in man, thereby permitting greater flexibility in breathing pattern, it has seemingly not eliminated the need for the synchronization of respiration and body motion during sustained running. Flying birds have independently achieved phase-locked locomotor and respiratory cycles. This hints that strict locomotor-respiratory coupling may be a vital factor in the sustained aerobic exercise of endothermic vertebrates, especially those in which the stresses of locomotion tend to deform the thoracic complex.

The capacity for sustained aerobic exercise (locomotion) is characteristic of both birds and mammals and has no doubt contributed to their evolutionary success. Mammalian locomotion in particular has been the object of intense investigation in recent years. Studies have been done to elucidate the characteristic movement patterns or "gaits" employed by various species (*1, 2*) as well as their biomechanical (*3–5*) and energetic (*6*) bases. Nonetheless, one basic aspect of mammalian locomotion has gone almost entirely without notice—namely, the manner in which mammals integrate respiration and locomotion. It is obvious, for example, that running mammals must effectively ventilate their lungs while in motion if sustained aerobic metabolism is to be achieved. But exactly how pulmonary function is accomplished under such conditions and to what extent body motion influences the respiratory process have not been determined by those concerned either with locomotor or respiratory phenomena. It now appears, however, that locomotor-respiratory integration must be included in any realistic evaluation of the form, function, and evolution of mammalian locomotor and respiratory mechanisms.

Physiological Evidence

Most of the evidence favoring an intrinsic linkage between locomotion and respiration in mammals has come from physiological experiments on anesthesized, decerebrate laboratory animals and from bicycle ergometer tests on humans. Early observations suggested that movement of the limbs could evoke changes in the breathing of anesthesized mammals (*7*). Subsequent studies have yielded many additional data in support of the neurogenic control of the respiratory response to exercise, especially the mechanism of hyperpnea (*8*). Although the source of such neurogenic stimuli is not known with certainty, various mechanoreceptors residing within the limbs have been implicated (*9*). For example, appropriate repetitive stimulation of somatic afferent nerves can lead to synchronized respiratory activity in cats (*10*), and partial entrainment of respiratory and stepping frequency has been observed in intact cats walking on a treadmill (*11*). However, central neuronal mechanisms, both hypothalamic (*12*) and spinal (*13*) may be capable of driving a proportioned response in locomotor and respiratory activity without proprioceptive input.

Human subjects may display complete or partial entrainment of respiratory rate to step or pedal frequency during tests on treadmills or bicycle ergometers (*14, 15*). However, the percentage of subjects exhibiting locomotor-respiratory synchronization in such experiments has varied greatly, and some investigators have found no evidence of entrainment (*16*). Questions of experimental design and analytical procedure have cast doubt on the results of some of these experiments (*15*). In particular, it is claimed that neurogenic factors have not been satisfactorily separated from possible metabolic influences on respiratory pattern. Experiments designed to eliminate this complication indicate that limb-based neurogenic mechanisms may have little, if any, effect on the entrainment of breathing to the pattern of limb movement (*15*).

Some physiological investigations provide strong evidence that locomotion can indeed influence respiratory pattern, particularly in quadrupedal mammals. The precise nature of the control mechanism is not understood, but both peripheral and central neurogenic elements are presumably involved. The human data are more equivocal, but some integration of respiratory and locomotor function seems evident (*14*), although perhaps not as rigorously enforced as in quadrupeds.

Even if locomotor control of respiration is accepted, information on its relative importance to the intact mammal or of its implications for locomotor and respiratory function under natural conditions is lacking. It is remarkable that there has been no serious effort to document the breathing patterns of mammals engaged in normal running behavior (*17*). If mammals have, in fact, evolved mechanisms to govern the interactions of the locomotor and respiratory systems, these mechanisms should be most apparent during sustained aerobic exercise, a behavior more often than not required for survival in natural settings.

Mechanical Constraints

Our interest in locomotor-respiratory coupling (LRC) was prompted by observations on the postcranial anatomy and running behavior of jackrabbits (*18*). This work suggested that running is likely to impose mechanical constraints on breathing that would require the respiratory cycle to be synchronized with gait.

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1) Locomotion and respiration both rely on cyclic movements in the same anatomic system, most specifically the thoracic complex (ribs, sternum, and associated musculature).

2) In quadrupedal species, the thoracic complex is subjected to repeated impact loading as the forelimbs alternately strike the ground.

3) The "upright" posture of therian mammals involves a support mechanism in which the anterior trunk is suspended by a muscular sling lashing the forelimb to the ribs and sternum (*19*). This design feature assures that the thoracic complex will be cyclically loaded in locomotion.

