

MECHANICS OF SIX-LEGGED RUNNERS

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Summary

Six-legged pedestrians, cockroaches, use a running gait during locomotion. The gait was defined by measuring ground reaction forces and mechanical energy fluctuations of the center of mass in *Blaberus discoidalis* (Serville) as they travelled over a miniature force platform. These six-legged animals produce horizontal and vertical ground-reaction patterns of force similar to those found in two-, four- and eight-legged runners. Lateral forces were less than half the vertical force fluctuations. At speeds between 0.08 and 0.66 ms⁻¹, horizontal kinetic and gravitational potential energy changes were in phase. This pattern of energy fluctuation characterizes the bouncing gaits used by other animals that run. *Blaberus discoidalis* attained a maximum sustainable stride frequency of 13 Hz at 0.35 ms⁻¹, the same speed and frequency predicted for a mammal of the same mass. Despite differences in body form, the mass-specific energy used to move the center of mass a given distance (0.9 J kg⁻¹ m⁻¹) was the same for cockroaches, ghost crabs, mammals and birds. Similarities in force production, stride frequency and mechanical energy production during locomotion suggest that there may be common design constraints in terrestrial locomotion which scale with body mass and are relatively independent of body form, leg number and skeletal type.

Introduction

Insect gaits and stepping patterns have been described extensively, because insects are used as models for the study of neural function (Delcomyn, 1981). However, few studies have directly addressed the mechanics of six-legged locomotion. The kinetics and kinematics of locomotion have been used primarily as a tool for understanding the interaction of peripheral force inputs and the neural control of locomotion (Delcomyn, 1985; Cruse, 1976). Graham (1983) suggested that the walking behavior of stick insects, as well as of other insects, is fundamentally different from that of birds and mammals. Stick insects simultaneously exert braking and propulsive forces during part of each stride. At certain periods during the leg cycle, the front or middle legs actively resist the forward motion of the body, producing a 'lurching' type of locomotion which may preclude mechanisms of energy exchange and transfer used in animals with different numbers of legs.

Key words: locomotion, mechanics, energetics, insects.

Despite differences in body size, body form, type of skeleton, leg number and leg orientation, animals as diverse as crabs, birds and mammals exhibit remarkable similarities in their locomotor mechanics. Quadrupedal and bipedal mammals, bipedal birds and eight-legged, sideways-running ghost crabs produce similar patterns of force and mass-specific energy changes during locomotion (Cavagna *et al.* 1977; Fedak *et al.* 1982; Heglund *et al.* 1982a; Blickhan and Full, 1987). These remarkable similarities reflect the common use of two basic mechanisms for minimizing energy expenditure by alternately storing and recovering energy. The first mechanism operates during walking. As the animal's center of mass rises and falls, kinetic and gravitational potential energy are exchanged rather than lost, in a manner analogous to a swinging pendulum or an egg rolling end over end (Cavagna *et al.* 1976, 1977; Heglund *et al.* 1982a). While hopping, trotting and galloping, animals use a second mechanism analogous to what occurs in a bouncing ball. In large animals, elastic elements such as tendons alternately store and release energy during each stride (Cavagna *et al.* 1964; Heglund *et al.* 1982b). Not only do birds, mammals and ghost crabs appear to use similar mechanisms of locomotion, but they also perform similar amounts of mechanical work per unit of mass (Heglund *et al.* 1982b; Blickhan and Full, 1987).

The results obtained from studies on ghost crabs indicate that the energy-conserving mechanisms which operate in vertebrates could be general features of legged locomotor systems. If this proves to be the case, then proposed explanations of mechanical similarity should not be based on morphology and physiology unique to birds and mammals. With data on only a single species of arthropod, the ghost crab, generalities may be premature. The locomotor mechanics of the most successful terrestrial animals, the insects, have not been examined. To address the question of whether fundamental patterns exist in the terrestrial locomotion of legged vertebrates and arthropods, we quantified the energetics of the center of mass of a six-legged insect, the cockroach, *Blaberus discoidalis*. This species was easily induced to run, and was of sufficient size to produce forces during locomotion which could be measured and resolved with our miniature force platform.

Materials and methods

Animals

Blaberus discoidalis (mean mass 2.6 g; $N=13$) were obtained from Carolina Biological Supply Company. Cockroaches were housed in individual plastic containers with a layer of cedar shavings. Animals were given water and Purina Puppy Chow, *ad libitum*. All cockroaches were kept on a local photoperiod at ambient temperatures ($24\pm 2^\circ\text{C}$).

Running track

A track was constructed with Plexiglas walls to contain the animals during filming and force measurements. A cardboard floor gave the animals sufficient

traction to prevent slippage. The force platform was inserted into the floor of the track, flush with the running surface and 50 cm from the start of the track. The animals ran into a darkened cardboard box placed 10–20 cm from the force platform.

Force measurements

We measured vertical and horizontal ground reaction forces using a miniature force platform based on a design by Heglund (1981). A platform measuring 10.7 cm × 6 cm × 0.06 cm and weighing 3.07 g was constructed of model aircraft plywood and mounted on four brass beams (Fig. 1). Semiconductor strain gauges were bonded to spring blades cut from the brass supporting beams at each corner of the platform. Cross-talk between vertical and horizontal outputs was less than 2%. Compensating gauges at each corner reduced drift due to temperature change. Loads in the range 0.001–0.1 N produced a linear response with a maximum variation across the platform of less than 7% (Fig. 2A). Test signals were digitally filtered using a Butterworth filter with zero phase shift. After repeated testing, we selected a cut-off frequency of 185 Hz (unloaded natural frequency of the platform = 400–650 Hz). This cut-off frequency did not result in amplitude modulation or loss of any signal components. Fig. 2B shows the effects of filtering and the phase response of the force platform for a known signal generated by a pendulum.

To measure lateral forces, we rotated the force platform 90°. Gauges which measured force in the horizontal direction were then in position to measure lateral forces. Vertical and lateral forces were measured simultaneously for each trial.

