# LEG DESIGN IN HEXAPEDAL RUNNERS

By R. J. FULL[1], R. BLICKHAN[2] and L. H. TING[1]

[1]*Department of Integrative Biology, University of California at Berkeley, Berkeley, CA 94720, USA* and [2]*A. G. Nachtigall, Zoologie, Universität des Saarlandes, D-6600 Saarbrücken, Germany*

## Summary

Many-legged animals, such as crabs and cockroaches, utilize whole-body mechanics similar to that observed for running bipeds and trotting quadrupedal mammals. Despite the diversity in morphology, two legs in a quadrupedal mammal, three legs in an insect and four legs in a crab can function in the same way as one leg of a biped during ground contact. To explain how diverse leg designs can result in common whole-body dynamics, we used a miniature force platform to measure the ground reaction forces produced by individual legs of the cockroach *Blaberus discoidalis*. Hexapedal runners were not like quadrupeds with an additional set of legs. In trotting quadrupedal mammals each leg develops a similar ground reaction force pattern that sums to produce the whole-body pattern. At a constant average velocity, each leg pair of the cockroach was characterized by a unique ground reaction force pattern. The first leg decelerated the center of mass in the horizontal direction, whereas the third leg was used to accelerate the body. The second leg did both, much like legs in bipedal runners and quadrupedal trotters. Vertical force peaks for each leg were equal in magnitude. In general, peak ground reaction force vectors minimized joint moments and muscle forces by being oriented towards the coxal joints, which articulate with the body. Locomotion with a sprawled posture does not necessarily result in large moments around joints. Calculations on *B. discoidalis* showed that deviations from the minimum moments may be explained by considering the minimization of the summed muscle forces in more than one leg. Production of horizontal forces that account for most of the mechanical energy generated during locomotion can actually reduce total muscle force by directing the ground reaction forces through the leg joints. Whole-body dynamics common to two-, four-, six- and eight-legged runners is produced in six-legged runners by three pairs of legs that differ in orientation with respect to the body, generate unique ground reaction force patterns, but combine to function in the same way as one leg of a biped.

## Introduction

Whole-body mechanics in two-, four-, six- and eight-legged runners can be

remarkably similar, despite variations in body form or morphology (Full, 1989, 1990). Pedestrians that vary in leg number and design can generate similar ground reaction force patterns. Running humans, trotting dogs, cockroaches and side-ways-running crabs can move their bodies by producing alternating propulsive forces. Two legs in a trotting quadrupedal mammal, three legs in an insect and four legs in a crab can act as one leg does in a biped during ground contact. The center of mass of the animal undergoes repeated acceleration and deceleration with each step, even when traveling at a constant average velocity (Blickhan and Full, 1987; Cavagna *et al.* 1977; Full and Tu, 1990, 1991; Heglund *et al.* 1982). Horizontal kinetic energy and gravitational potential energy of the center of mass fluctuate in phase. Trotting quadrupedal mammals, such as dogs, generate this common mechanical pattern by producing nearly the same force pattern with each leg (Alexander, 1977a). In fact, successful trotting quadrupedal robots have been designed so that the kinetics of each leg is the same, differing only in relative phase (Raibert *et al.* 1986). In the present study we test the hypothesis that each of the three legs of a hexapedal runner functions in a similar manner to produce whole-body mechanics comparable to that of bipedal runners and quadrupedal trotters. Similarities between mammalian and arthropod whole-body mechanics suggest that rigid constraints may exist on the possible mechanisms by which a leg can function during running.

Data from the few studies on the kinetics of terrestrial locomotion in arthropods do not support the hypothesis that all the legs generate similar ground reaction force patterns. Unfortunately, because these studies have focused primarily on questions dealing with neural function, few investigations have correlated kinematics (i.e. description of stepping patterns) with the actual kinetics of locomotion (Delcomyn, 1985). Moreover, most investigations have examined animals moving at very low speeds.