4) While running, the body is alternately accelerated and decelerated in the horizontal and vertical planes (*4*). Because the visceral mass is not firmly connected to the body frame, it can be expected to shift position within the abdominal cavity. Because visceral motion will be somewhat out of phase with that of the musculoskeletal frame, the abdominal mass potentially constitutes a "visceral piston," the movements of which could influence respiration by altering intra-abdominal and intrathoracic volume (and pressure).

5) In small to medium-sized mammals with limber backs, vertebral flexion and extension may contribute importantly to stride length (*20*) and may also result in major changes of body shape and internal volume, including that of the thoracic cavity.

These and other biomechanical considerations lead to the simple proposition that locomotion and respiration are not independent phenomena in running mammals. This is based on the assumption that locomotion imposes limits on respiratory function and that breathing must therefore be made to fit the locomotor cycle. A clear expectation is that the locomotor and respiratory cycles will be appropriately integrated so as to avoid antagonistic interactions. This reasoning points to a model of LRC in which phase locking of the two functions is predicted. What evidence is there to support this hypothesis?

Quadrupedal Mammals

Initial observations led us to predict an LRC ratio of 1:1 (one stride per breath) in fast-running jackrabbits (*21*). This idea was subsequently tested by training a young hare (*Lepus californicus*) to run on a motorized treadmill. High-speed frontal films provided a simultaneous record of breathing and gait (*22*). At slower running speeds, the jackrabbit utilized the half-bound gait, and respiratory movements were observed to be synchronized with the footfall cycle (Fig. 1). There were two complete breathing cycles per locomotor cycle (stride), thereby yielding an LRC ratio of 0.5:1 or 1:2. At higher speeds, the hare abruptly switched to the expected coupling ratio of 1:1, thereby halving its breathing frequency (Fig. 1A). This pattern was maintained as the animal gained speed. When forced to run near the transition speed (approximately 4.2 strides per second), the young jackrabbit repeatedly shifted between the two coupling ratios (*23*).

Inspection of the ventilatory and footfall patterns (Fig. 1B) shows that the 1:2 coupling program is associated with asymmetric breathing. A short inhalation is taken during that portion of the stride interval in which the forelimbs are in contact with the treadmill and the thoracic complex is under load. A substantially longer inhalation occurs when the body is supported by the hind limbs and the rib cage is unloaded. The shift from 1:2 to 1:1 coupling as speed and thoracic loading increases appears to involve the selective elimination of the shorter (and shallower?) breath while retaining the longer (deeper?) ventilatory cycle.

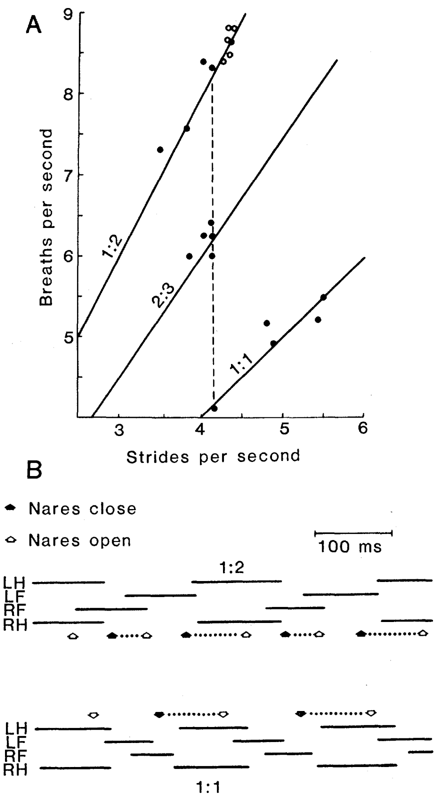

Fig. 1. (A) Relation between breathing and stride frequency in a young hare (*Lepus californicus*) running on a treadmill. Each data point is the mean of three consecutive strides. Solid points are data obtained when the animal was immature (approximately 500 grams); open points were obtained when it was subadult (approximately 1000 grams). (B) Comparison of limb support and respiratory sequences in the hare while it was running on a treadmill at LRC ratios of 1:2 and 1:1. Inhalation phases are indicated by dotted segments. See text, (*22*), and (*23*). Abbreviations: *LF* and *RF*, left and right forelimbs; *LH* and *RH*, left and right hind limbs.