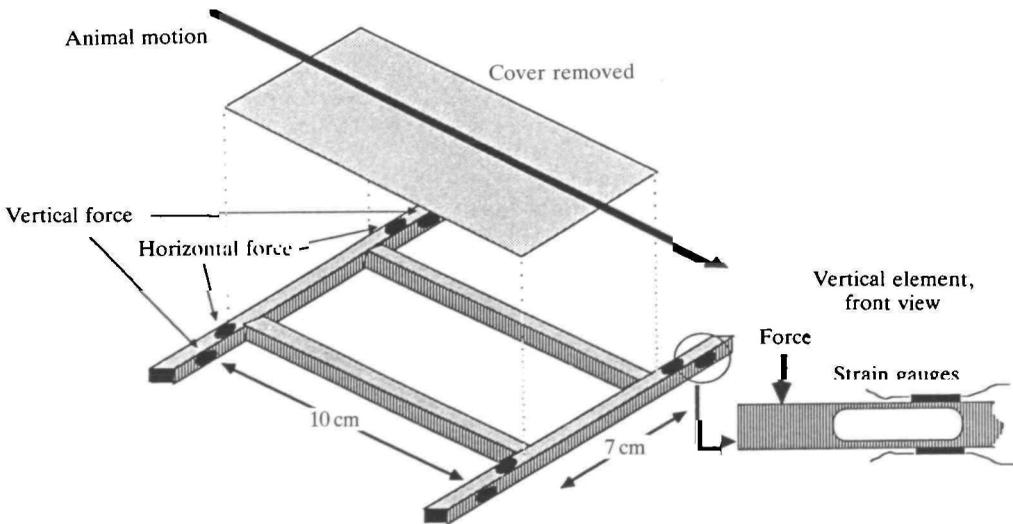


Fig. 1. (A) Miniature force platform. Semiconductor strain gauges mounted on spring blades are sensitive to vertical and horizontal deformation of the beams caused by forces exerted when the animal moves over the wooden cover (see Heglund, 1981).

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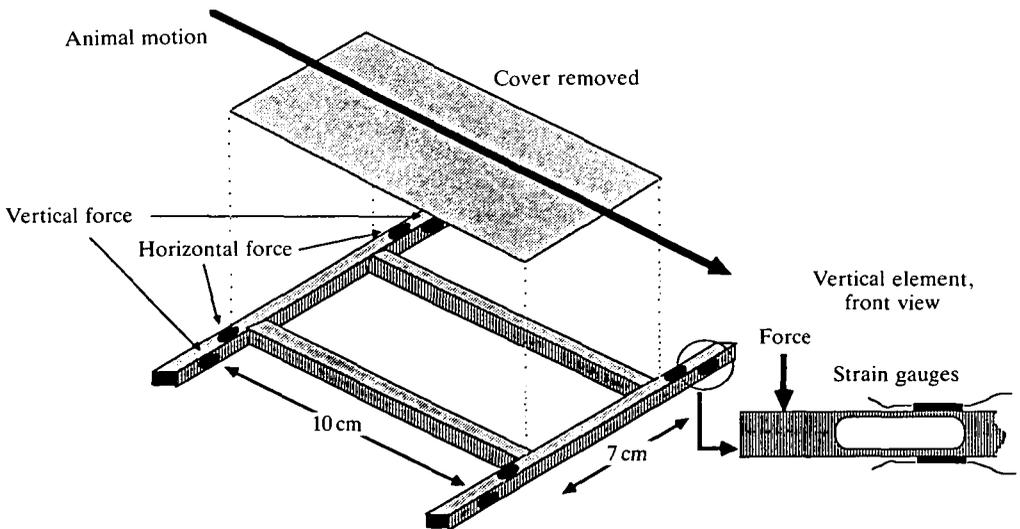


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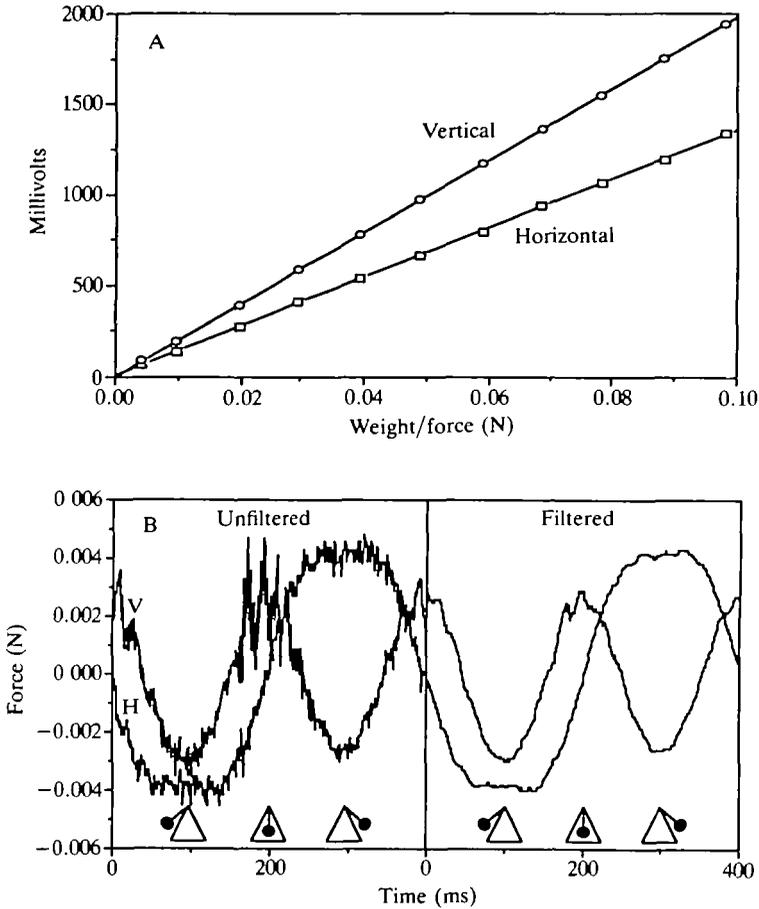


Fig. 2. Force platform performance measures. (A) Calibration curves for vertical and horizontal force. Both calibrations produced a linear output for the range of forces the animals generated (mean of $N=6$ at each weight; $r^2=1.00$ for both functions; bars showing \pm S.E.M. are not shown because they are smaller than the size of the points). (B) Vertical (V) and horizontal (H) forces generated by a pendulum attached to a stand and placed on the force platform. Forces produced by the swinging pendulum (position shown at the bottom of the figure) match theoretical predictions. Signal conditioning (i.e. filtering; left vs right side of figure) did not affect signal amplitude or phase relationships.

Data acquisition

Signals from each force platform channel were amplified (Vishay, Measurements Group), and collected by an analog to digital converter (C-100, Cyborg) interfaced with a computer (IBM PC/AT). Force signals were sampled at a frequency of $1000 \text{ samples s}^{-1}$. Integrations of force records were performed using data acquisition and analysis software (Discovery, Cyborg). Energy fluctuations were calculated using macros linked in electronic spreadsheets (Lotus).

Kinematic analysis

Each trial was taped using a video camera (Video Logic CDR460) capturing 60 frames s^{-1} . Top and lateral views were filmed simultaneously by placing a mirror at a 45° angle above the track. A digital timer placed in the camera's field enabled us to synchronize video and force records. Video frames were grabbed and the coordinates of the leg positions at each frame were digitized into a computer (IBM PC/AT) with a video analysis system (Peak Performance Technologies Inc.).