Three-dimensional ground reaction force vectors for the legs of standing and slowly walking spiders differ depending on the leg measured (Blickhan and Barth, 1985; R. Blickhan, unpublished data). Legs four and five of rock lobsters walking under water also produce unique force patterns (Clarac and Cruse, 1982; Cruse *et al.* 1983). Leg four appears to control movement, whereas leg five functions as a strut. In crayfish, leg three exerts the largest vertical force, whereas leg four produces most of the propulsive force (Klärner and Barnes, 1986). Cruse (1976) demonstrated that pro-, meso- and metathoracic legs in a walking stick insect each generate a distinct ground reaction force pattern. Harris and Ghiradella (1980) used a photoelastic substratum to estimate the magnitude of vertical force and the direction of total force at the tarsus of each leg in crickets. Vertical force patterns are distinct in the second and third legs.

Hughes (1952) proposed a simple model for the function of insect legs. Legs could function as levers, inclined struts or both simultaneously, depending on the direction of the ground reaction force vector. A leg functions as a strut if the ground reaction force vector is directed back towards the joint. If a significant horizontal accelerating force directs the ground reaction force in an anterior

direction, then the leg functions as a lever in the horizontal direction. Hughes (1952) reported that the first leg of cockroaches functions as a lever, while the second and third legs function as inclined struts. Yet the legs of stick insects do not appear to follow this simple model (Cruse, 1976). First and second legs in stick insects can act as levers or inclined struts, depending on the direction considered. Graham (1983) related these single-leg force patterns to changes in whole-body velocity. He concluded that the mechanics of walking in stick insects is fundamentally different from that of bipeds and quadrupeds. Stick insects employ a lurching gait during which legs push against one another during a step. The 'unusual behavior' of the stand–push–recover system was hypothesized to increase energy cost significantly.

In the present study we determine three-dimensional ground reaction force vectors for individual legs of the cockroach *Blaberus discoidalis*. More importantly, we attempt to link the kinematics and kinetics of single legs to the whole-body movement of a running hexaped.

## Materials and methods

### Animals

*Blaberus discoidalis* (Serville) were obtained from Carolina Biological Supply Company. The average mass of the animals used was $2.1\pm0.7$ g (S.D.). The cockroaches were individually housed in plastic containers, and given dog food and water *ad libitum*.

### Force platform

The animals were induced to run on a cardboard surface along a straight running track (6 cm in width). A force platform was placed just below, but not in contact with, the running track. Two small rectangular holes (20 mm in length and 10 mm in width) were cut in the track to expose areas of the force platform at positions where it was likely that a single leg would contact the ground (i.e. spaced 34 mm apart). Small cardboard pads were glued on these exposed areas of the force platform so that the running track was flush with the pads attached to the force platform. The running track was rigid enough to support the weight of the cockroach without interfering with the force platform signal.

The force platform was sensitive to vertical, horizontal and lateral force components. The platform was constructed of model airplane plywood and mounted on four brass beams, which had 24 semi-conductor strain gauges bonded to spring blades (Full and Tu, 1990). Variation in force across the platform was less than 7%. Loads in the range 0.001–0.1 N produced a linear response. Forces as small as 3% of the animal's body weight could be resolved. Data were corrected for crosstalk, which ranged from 1 to 13%. The correction coefficients were determined from readings taken when the platform was loaded with known vertical, horizontal and lateral loads. After correction for crosstalk, force signals

were accurate to 1 %. The unloaded natural frequency of the force platform was 400–650 Hz.

The signals from the force platform were amplified (Vishay, Measurements Group) and sampled by computer (IBM PC/AT) *via* an analog-to-digital converter (C-100, Cyborg) at 1000 samples s$^{-1}$. The signals were collected using data acquisition and analysis software (Discovery, Cyborg) that also digitally filtered the data (185 Hz Butterworth filter with zero phase shift) and made baseline corrections.

### Video analysis system

Each trial was videotaped at 120 frames s$^{-1}$. Two views were filmed simultaneously by placing a mirror above the track at 45° and filming from the side. From the videotapes, it was possible to determine which leg had touched the exposed area of the force platform in each trial. In addition, the three-dimensional positions of the incident leg, the head and the abdomen of each animal were digitized into a computer using a motion analysis system (3D version, Peak Performance Technologies, Inc.). These data allowed calculation of the average speed of the animal, as well as the relative position of the legs for each trial. Only trials of constant average velocity (i.e. net changes in velocity did not exceed 20 %) were analyzed.