Our investigation was next extended to free-running domestic dogs, horses, and humans. Simultaneous recordings of gait and respiration were obtained with a small stereophonic cassette recorder fastened to the subject. Breathing sounds were obtained on one channel from a miniature microphone placed inside an open-ended Styrofoam cone mounted over (humans) or immediately in front of the nose and mouth. The second channel recorded footfalls from an impact device fixed to the right forelimb (quadrupeds) or leg (humans) (*24*). All subjects were tested while running over flat ground.

Recordings were made on three large dogs (27 to 50 kilograms) while they were running beside a bicycle or automobile carrying their owners (*25*). In all three animals, breathing was found to be synchronized with the locomotor cycle. The LRC ratio was 1:1 during the trot and gallop. There appeared to be no attempt to alter this ratio even when the animals were run at speeds that caused them repeatedly to cross the trot-gallop transition.

Simultaneous recordings of gait and lung ventilation were also obtained from four horses (*25*). The animals (with rider) were tested while they ran distances of 200 yards to 1 mile. The gaits examined were the trot, canter (slow gallop), and fast gallop. Transitions between these gaits were recorded for each animal. All four horses displayed locomotor-respiratory integration, especially in the asymmetric gaits (canter and gallop) (*26*). Representative recordings of gait (footfall) and breathing during a trot and gallop are shown in Fig. 2, A and B. As in dogs, the fundamental coupling ratio was 1:1 in each gait. However, one horse, an 18-year-old gelding with little regular exercise, sometimes switched its breathing to an LRC ratio of either 2:1 or 3:1 for brief intervals (four to eight strides) while galloping. Two other horses, both 7-year-old geldings and regularly exercised, displayed no inclination to break from the 1:1 coupling pattern, even during galloping runs up to a mile in length. Although breathing and gait can be tightly coupled in the trot (Fig. 2A), more than half of our recordings of this gait in horses showed an absence of strict phase locking, and breathing was sometimes erratic. Rigorous coupling was almost always in evidence during the canter and gallop.

A detailed picture of the relation between the locomotor and ventilatory cycles of a horse in the canter and gallop is provided in Fig. 3 as reconstructed from slow-motion films of the same animal (*27, 28*). It permits a side-by-side comparison of the actual recordings of footfall and breathing sound, together with the limb support sequence, body position, and a theoretical loading curve for the thoracic complex. These data provide a clear indication of the actual pattern of locomotor-respiratory integration in a running mammal. They also seem to confirm our initial assumption that biomechanical constraints dictate the coordination of gait and breathing.

Inhalation and exhalation during the canter are represented by large, distinct bursts of sound (Fig. 3, left). The two phases of the pulmonary cycle are normally separated by a brief end-inspiratory pause (EIP). A critical feature is the timing of the respiratory cycle relative to thoracic loading. Thus, inhalation is more or less coincident with the departure of the lead forelimb (left in this case) from the ground and, therefore, the start of the off-loaded phase of the thoracic cycle. At this point, the horse leaves the ground and enters the floating or gathered suspension phase (position 4 in Fig. 3A). Air continues to flow into the lungs during the initial or on-loading portion of the thoracic cycle but truncates rapidly and appears to cease altogether (that is, EIP begins) as compressive loading of the rib cage escalates. Exhalation begins explosively near the point at which the thoracic complex experiences its peak load.

In the gallop, breathing remains coupled to gait, but significant adjustments are made. The most important of these adjustments is a phase shift (leftward) in the ventilatory cycle, with the result that it is now "in phase" with the thoracic loading cycle. Hence, in the fast gallop, inhalation is confined to the off-loaded interval when the horse is either entirely off the ground or is supported by the rear limbs only. Conversely, exhalation starts as the first (trailing) forelimb touches the ground and thoracic loading begins. Other adjustments of the respiratory cycle associated with the transition from canter to fast gallop are (i) increased breathing rate, (ii) loss of the EIP interval, and (iii) a probable reduction in tidal volume (*29*).

Humans

Humans alone among modern mammals utilize a striding bipedal gait. Paleontologic evidence suggests that bipedalism was the frequent or habitual mode of travel in the australopithecine predecessors of *Homo* (*30*). One important consequence of this unusual locomotor pattern is that the thoracic complex is no longer subjected to direct impact loading. It is necessary to ask, therefore, whether human runners are thereby released from the constraints seemingly imposed on the respiratory mechanism of quadrupedal runners. The answer appears to be no and yes.

Our sample of human runners included both experienced, conditioned runners and persons having little or no serious running experience (*31*). All subjects were tested while running on a quarter-mile outdoor track. The distances run varied from 0.25 to 1.25 miles (0.40 to 2.01 kilometers). The recordings included footfall and breathing signals during slow, moderate, and fast running speeds and, in some cases, walking in the "cooling off" period immediately following a run.