Speed

An animal's speed was calculated from the video recordings by dividing the force platform length by the time taken to cross the platform. This value was checked independently with the force records by dividing the length of the force platform plus the body length of the animal by the duration of the vertical force recording. The two methods produced values in agreement to within 10%. In the case of some very high-speed trials ($>0.60 \text{ m s}^{-1}$), for which the video record was less precise for speed determination, only the latter method was used.

Stride period and frequency

At speeds above 0.14 m s^{-1} , the maxima and minima of the vertical force recording clearly defined each stride period (i.e. one complete cycle of protraction and retraction of a leg). Synchronization of the video recordings with the force recordings showed that the stride periods determined by the force record agreed with those recorded on the video tape. At the slowest speeds, the vertical force patterns were less clear, and stride periods were determined by video analysis alone. Stride frequencies were calculated from the duration of the stride or strides selected from the trials used for energy analysis.

Velocity and displacement of the center of mass

The horizontal and lateral velocity of the center of mass were calculated by integrating the horizontal and lateral force recordings, respectively. The vertical velocity of the center of mass was calculated from integration of the vertical force recording, minus the body mass. An additional integration of the vertical velocity yielded the vertical displacement of the center of mass. The animal's average speed was used as the integration constant for the horizontal velocity of the center of mass. The integration constants for the vertical and lateral component of velocity and for the vertical displacement of the center of mass were assumed to be zero. Drift in the horizontal and vertical force signals was negligible (Fig. 3). Trials in which the animal changed direction or bumped into the walls of the track were rejected. Time segments from each trial were selected for analysis if they contained an integral number of strides and if the sum of the increases and decreases in speed was within 10% of the animal's average speed.

Energy calculations

Calculations of the energy fluctuations of the center of mass were performed as in Blickhan and Full (1987), Cavagna (1975) and Heglund *et al.* (1982a). The horizontal, lateral and vertical kinetic energies of the center of mass (E_k) were calculated from the equation: $E_k = \frac{1}{2}M_b v^2$, where v is the horizontal, lateral or vertical velocity and M_b is the body mass. The gravitational potential energy of the center of mass (E_p) was calculated from the vertical displacement (h) and the gravitational acceleration (g) according to the equation: $E_p = M_b g h$. The total energy of the center of mass (E_{cm}) was the sum of the vertical and horizontal kinetic energies and the gravitational potential energy at each sampling period (1 ms). The power needed to lift and accelerate the center of mass (\dot{E}_{cm}) was calculated from the sum of the positive increments of E_{cm} over an integral number of strides, divided by the duration of the strides.

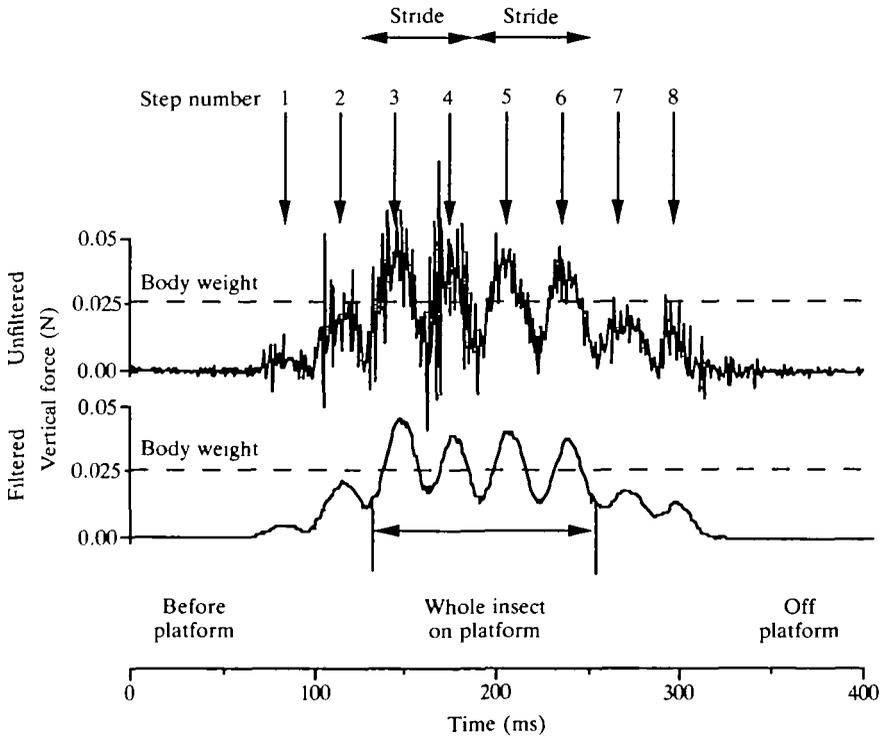


Fig. 3. Unprocessed and filtered vertical ground reaction force. No force fluctuations were recorded before the animal stepped on the platform. As the animal first stepped on the platform with one or two legs, a force signal was generated. Each step taken by the insect was correlated with a vertical force maximum. Two steps or two complete vertical force cycles equalled one stride, since the animals were using an alternating tripod gait in which three legs moved synchronously. When the insect was completely on the platform, the vertical force oscillated around the body weight. Vertical force decreased to zero as the animal left the platform. Signal processing (i.e. filtering) did not affect the phase or amplitude of the signal. No baseline correction was necessary.

Results

Gait and ground reaction forces

As a cockroach moved over the force platform, distinct maxima and minima were apparent in the ground reaction forces (Fig. 3). Each vertical force maximum was correlated with a step observed on the video tape. The period of two vertical force cycles was correlated with a stride period (i.e. the length of time required to complete one leg cycle). Video analysis showed that cockroaches used an alternating tripod gait at speeds from 0.08 to 0.66 m s⁻¹. The right front, left middle and the right hind legs all moved simultaneously in a step, while each moved out of phase with its contralateral pair (Fig. 4A). Maximal horizontal accelerating force occurred near the end of retraction. Maximal horizontal decelerating force occurred as one set of legs contacted the ground following protraction, while the other set began retraction. Over most of the speed range tested, the summed forces of the legs produced two discrete maxima on the vertical recordings during each stride (Fig. 4B, t_1 and t_3). Vertical force decreased to below body weight (Fig. 4B, t_2) as the center of mass rose (Fig. 4F) following upward acceleration by the legs (Fig. 4D). As the center of mass fell, the vertical force increased. Horizontal force increased as the legs accelerated the center of mass forward, and decreased as the legs produced braking forces at the end of each step (Fig. 4C,E). Below 0.14 m s⁻¹, the movements of the three legs comprising each alternating tripod were not as tightly coupled as during faster speeds, resulting in small vertical force maxima which corresponded to discrete steps by individual legs. The overall pattern of horizontal force, however, did not change as a function of speed.