Force and position data were synchronized by matching the first video frame showing ground contact with the initial rise in the force data. The number of video frames in which a leg was in contact with the ground was in agreement with the duration of the vertical force recordings to the accuracy of the framing rate of 120 Hz. Only trials during which the animal stepped completely on the force platform were accepted.

### Coordinate system for analysis

Animals were made to run from left to right. Both video and force data were collected for legs on the right side of the body and analysed using a common coordinate system. A rectangular coordinate system was chosen such that the positive $x$-axis pointed laterally towards the right side of the animal; the $y$-axis, or the horizontal, corresponded with the direction of motion and the $z$-axis was directed vertically (Fig. 1). Ground reaction force vectors from the right set of legs with a negative $x$, or lateral, component pointed towards the body. A negative $y$, or horizontal, component decelerated the body in the direction of motion; a positive $y$ component accelerated the body. Positive vertical forces indicated the support of weight. The maximum or minimum magnitudes, or extrema, of the ground reaction forces are referred to as $F_L$, $F_H$ and $F_V$ for the lateral, horizontal and vertical directions, respectively.

To illustrate the direction of the force vectors, force data were plotted in two projections, lateral and posterior. These orthogonal views corresponded to the primary axes of the coordinate system, such that the plane of projection was always perpendicular to an $x$, $y$ or $z$ force component (Fig. 1). The posterior
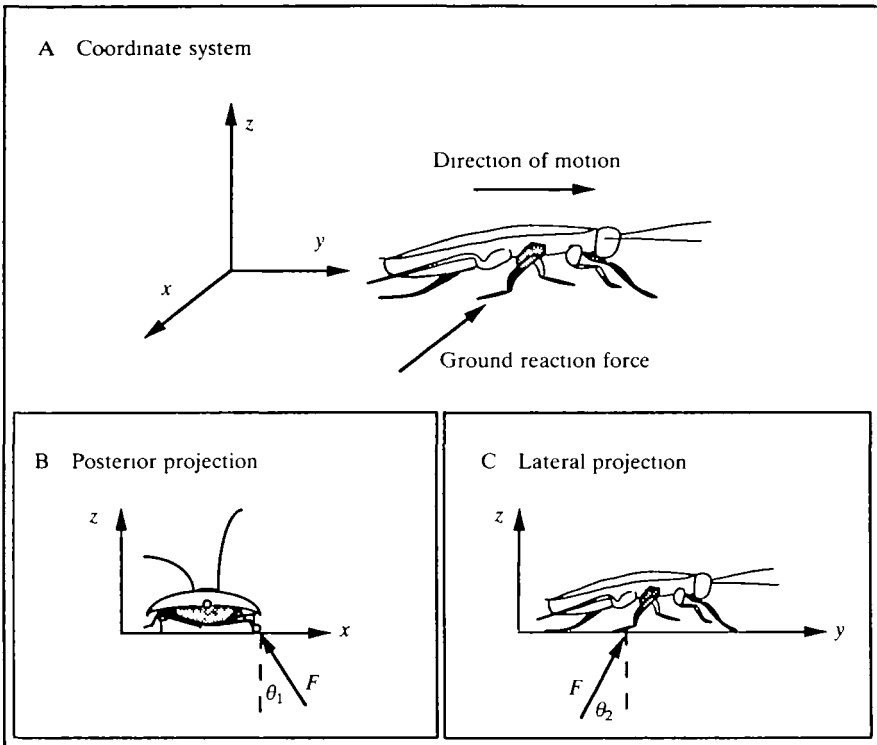
Fig. 1. Coordinate system and projections for ground reaction forces and position data. (A) Coordinate system. The $x$-axis is directed laterally towards the right. The $y$-axis points along the direction of motion, and the $z$-axis vertically upwards. (B) Posterior projection. The actions of the lateral and vertical force components are resolved. The angle of the projected peak force ($\theta_1$) was calculated with respect to the vertical. (C) Lateral projection. The actions of the vertical and horizontal force components are shown. Angles of peak forces ($\theta_2$) were calculated with respect to the vertical.

projection (Fig. 1B) illustrates the magnitude and direction of lateral and vertical forces. The angle of the peak force with respect to the vertical ($z$-axis) is referred to as $\theta_1$. The lateral projection (Fig. 1C) compares the vertical and horizontal force components where the angle of the peak force with respect to the $z$-axis is $\theta_2$.