In the experienced human runners, breathing and gait were as tightly coupled as in quadrupeds (Fig. 2, C and D). Phase-locked locomotor and respiratory cycles were observed in these individuals for runs of up to 1.25 miles, the greatest distance for which we have a continuous recording (*32*). In the most experienced (marathon) runners, phase locking occurred within the first four or five strides of a run. Less experienced runners required somewhat longer distances before breathing and gait were fully coupled. In all cases, however, it was evident that breathing was entrained to gait and not the reverse. Breathing often remained locked to body motion for variable periods of time when runners slowed to a walk at the end of a run.

The inexperienced runners typically showed little or no tendency to synchronize gait and respiration (*33*). This was true even in individuals in good physical condition who maintained regular exercise programs other than running (for example, swimming). Although such persons were almost always able to maintain a steady limb rhythm (that is, stride frequency), their concurrent respiratory cycles were characterized by marked irregularities of frequency and amplitude. This contrasts sharply with the clockwork precision of the LRC observed in experienced human runners.

An important difference between humans and those quadrupedal species so far examined lies in the apparent range of LRC ratios available to human runners. Although quadrupeds are largely confined to a 1:1 ratio, humans use at least five distinct coupling patterns. The predominant ratio for man appears to be 2:1 (Fig. 2C). This ratio can be used over a wide range of speeds and stride frequencies (*34*). Slower sustained running speeds are frequently accompanied by a ratio of 4:1 (Fig. 2D). Experienced runners commonly began a run with a 4:1 ratio and later switched to 2:1 as the run progressed (Fig. 2E). Shifts in coupling ratio occurred quickly and smoothly over just a few strides. This was also the case in quadrupedal species. In humans, these abrupt changes in breathing pattern are often not associated with detectable changes of gait. Most alterations in

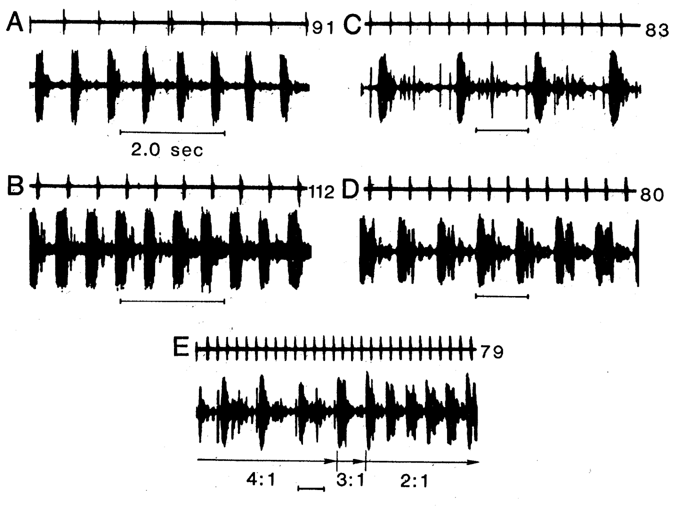

Fig. 2. Oscilloscope records of gait and breathing in free-running mammals. Upper trace in each record is footfall of right forelimb (horses) or leg (human). Lower trace is breathing pattern as recorded from a microphone in a face mask. (A) Horse at trot; (B) horse at gallop; (C) human at 4:1 coupling ratio; (D) human at 2:1; and (E) human during shift from 4:1 to 2:1. Number following upper trace is stride rate per minute. Time scale is 2.0 seconds in all cases. (A) and (B) were recorded from different horses; (C) to (E) were recorded from the same human during a single run. Prominent bursts in the breathing signal are exhalations.

coupling ratio appear to be triggered by involuntary stimuli, and most of our runners were unaware of shifting from 4:1 to 2:1, even though this represented an abrupt change in respiratory frequency. Other sustained LRC ratios observed in humans running at moderate speed were 3:1, 2.5:1 (5:2), and 1.5:1 (3:2). Our data indicate that an LRC ratio of 1:1 is not normally used by humans on flat ground (*35*). This ratio may be sustained, however, while ascending (and descending?) sloped surfaces wherein cyclic loading of the body is high, stride frequency is relatively low, and metabolic demand is intensified (*36*).