Lateral force fluctuations were less than half the magnitude of the vertical force fluctuations (Fig. 5). Because lateral forces were less regular than vertical or horizontal forces, we performed a Fourier transform on vertical and lateral force signals that had been recorded simultaneously. Both vertical and lateral force patterns showed the greatest spectral magnitude at one frequency over the range of speeds measured. The ratio of vertical to lateral signal frequency was 1.8 ± 0.1 (s.d.) for 20 trials. The period of the lateral force signal was twice that of the vertical signal. Each lateral force maximum or minimum was in phase with the maxima of vertical force (Fig. 5B, C). When an animal accelerated forwards and upwards, it also generated a lateral force which pushed it towards the side with only a single leg of the tripod on the ground (Fig. 5A, with arrows, and B). The maximum lateral force showed some variation in phase with respect to the vertical force. The phase relationship depended on whether the animal first pushed to the side, and then pushed upwards and forwards, or whether it pushed upwards and forwards and then to the side.

Phase relationship between horizontal kinetic and gravitational potential energy

Fig. 6A shows the phase relationship between horizontal kinetic and gravitational potential energy (Fig. 4H, I). Both signals were considered to be periodic

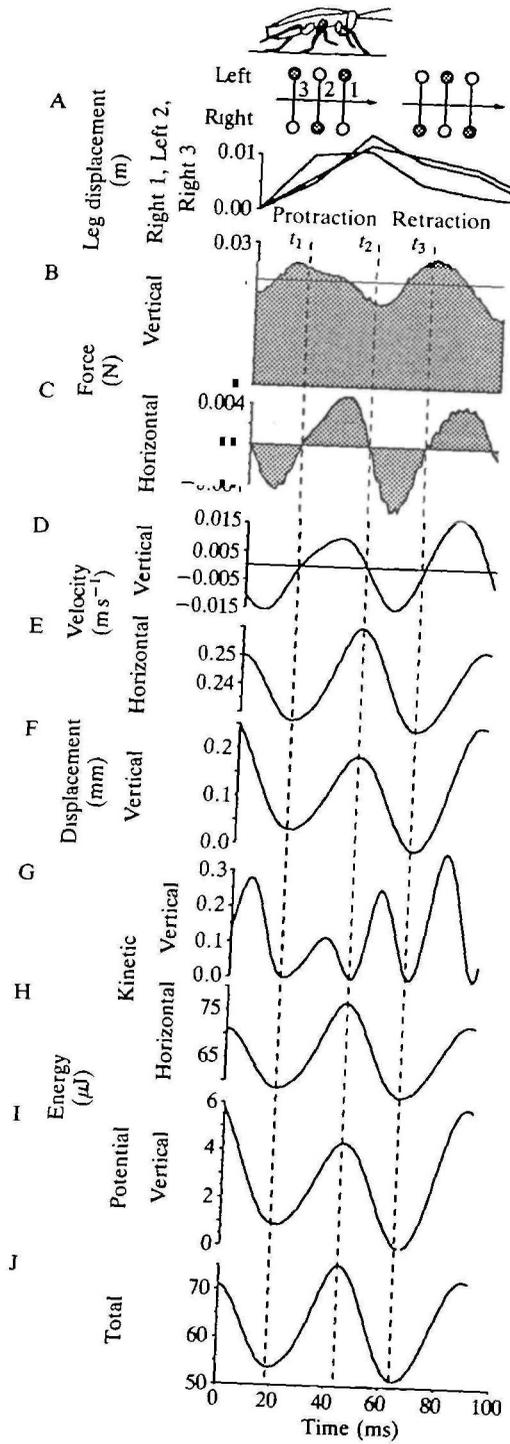


Fig. 4

Fig. 4. Gait, force, velocity, displacement and energy of the center of mass during one stride (i.e. one complete leg cycle) of a 2.3 g (0.022 N) cockroach travelling at just less than 0.25 m s^{-1} . (A) Tarsal leg position relative to the body in which maxima show leg in complete protraction and minima show leg in complete retraction. The gait used was an alternating tripod in which the right front, left middle and right hind legs all moved simultaneously, while each moved out of phase with its contralateral pair. In the gait diagram filled circles represent legs on the ground (retracting), whereas open circles show legs in protraction. (B) Vertical and (C) horizontal forces obtained from the force platform; (D) vertical and (E) horizontal velocity calculated by integration of the force recordings; (F) vertical displacement obtained from integration of the vertical velocity tracing; (G) vertical kinetic energy; (H) horizontal kinetic energy; (I) gravitational potential energy and (J) total energy fluctuations of the center of mass (E_{cm}). Horizontal line in B represents the animal's weight.

functions that repeat every step (i.e. every half of the stride period shown in Fig. 4 from time $t=0$ to t_2). If the maximum of gravitational potential energy for one step was in phase with the nearest maximum of horizontal kinetic energy, we defined this as a zero phase shift. If the nearest maximum of horizontal kinetic energy preceded the nearest maximum of gravitational potential energy, the shift was considered negative. If the nearest maximum of horizontal kinetic energy followed the maximum of gravitational potential energy, the shift was considered positive. If the horizontal kinetic and gravitational potential energy were completely out of phase, the phase shift would equal $\pm 180^\circ$. The mean phase shift was -7.6 ± 7.6 (s.e.) and was not significantly different from zero. Horizontal kinetic and gravitational potential energy were in phase. Phase shift was not a significant function of speed ($F_{(1,46)}=4.0$, $P>0.05$; $r^2=0.08$, therefore the slope, β , was zero).

Energy recovery

The alternating tripod gait used by the cockroaches did not result in energy conservation by pendulum-like energy exchange. Vertical potential energy changes tended to be in phase with fluctuations in horizontal kinetic energy at all speeds (Figs 4H, I, 6A). The magnitude of energy recovery can be calculated by comparing the mechanical energy needed to sustain a constant forward speed if no energy exchange occurred, with the amount of energy actually expended. Energy recovery can be expressed by the following equation:

$$\% \text{ recovery} = \frac{(\Sigma \Delta E_k + \Sigma \Delta E_p - \Sigma \Delta E_{\text{cm}})100}{\Sigma \Delta E_k + \Sigma \Delta E_p},$$

where $\Sigma \Delta E_k$, $\Sigma \Delta E_p$ and $\Sigma \Delta E_{\text{cm}}$ are the sums of the positive changes in the kinetic, potential and total energy of the center of mass, respectively. In an ideal system in which pendulum-like energy exchange occurs, energy recovery will be 100%. For the cockroaches, recovery values varied around a mean of 15.7% (Fig. 6B). The