All values given in the text are presented as mean ± S.E.

## Results

### Gait

The average running speed found in 42 force recordings ($N=3$ animals) was $37.8 \pm 7.5 \, \text{cm s}^{-1}$. Cockroaches used an alternating tripod gait. The first and third legs on one side of the body moved simultaneously with the second leg on the opposite side. Each leg moved 180° out of phase with its contralateral pair.

*Prothoracic leg*

## Force patterns

The force patterns produced by the prothoracic or first leg exhibited single peaks or extrema (Fig. 2A). $F_V$ was $49\pm3\%$ of body weight and was always larger than $F_H$ and $F_L$. $F_H$ averaged $46\pm5\%$ of $F_V$ and $F_L$ averaged $49\pm2\%$ of $F_V$
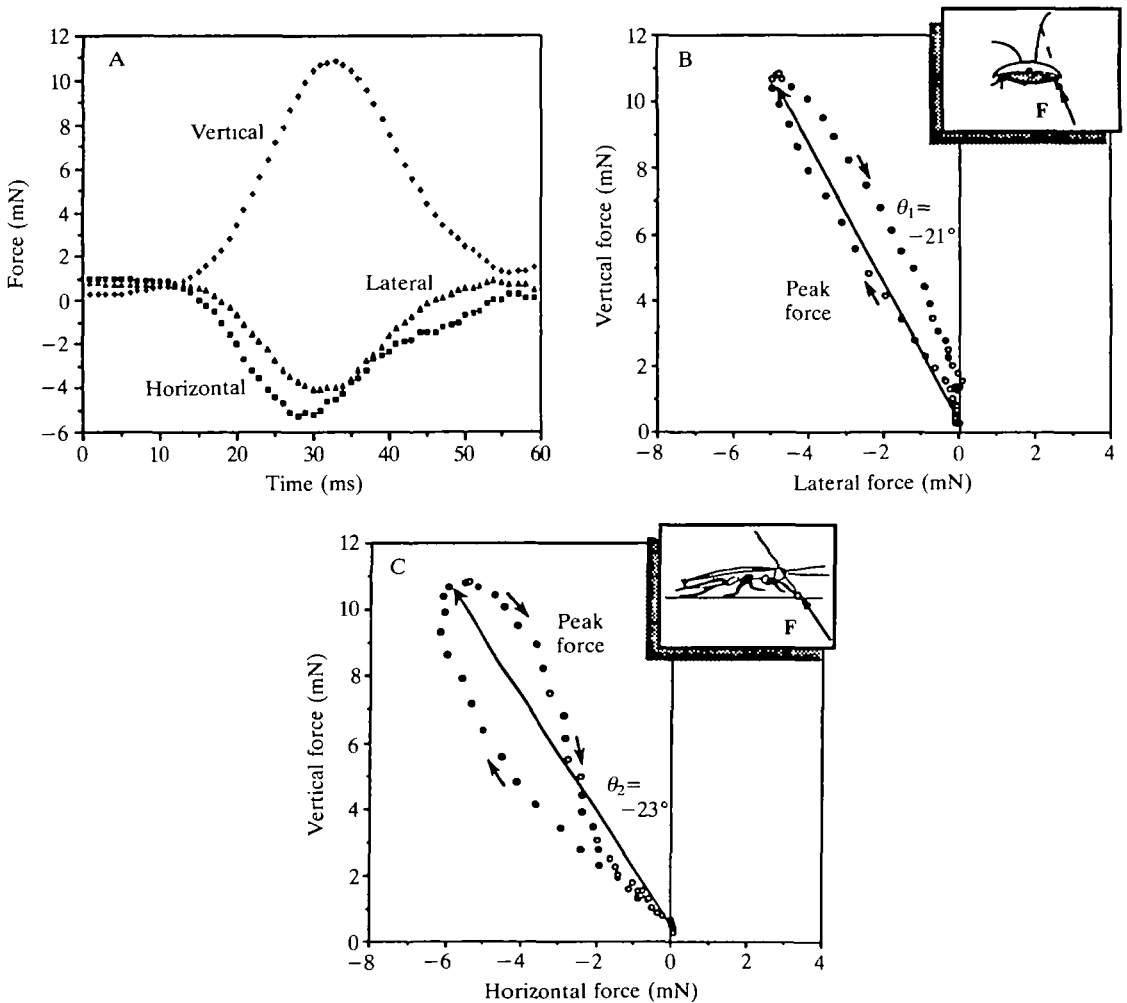