The integrated 2:1 locomotor-respiratory cycle of an experienced human runner is depicted in Fig. 4. The pattern is more complex than that of the horse, primarily in that a single ventilatory cycle is spread over two complete locomotor cycles or strides (four steps). Just as in quadrupeds, bulk flow of air to and from the lungs occurs in discrete pulses rather than as smooth biphasic flow. Exhalation begins in the floating phase of the locomotor cycle. Most air is expelled in a large initial burst (*E*) beginning at or very near the impact of the left foot. A smaller secondary burst (*E*′) during the subsequent support phase of the right foot completes the exhalation portion of the respiratory cycle. Inhalation is also commonly represented by two bursts (*I* and *I*′), both of much lower amplitude than those of exhalation (*24*). Inhalation is nearly always followed by a pronounced EIP interval. This pause begins with the push-off or reacceleration phase of support at a time when body loading is presumably greatest. It continues until the body reaches the top of its trajectory in the float phase. The time spent in exhalation is noticeably longer than that devoted to inhalation.

Human runners in whom breathing and gait are tightly coupled are "footed"; that is, the beginning and end of a respiratory cycle are associated with the same footfall when even coupling ratios are used (4:1 or 2:1). Therefore, the ventilatory cycle is keyed to a particular foot and remains so for run after run, and even during transitions between coupling patterns (Fig. 2E). Thus, the runner depicted in Fig. 4 is left-footed. This illustration also reveals that the gait of experienced runners can be decidedly asymmetric, a fact previously documented in elite distance runners (*37*). The result is that the center of gravity is raised higher during push-off by one leg than the other; consequently, body loading is expected to be asymmetric as well (*28*). It remains to be seen, however, whether this phenomenon is the natural consequence of the integration of gait and breathing.

Implications

The data we have reviewed, although limited, leave little doubt that mammalian LRC is a real and potentially significant phenomenon. This realization is at once exciting and distressing. It is exciting because with it comes a whole family of new questions, problems, and issues relating to the structure and function of the mammalian respiratory and locomotor mechanisms. It is disturbing in that nearly all current models of mammalian ventilatory mechanics (*38*), locomotor energetics (*6*), and gait selection (*1, 2, 5, 39*) have been framed without consideration of the constraints that may be imposed on locomotor and respiratory function by virtue of their linkage. The LRC concept therefore has numerous implications for future studies in these areas. Here, we restrict our attention to a small sampling of these.

Our findings, together with those already available for birds (*40, 41*), indicate that locomotor-respiratory integration may be a general requirement for sustained aerobic activity among endothermic vertebrates. This is probably especially true for those species in which the thoracic complex is subjected to cyclic mechanical loading as a result of propulsive activity. In mammals at least, the foundation of the integrative mecha-