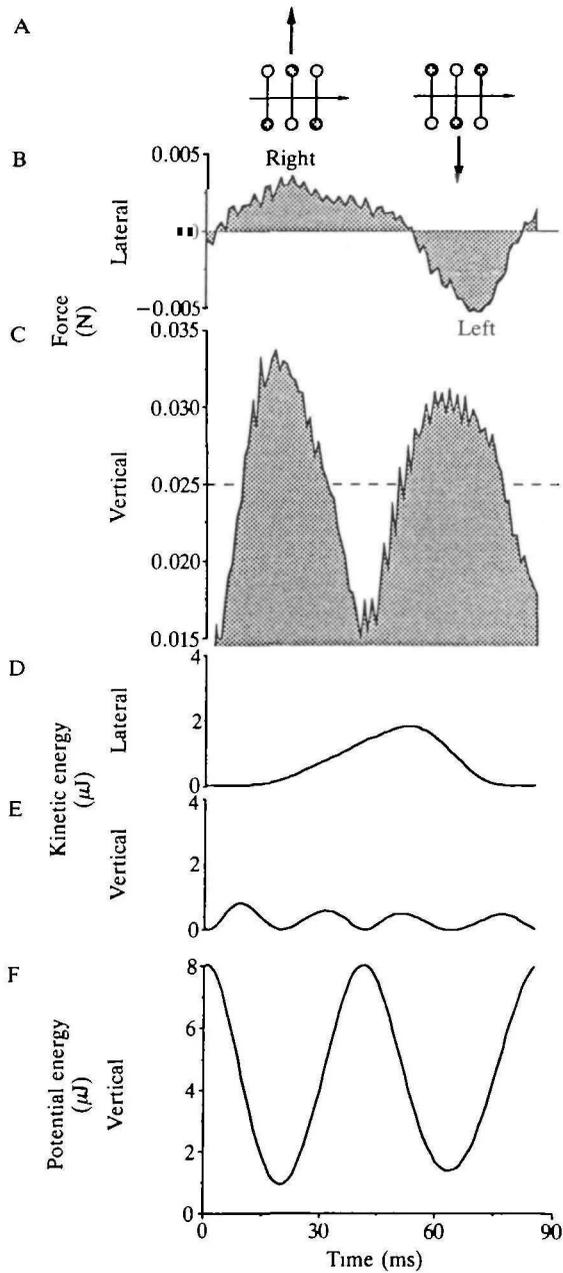


Fig. 5

percentage of energy recovered did not vary as a function of speed ($F_{(1,50)}=0.27$, $P=0.60$, therefore the slope, β , was zero; Fig. 6B).

Stride frequency

Stride frequency increased linearly with speed from 0.08 m s^{-1} to approximately

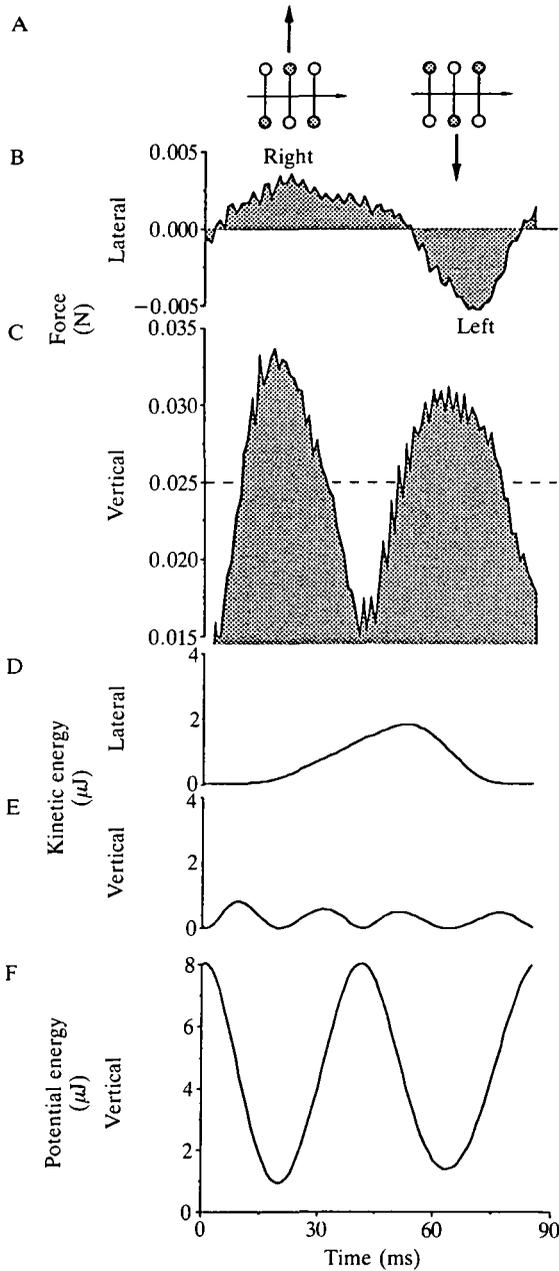


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Fig. 5. Lateral and vertical force production compared for one stride period of an animal running at 0.36 m s^{-1} . (A) Lateral forces were generated by the side of the body with two legs on the ground (represented by filled circles in gait diagram), causing the animal to move laterally in the direction shown by the arrows. Fluctuations in (B) lateral force, (C) vertical force (dashed line represents body weight), (D) lateral kinetic energy, (E) vertical kinetic energy and (F) gravitational potential energy. Positive lateral force values represent a push to the right. Negative lateral force values represent a push to the left. Fluctuations in lateral force were smaller than vertical force changes. The magnitudes of vertical and lateral kinetic energy changes were small compared with those of potential energy. The magnitudes of vertical and lateral kinetic energy changes had little effect on the total energy fluctuations of the center of mass.

0.35 m s^{-1} (Fig. 7). Above this speed, stride frequency attained a maximum. Increases in speed above 0.35 m s^{-1} were achieved by increasing stride length.

Mechanical energy of the center of mass

The mass-specific power used to lift and accelerate the center of mass (\dot{E}_{cm} , W kg^{-1}) increased linearly with speed (v , m s^{-1}): $\dot{E}_{\text{cm}} = 0.89 \pm 0.097v$ (S.E.) $- 0.029$ (Fig. 8). At speeds between 0.08 and 0.23 m s^{-1} , gravitational potential energy and horizontal kinetic energy changes were approximately equal in magnitude. Fluctuations in lateral kinetic energy were more comparable to fluctuations in vertical kinetic energy, but less than one-tenth that of changes in potential energy (Fig. 5D, E, F). The contributions of vertical and lateral kinetic energy fluctuations to the total energy changes of the center of mass were negligible. As speed increased, the mechanical power used to accelerate the center of mass forward increased, whereas the mechanical power used to accelerate the center of mass upwards did not show a systematic change with speed. Consequently, at the fast speeds, the total mechanical power was determined primarily by the fluctuations in horizontal kinetic energy.