Fig. 2. Prothoracic leg ground reaction force patterns. (A) Lateral, horizontal and vertical forces as a function of time for one step. (B) Posterior projection. Vertical force as a function of lateral force during a single step. Arrows indicate the direction of change with time. At mid-stance, the direction of the ground reaction force was towards the body of the cockroach during the step at an angle ($\theta_1$) of 21° from the vertical. (C) Lateral projection. Horizontal force as a function of vertical force during a step. At peak force, the angle ($\theta_2$) of the horizontal force with the vertical was −23°. F, force vector.

Table 1. *Average  ground  reaction  force  extrema  produced  by  single  legs  of  a*
*cockroach*

| Leg | $F_V$ (mN) | $F_H$ (mN) | $F_L$ (mN) |
|---|---|---|---|
| Prothoracic | 10.4±0.6 | 4.9±0.4 | 5.1±0.4 |
| Mesothoracic | 9.8±0.6 | 4.0±0.6 | 5.1±0.5 |
| Metathoracic | 11.9±0.9 | 4.9±0.7 | 3.2±0.9 |

$F_V$, ground reaction force extrema in the vertical direction; $F_H$, ground reaction force extrema in the horizontal direction; $F_L$, ground reaction force extrema in the lateral direction.

Values are mean ± s.e. $N$=15, 11 and 14 for pro-, meso- and metathoracic legs, respectively.

(Table 1). $F_L$ showed a significant correlation with $F_V$ ($F_{(1,11)}$=16.6, $P$=0.002; $r^2$=0.62).

## Direction of forces

The vertical ground reaction force component ($z$) was directed upwards for the support of weight. No recordings of negative vertical force were measured in any of the trials. The lateral ($x$) and horizontal ($y$) force components were negative throughout the step, so that the force vector was directed towards the body of the animal. Vertical forces increased and decreased in proportion to lateral forces, so that the direction of the force was relatively constant throughout the step (Fig. 2B). The angle $\theta_1$ was −26±1°. In the lateral projection, horizontal force opposed the direction of motion. The angle $\theta_2$ for the first leg was −24±2° from the vertical (Fig. 2C).

## Forces relative to body position

Although the forces were relatively constant in direction with respect to the ground throughout a single step, the direction of the force changed with respect to the animal's body position. The end of the tarsus stayed in the same position on the ground throughout the step, but the leg moved with respect to the body, as did the force vector.

In the lateral projection, the direction of the force vector shifted posteriorly, reflecting the angular movement of the leg with respect to the body. The force vector was aligned approximately along the leg, towards the coxal region of the thorax (Fig. 3A). In the posterior projection, the position of the tarsus did not move in relation to the body. The force vectors were relatively constant in direction with respect to the animal and were directed towards the coxa of the first leg (Fig. 3B).