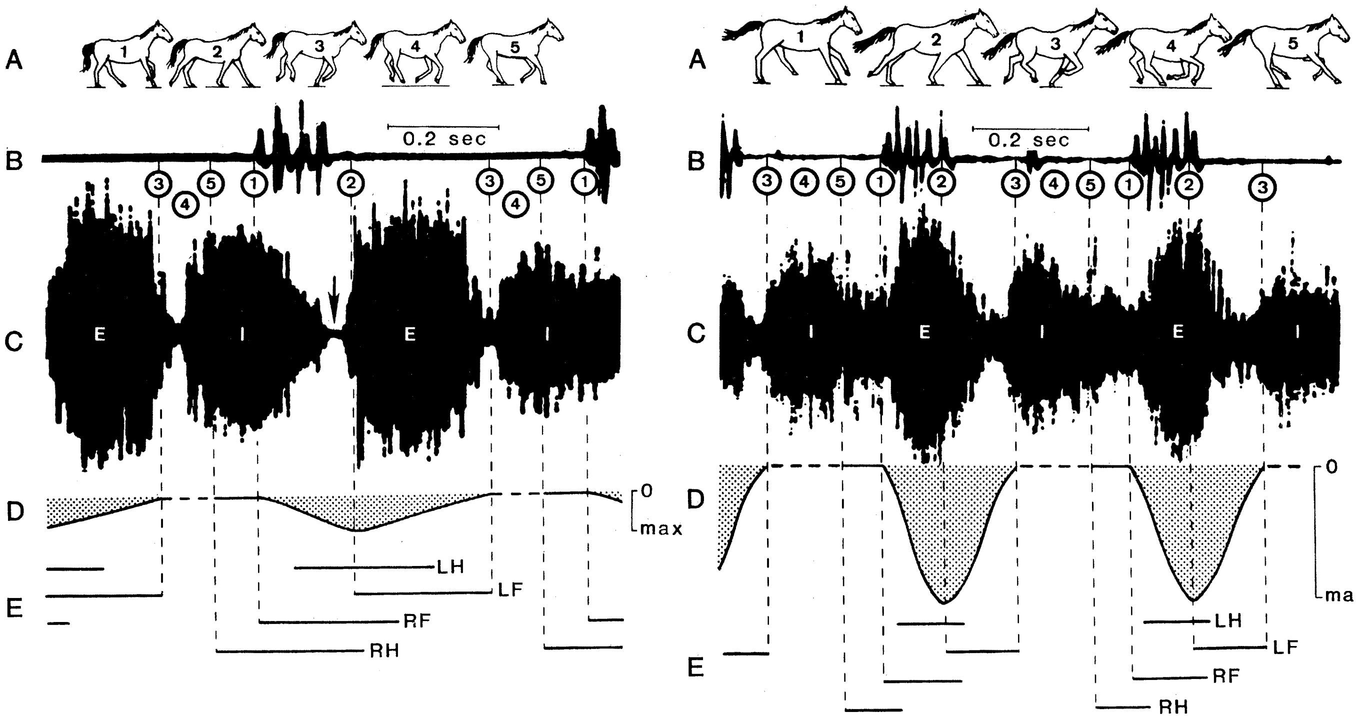

Fig. 3. Relationships of locomotor and respiratory cycle in the same horse at a canter (left) and gallop (right). (A) Tracings of body position at five selected points in locomotor cycle. (B) and (C) Oscilloscope tracings of footfall and breathing. (D) Hypothetical loading profile for thoracic complex (*28*). (E) Standard support diagram for the gait. Loading increases in the gallop as the animal spends a larger fraction of each stride off the ground. The arrow indicates the end-inspiratory pause. Abbreviations: *E*, exhalation; *I*, inhalation; *LF* and *RF*, left and right forelimbs; *LH* and *RH*, left and right hind limbs. See text for discussion.

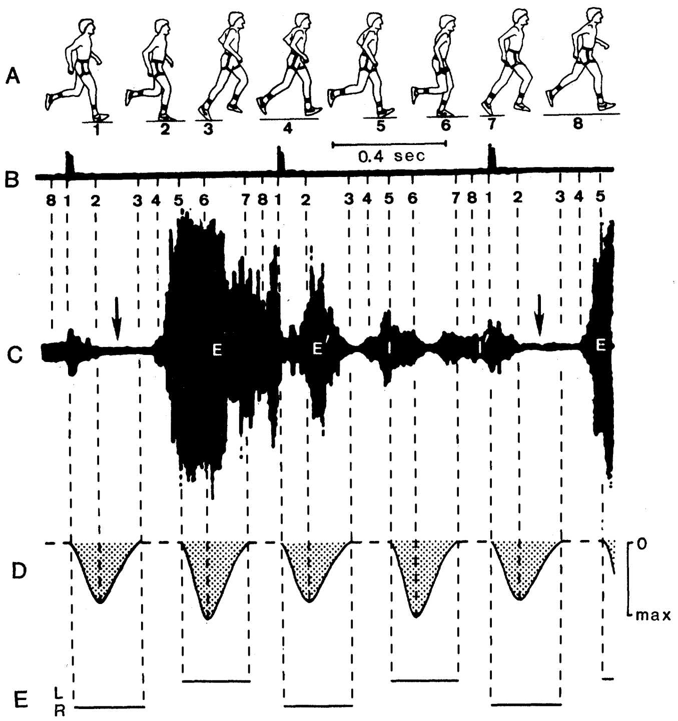

Fig. 4. Relation of gait to respiratory pattern coupled at 2:1 in an experienced human runner. Parameters are same as in the previous illustration except that the loading cycle applies to the body as whole rather than just to the thorax. Note the asymmetry of gait and the pronounced end-inspiratory pauses. See text for discussion.

nism for locomotion and breathing may be quite ancient. The mechanism is known to exist in at least four orders of mammals (Primates, Carnivora, Perissodactyla, and Lagomorpha). Unless independently acquired, some form of locomotor-respiratory integration must have been present in the common ancestor of these lineages. Such an animal would have been a small, primitive eutherian of middle or late Cretaceous period (*42*). It is likely to have been of ambulatory but certainly not cursorial locomotor habit. Therefore, although LRC would seem to have its greatest advantage in duration runners, the underlying regulatory mechanisms may have first developed in early mammals with little or no capacity for such activity. It is not yet known whether gait and respiration are phase locked in marsupials. If this should prove to be the case, then LRC may well be a primitive therian trait perhaps related to the development of upright posture and a peculiar shoulder complex that suspends the trunk from the ribs and sternum. If so, we would not expect synchronization of gait and breathing in monotremes, which lack this form of body suspension.