Discussion

Gait, ground reaction forces and energy fluctuations of the center of mass

Over nearly the whole speed range tested, *B. discoidalis* utilized an alternating tripod stepping pattern similar to the symmetrical running gaits of other insects (Hughes, 1952; Delcomyn, 1971), eight-legged ghost crabs (Blickhan and Full, 1987) and trotting four-legged vertebrates (Fig. 4A). Two sets of proplusors moved the body. Cockroaches have been described as using a speed-independent 'walking' gait at intermediate and fast speeds and a speed-dependent 'walking' gait at very slow speeds (Delcomyn, 1971; Kozacik, 1981). However, Spirtio and Mushrush (1979) found speed independence at very low stride frequencies. In some cases, the transition between these 'gaits' may be graded (Hughes, 1952). Hughes (1952) concluded that cockroach 'walking' and 'running' are indistinguishable.

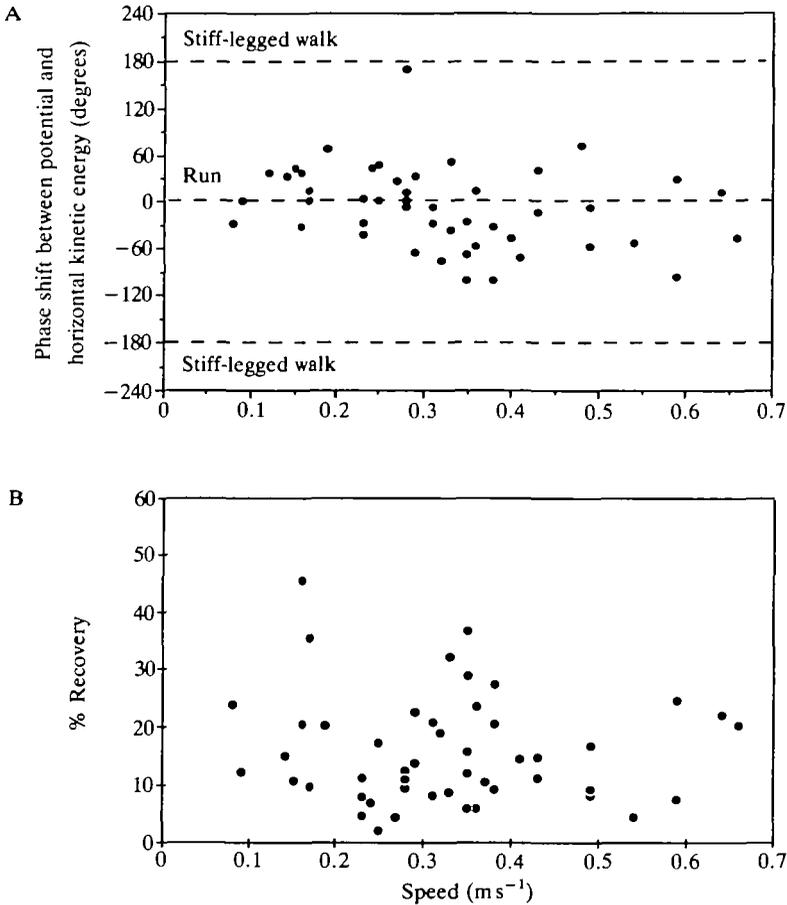


Fig. 6. (A) Phase shift between horizontal kinetic and gravitational potential energy. Cockroaches showed a near-zero phase shift similar to that found in running mammals and ghost crabs. Insufficient evidence was obtained to support the use of a pendulum-like, stiff-legged walk (180° phase shift). (B) Percentage energy recovery as a function of speed. Energy recovery by pendulum-like energy exchange did not vary as a function of speed for cockroaches, whereas crabs at slow speeds can recover or transfer as much as 50% of the energy (Blickhan and Full, 1987).

In the present study we used stepping pattern, stride frequency and mechanics to define walking and running. Data on *B. discoidalis* suggest that cockroaches used a running gait at nearly all speeds. We found no evidence of a walking gait in which a pendulum-like energy exchange was used, even at stride frequencies as low as 3 Hz. At very slow speeds, locomotion became intermittent, and only rarely did cockroaches sustain a constant average speed for more than a few strides. Similar results have been reported for mammals such as squirrels and chipmunks (Heglund *et al.* 1982a).

Pendulum-like energy exchange can characterize walking gaits. Analysis of whole-body mechanics in walking birds and mammals has revealed that horizontal kinetic

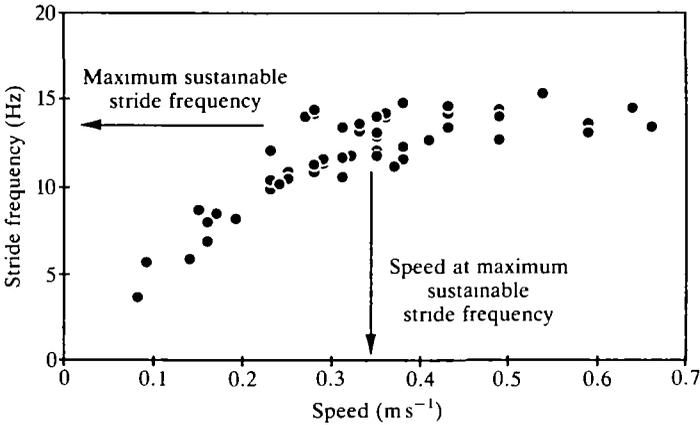


Fig. 7. Stride frequency as a function of speed. Cockroaches attained a maximum sustainable stride frequency at the same speed (0.35 m s^{-1} for a 2.6 g cockroach) predicted by scaling stride frequency at the trot–gallop transition with body mass using the relationship derived for quadrupeds (Heglund *et al.* 1974).

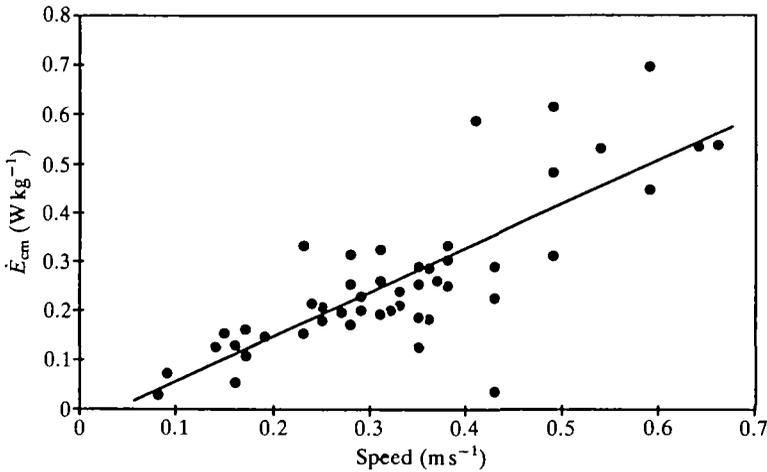


Fig. 8. Mechanical power used to lift and accelerate the center of mass (\dot{E}_{cm}) as a function of speed (v). \dot{E}_{cm} was calculated on the basis of an integral number of strides. $\dot{E}_{\text{cm}} = 0.89 \pm 0.097v - 0.029$.

energy and gravitational potential energy fluctuate out of phase, allowing energy transfer (Cavagna *et al.* 1977). Energy transfer or recovery by walking birds and mammals reduces the energy required to sustain a constant speed by 55–70% (Cavagna *et al.* 1977; Heglund *et al.* 1982a). Pendulum-like energy exchange is not restricted to two- and four-legged walkers. We have discovered similar results in a

sideways travelling, eight-legged ghost crab (Blickhan and Full, 1987). Horizontal kinetic energy and gravitational potential energy in *B. discoidalis* fluctuated in phase (Fig. 6A). The low recovery values indicated that cockroaches did not utilize an effective pendulum-like mechanism of energy conservation at any speed (Fig. 6B).

Cockroaches used a running gait over the entire speed range we observed. These six-legged runners produced patterns of ground reaction forces that are virtually indistinguishable from those produced by trotting eight-legged crabs and four-legged mammals and running bipeds (Fig. 4B,C; Cavagna *et al.* 1964, 1977). The symmetrical oscillation of vertical force (i.e. duration and amplitude of vertical force above and below body weight) supports our hypothesis that cockroaches were running or bouncing with a step frequency near their natural frequency (Cavagna *et al.* 1988). The shape of the vertical force (F_v) pattern can also be described at any time T by a modified Fourier series (Alexander and Jayes, 1978), where $F_v = a[\cos(\pi/T) - q\cos(3\pi/T)]$ from the time a foot is set down ($-T/2$) to when it is lifted ($+T/2$). For *B. discoidalis*, the shape factor describing the force pattern ($q = -0.1$ to 0) and duty factor (the fraction of a stride duration a foot is on the ground, $\beta = 0.5$) corresponded to a trot when compared with two- and four-legged vertebrates.

The time course of mechanical energy fluctuations is also a defining feature of vertebrate running gaits. During running or bouncing gaits, horizontal kinetic and gravitational potential energy of the center of mass fluctuate in phase. Based on these relationships of energy transfer and leg movement, we found that eight-legged ghost crabs show a transition from walking to slow running or trotting (Blickhan and Full, 1987). By these criteria, the alternating tripod gait used by *B. discoidalis* was a run, similar to the bouncing gaits of two-, four- and eight-legged animals (Fig. 6; Blickhan and Full, 1987; Cavagna *et al.* 1977; Heglund *et al.* 1982a). *Blaberus discoidalis* did not attain an aerial phase although, at the fastest speeds, vertical force decreased to less than one-fifth of the animal's weight. The absence of an aerial phase does not exclude the gait from being a run or a trot. Human subjects running with increased knee flexion adopt a gait in which vertical displacement of the center of mass decreases and the aerial phase is reduced to zero (McMahon, 1985).

Results from our present study on cockroaches suggest that insect locomotion is fundamentally similar to locomotion in two- and four-legged vertebrates. However, one investigator's study of 'walking' in stick insects reached a different conclusion. Stick insects walk using 'lurching' locomotion during which legs simultaneously exert braking and propulsive forces during part of the stride cycle (Graham, 1983). The resulting velocity changes of the body relative to the leg movements are unlike those which characterize vertebrate walking. Patterns of horizontal velocity fluctuations seen in cockroach locomotion are similar to those described in stick insects, yet cockroaches attained high speeds. The pattern of horizontal velocity fluctuations is actually similar in cockroaches and running, as opposed to walking, vertebrates. The use of lurching gaits by insects would be

expected to increase metabolic costs greatly (Graham, 1983). However, locomotor economy in *B. discoidalis* is not significantly different from that of other pedestrians of a similar mass (Herreid and Full, 1984; R. J. Full and A. Tullis, in preparation). Graham (1983) hypothesized that the type of walking behavior observed in stick insects may be necessary for insects to maintain static stability. Our preliminary data indicate that, at high speeds, cockroaches may not rely on static stability, but use dynamic adjustments instead. Rather than being a general feature of insect locomotion, lurching gaits may be a phenomenon restricted to slow walking speeds, or peculiar to stick insects.

Stride frequency

As quadrupedal mammals increase speed, they typically switch from a trot to a gallop. Further increases in speed are achieved by increasing stride length, while stride frequency remains relatively constant. Among mammals, both speed and maximum sustainable stride frequency at the trot-gallop transition scale predictably as a function of body mass (Heglund *et al.* 1974). Smaller mammals switch from a trot to a gallop at lower speeds and higher stride frequencies than larger mammals. We have shown that eight-legged ghost crabs follow this same trend (Blickhan and Full, 1987). Surprisingly, *B. discoidalis* attained a maximum sustainable stride frequency as it increased speed (Fig. 7). To our knowledge this is the first demonstration of a maximum sustainable stride frequency in insects, although data from Delcomyn (1971) suggest the possibility for another species of cockroach. The maximum sustainable stride frequency and the speed at which it was attained scaled as predicted from data on quadrupedal mammals (Heglund *et al.* 1974).

Patterns of stride frequency, speed and ground reaction force for six-legged *B. discoidalis*, eight-legged crabs and two- and four-legged vertebrates suggest that animals representing a great diversity of body forms may operate in a similar manner, while running at 'comparable' speeds (Full, 1989). For the first time, quantification of stride frequency, external force production and energy fluctuations may allow comparisons of 'equivalent' gaits in very different morphological designs. The following simple calculation using a scaling model supports this possibility.

The hypothesis of dynamic similarity for terrestrial locomotion predicts that animals of different size will move in a similar fashion whenever they move at speeds proportional to the square roots of their effective leg length or hip height (Alexander and Jayes, 1983). Dynamic similarity is achieved when Froude numbers (the ratio of inertial to gravitational forces, u^2/gl , where u represents speed, g is acceleration due to gravity and l is a general characteristic of length such as hip height) are equal. Based on its Froude number (2–3 where $l=0.4$ cm), *B. discoidalis* is predicted to show a gait change between 0.3 and 0.4 m s⁻¹. This corresponds to the speed at the maximum sustainable stride frequency and is the speed at which quadrupeds change from a trot to a gallop. Precise definition of a

gait change in *B. discoidalis* at the maximum sustainable stride frequency must await further kinematic analysis.

It appears that the observed patterns of force production, mechanical energy fluctuation and stride frequency or period could be described by a model based on an oscillating spring and mass system (R. Blickhan, unpublished results; Cavagna *et al.* 1988; McMahon, 1985). The fact that six- and eight-legged runners produce force patterns similar to those in mammals suggests a comparable whole-body stiffness. Animals may very well operate as tuned mechanical spring systems possessing similar spring-like characteristics (R. Blickhan, unpublished results; McMahon, 1985; Taylor, 1985). Similarities in mechanics may be due to similar material properties of the muscles or connective tissues.