The LRC model also raises questions regarding current ideas on locomotor and respiratory function in running mammals. For example, in quadrupedal mammals, stride frequency increases linearly with increasing speed in the walk and trot, but remains essentially constant in the gallop (*43*). Because speed is the product of stride rate and stride length, nearly all gains in speed above the trot-gallop transition must result from longer stride. If breathing and gait are coupled at a 1:1 ratio, breathing rate will likewise become approximately fixed as the gallop begins. Since oxygen consumption continues to rise linearly with speed in the gallop up to the point of maximum aerobic capacity (*44*), we must ask how the mammal meets the increased demand for air without adjusting its breathing frequency.

If oxygen consumption is assumed to be a constant fraction of lung ventilation (that is, tidal volume times respiratory rate), this can only mean that compensation is accomplished by increasing the depth (tidal volume) of each breath, since respiratory rate is fixed by stride frequency. This implies that tidal volume may be proportional to stride length in a galloping mammal. To appreciate this possibility, one needs only to consider that in small and medium-sized mammals, stride length in the gallop is achieved through increased oscillation of the axial skeleton, including the thoracic region. Such a mechanism for adjusting lung ventilation would presumably be unavailable to those large cursorial species (for example, horses) that run with rigid vertebral columns.

One fact that emerges clearly is that respiratory rate is not an independent variable in exercising (running) mammals. When tied to gait, this important respiratory parameter must vary directly with stride frequency. Any adjustment in breathing rate at any given running speed must therefore require a change of coupling ratio. Such switches of ratio are now known to occur in rabbits, horses, and humans. Exactly how widespread this ability is among running mammals is not known, but available data suggest that the variety of ratios employed by humans is exceptional. The basic coupling ratio for quadrupeds is apparently 1:1, and some species may be confined to it (for example, dogs). In humans, 2:1 is the dominant ratio, but at least five others (4:1, 5:2, 3:1, 3:2, and 1:1) are available when needed. One result of this difference is that at any particular stride frequency, the respiratory rate of a human can be substantially lower than that of a quadruped. A possible explanation for the flexibility of coupling patterns in humans could be the relaxation of mechanical constraints associated with the adoption of a bipedal habit (*45*).

The functional significance of variable or selectable coupling ratios is one of the more intriguing issues to arise from the LRC concept. As a consequence of the elastic resistance of the thorax, airway resistance and dead space volume, there presumably exists a specific rate and depth of breathing that optimizes ventilatory efficiency (*46*). It would be surprising, therefore, if such shifts in breathing pattern during running were not related to the control of respiratory efficiency and, thereby, the overall energetic cost of locomotion. There is now evidence that among quadrupeds, changes of gait (for example, from trot to gallop) act to minimize the incremental cost of transport as running speed increases (*39*). However, even though the trot-gallop transition may entail a major adjustment in the locomotor program, there is no departure from the 1:1 coupling pattern in either horses or dogs. Humans differ in that increases in running speed are not attended by changes of gait. The inability of humans to change gait while running implies that their exceptional capacity to alter breathing pattern could to some extent represent an alternative strategy for regulating energetic cost. In this view, variable coupling in humans becomes a kind of pulmonary gearing mechanism within a fixed locomotor program.

If gait constrains respiration, it is conceivable that respiration may in some instances affect or even dictate locomotor pattern. The possibility that vertebral oscillation during the gallop of lighter-bodied mammals could be a means of regulating depth of breathing has already been mentioned. Similarly, respiratory limitations may provide an explanation for why larger cursors normally retain only a single suspension (that is, gathered) in the gallop (*2*). Elimination of the extended suspension stage means that the fall of the body is first broken by the hind limbs, thereby avoiding full impact on the thoracic complex (see Fig. 3). Thus, although horses appear to choose speeds within their various gaits that minimize energetic cost (*39*), until such factors as stride frequency, stride length, and integrated breathing pattern are also examined, respiratory constraints cannot be excluded as a determinant of optimal gait selection in mammals.