Mechanical energy of the center of mass

The mechanical energy of the center of mass (E_{cm}) represents one component of the total mechanical energy generated during locomotion (Heglund *et al.* 1982*b*). The internal energy (E_i) produced to accelerate the limbs relative to the body, elastic strain energy (E_e) and the transfer of energy between segments add to the total mechanical energy of the system. The largest fraction of the energy appears to be involved in lifting and accelerating the center of mass, E_{cm} . However, in large fast-moving mammals E_i can equal or exceed E_{cm} (Heglund *et al.* 1982*b*). The magnitude of E_e is unknown.

The rate of mass-specific mechanical work used to move the center of mass of a cockroach increased with speed and was not significantly different from that used by a mammal, bird or ghost crab moving at the same speed (Fig. 8). The amount of mechanical energy generated to move 1 kg of animal 1 m is approximately 1 J, regardless of body form. The contribution of E_i remains to be quantified. However, the combined limb-mass relative to the body is small for *B. discoidalis*, and trunk rocking appears to be minimal. Consequently, the contribution of E_i is likely to be smaller than the upper limit of 32% estimated for ghost crabs (Blickhan and Full, 1987). The magnitude of E_e for *B. discoidalis* is not known, although the ability of small animals to store and recover elastic strain energy may be limited (Biewener *et al.* 1981). Large mammals using bouncing gaits can alternately store and recover energy in elastic elements, such as tendons. Recovery of this elastic strain energy would reduce the mechanical energy that must be generated by muscles to maintain a constant running speed.

In summary, similarities in force production, stride frequency and mechanical energy production during locomotion suggest that there may be common design constraints for terrestrial locomotion, which scale with body mass and are relatively independent of body form, leg number and skeletal type.

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References

- ALEXANDER, R. McN. AND JAYES, A. S. (1983). A dynamic similarity hypothesis for the gaits of quadrupedal mammals. *J. Zool. Lond.* **201**, 135–152.
- ALEXANDER, R. McN. AND JAYES, A. S. (1978). Vertical movements in walking and running. *J. Zool., Lond.* **185**, 27–40.
- BIEWENER, A., ALEXANDER, R. McN. AND HEGLUND, N. C. (1981). Elastic storage in the hopping of kangaroo rats (*Dypodomus spectabilis*). *J. Zool., Lond.* **195**, 369–383.
- BLICKHAN, R. AND FULL, R. J. (1987). Locomotion energetics of the ghost crab. II. Mechanics of the centre of mass during walking and running. *J. exp. Biol.* **130**, 155–174.
- CAVAGNA, G. A. (1975). Force platforms as ergometers. *J. appl. Physiol.* **39**, 174–179.
- CAVAGNA, G. A., FRANZETTI, P., HEGLUND, N. C. AND WILLEMS, P. (1988). The determinants of the step frequency in running, trotting and hopping in man and other vertebrates. *J. Physiol., Lond.* **399**, 81–92.
- CAVAGNA, G. A., HEGLUND, N. C. AND TAYLOR, C. R. (1977). Mechanical work in terrestrial locomotion: Two basic mechanisms for minimizing energy expenditure. *Am. J. Physiol.* **233**, R243–R261.
- CAVAGNA, G. A., SAIBENE, F. P. AND MARGARIA, R. (1964). Mechanical work in running. *J. appl. Physiol.* **19**, 249–256.
- CAVAGNA, G. A., THYS, H. AND ZAMBONI, A. (1976). The sources of external work in level walking and running. *J. Physiol., Lond.* **262**, 639–657.
- CRUSE, H. (1976). The function of legs in the free walking stick insect, *Carausius morosus*. *J. comp. Physiol.* **112**, 135–262.
- DELCOMYN, F. (1971). The locomotion of the cockroach *Periplaneta americana*. *J. exp. Biol.* **54**, 443–452.
- DELCOMYN, F. (1981). Insect locomotion on land. In *Locomotion and Energetics in Arthropods* (ed. C. F. Herreid and C. R. Fourtner), pp. 103–125. New York: Plenum Press.
- DELCOMYN, F. (1985). Insect locomotion: past, present and future. In *Insect Locomotion* (ed. M. Gewecke and G. Wendler), pp. 1–18. Berlin: Paul Parey.
- FEDAK, M. A., HEGLUND, N. C. AND TAYLOR, C. R. (1982). Energetics and mechanics of terrestrial locomotion. II. Kinetic energy changes of the limbs and body as a function of speed and body size in birds and mammals. *J. exp. Biol.* **79**, 23–40.
- FULL, R. J. (1989). Mechanics and energetics of terrestrial locomotion: From bipeds to polypeds. In *Energy Transformation in Cells and Animals* (ed. W. Wieser and E. Gnaiger), pp. 175–182. Stuttgart: Thieme.
- GRAHAM, D. (1983). Insects are both impeded and propelled by their legs during walking. *J. exp. Biol.* **104**, 129–137.
- HEGLUND, N. C. (1981). A simple design for a force-plate to measure ground reaction forces. *J. exp. Biol.* **93**, 333–338.
- HEGLUND, N. C., CAVAGNA, G. A. AND TAYLOR, C. R. (1982a). Energetics and mechanics of terrestrial locomotion. III. Energy changes of the centre of mass as a function of speed and body size in birds and mammals. *J. exp. Biol.* **79**, 41–56.
- HEGLUND, N. C., FEDAK, M. A., TAYLOR, C. R. AND CAVAGNA, G. A. (1982b). Energetics and mechanics of terrestrial locomotion. IV. Total mechanical energy changes as a function of speed and body size in birds and mammals. *J. exp. Biol.* **97**, 57–66.
- HEGLUND, N. C., TAYLOR, C. R. AND McMAHON, T. A. (1974). Scaling stride frequency and gait to animal size: mice to horses. *Science* **186**, 1112–1113.
- HERREID, C. F. AND FULL, R. J. (1984). Cockroaches on a treadmill: aerobic running. *J. Insect Physiol.* **30**, 395–403.
- HUGHES, G. M. (1952). The coordination of insect movements. I. The walking movements of insects. *J. exp. Biol.* **29**, 267–284.
- KOZACIK, J. J. (1981). Stepping patterns in the cockroach, *Periplaneta americana*. *J. exp. Biol.* **90**, 357–360.
- McMAHON, T. A. (1985). The role of compliance in mammalian running gaits. *J. exp. Biol.* **115**, 263–282.

- SPIRITO, C. P. AND MUSHRUSH, D. L. (1979). Interlimb coordination during slow walking in the cockroach. I. Effects of substrate alteration. *J. exp. Biol.* **78**, 233–243.
- TAYLOR, C. R. (1985). Force development during sustained locomotion: a determinant of gait, speed and metabolic power. *J. exp. Biol.* **115**, 253–262.