Finally, our study provides a clear answer to the long-standing question of whether locomotion is a significant regulatory factor in mammalian respiration. It is. The data from free-running mammals strongly support the concept of neurogenic control, but do not indicate the relative importance of peripheral as opposed to central mechanisms in such control. Nonetheless, our data provide nearly as convincing evidence that neurogenic factors alone cannot account for respiratory patterns in running mammals. The shift of LRC ratio in human runners (from 4:1 to 2:1) occurs without any detectable alteration in the motor program. This indicates that other stimuli, probably metabolic, trigger the change of breathing. But it is equally clear that such adjustments in respiratory pattern are only possible within rather specific boundaries imposed by locomotor constraints.

That a detailed examination of the interactions between locomotion and respiration in mammals has been delayed so long is surprising, especially in view of the early recognition (*47*) and subsequent investigation of this issue in birds (*40, 41*).

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19. Principal components of this sling are the serratus ventralis (serratus anterior of man), levator scapulae, and pectoralis muscles.
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21. D. M. Bramble and D. Carrier, *Am. Zool.* **19**, 909 (1979).
22. Synchronized high speed film and whole body plethysmographic recordings of *Lepus* and *Oryctolagus* established that the inhalation and exhalation phases of the respiratory cycle were associated with distinct movements of the nose and narial valves.
23. When more fully grown, the hare was constrained by treadmill size. It would not or could not obtain sufficient speed to shift to the 1:1 ratio.
24. The microphone (Sony ECM-150) was highly directional, giving strong exhalation but weaker inhalation signals. The recorder was an AIWA TP-S30. Recordings were analyzed on a dual-beam storage oscilloscope (Tektronix 5111) and chart recorder (Gould 2400).
25. The dogs were a golden retriever and two Doberman pinschers; the horses were two quarter horses, one thoroughbred, and one mixed-breed Morgan.
26. Nostril movements obtained from high-speed (144 frames per second) films of galloping Mongolian wild horses (*Equus przewalskii*) indicate 1:1 coupling of locomotion and breathing.
27. The films (64 frames per second) were studied frame by frame on a motion analyzer (Vanguard). The timing of various events in the cycle was averaged over several smooth strides covered by the taped breathing and footfall record. This permitted a statistical fit between film and tape records with the footfall signal providing a convenient synchronization marker.
28. Body loading profiles (Figs. 3D and 4D) are based on the kinematic profile of the subject. Magnitude is proportional to the amount of time spent in the air relative to that on the ground. Peak gravitational load corresponds with the lowest point of the center of gravity during the support phase, an expectation consistent with actual force platform records (*4*).
29. Our recordings tended to show an inverse relation between the rate and amplitude of the exhalation signal. Hörnicke *et al.* (*17*) reported an inverse relation between breathing frequency and tidal volume in their horses.
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31. Twelve individuals (eleven males and one female, aged 20 to 45) were studied. Six were experienced runners and had individual exercise programs varying from 15 to 70 miles per week. The other six individuals had had little or no regular running experience.
32. This recording was from an experienced marathon runner (best time, 2 hours and 40 minutes) and was obtained shortly after the completion of an 8-mile training run.
33. One inexperienced runner demonstrated substantial coupling (2:1) but his breathing amplitude was erratic. Other runners in this category showed occasional coupling for brief intervals (five to ten strides) but did not sustain this pattern.
34. One experienced runner used a ratio of 2:1 over stride rates extending from 56 per minute in a cooling-off walk to 170 per minute in a moderate sprint.
35. Data provided by J. Daniels and N. Oldridge [*Med. Sci. Sports* **2**, 107 (1970)] indicate that, under stress, one of their world-class runners sustained a 1:1 ratio at a 3-mile race-pace during high altitude acclimatization tests. Their other runners appear to have used the 2:1 ratio.
36. The metabolic cost of running uphill is substantially higher than running on a horizontal surface, especially for larger mammal [D. B. Dill, *J. Appl. Physiol.* **20**, 19 (1965); C. R. Taylor, S. L. Caldwell, V. J. Rowntree, *Science* **178**, 1096 (1972); Y. Cohen, C. T. Robbins, B. B. Davitt, *Comp. Biochem. Physiol. A*, **61**, 43 (1978)].
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45. Although we have no data from bipedal saltatory mammals, the marked vertical oscillation of the vertebral column in these animals leads us to predict that their breathing and gait are rigidly coupled at a 1:1 ratio.
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48. We thank D. Alstad, J. Beck, A. Beck, S. Fakkema, C. Herl, K. Morton, and B. Wicks for the use of their animals in this study; L. Radinsky and K. Thomas for data on human running performance; and M. Hildebrand, C. Gans, G. Goslow, S. Emerson, and L. Radinsky for comments on the manuscript. This study was supported by funds from NIH biomedical research support grant RR07092 to the University of Utah.