## Mesothoracic leg

### Force patterns

The largest force component in the mesothoracic leg of the cockroach was in the vertical direction, attaining a maximum at near mid-step (Table 2). The vertical
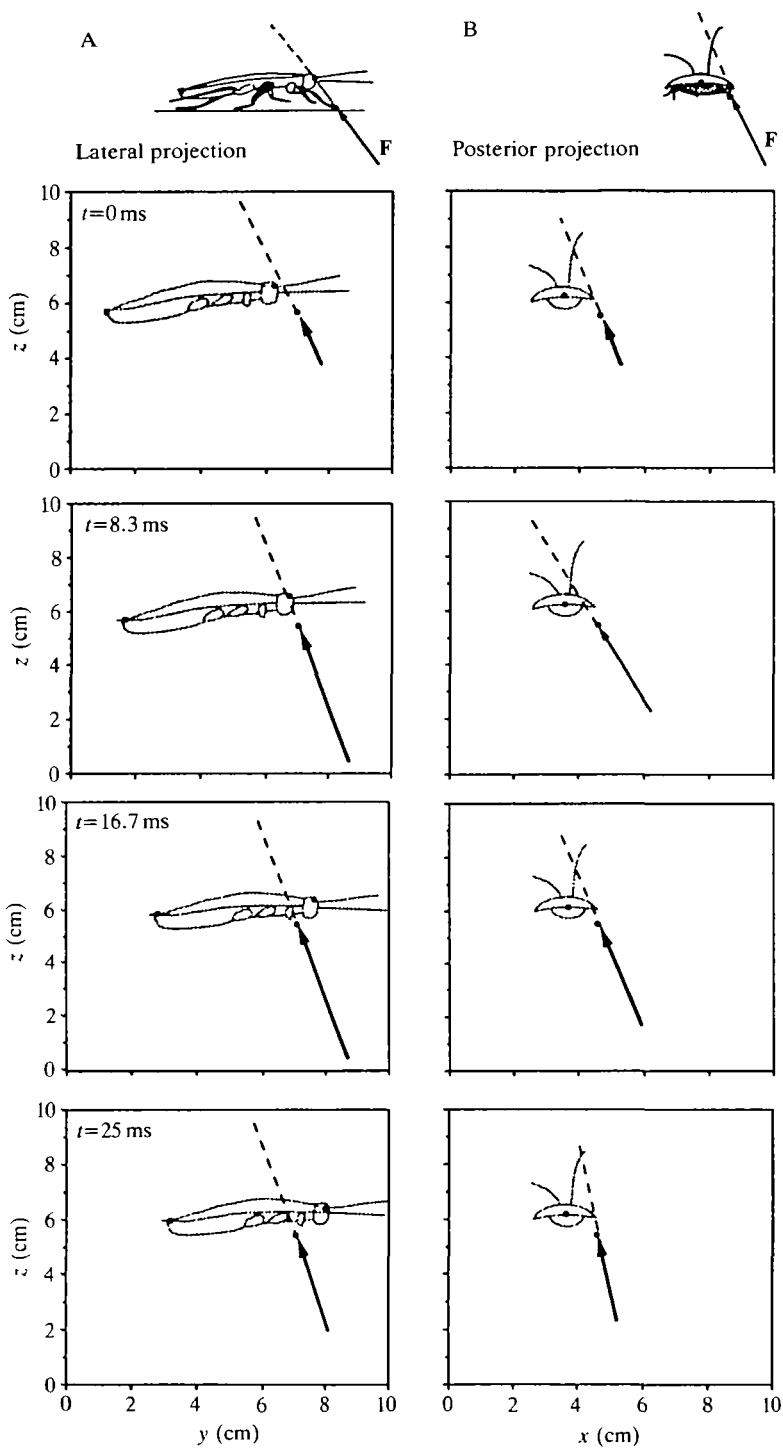
Fig. 3

Fig. 3. Ground reaction forces of the prothoracic leg with respect to body position. The vertical series of plots shows four combined plots for the force vector (**F**) and the positions of the head, abdomen and tarsus of the first leg corresponding to the video frames for that step. (A) Lateral projection. (B) Posterior projection. Throughout the step, the force vector was directed towards the body.

Table 2. *Single leg peak force phase relationships relative to the duration of vertical force*

| Leg | Peak force phase | | | |
| --- | --- | --- | --- | --- |
| | $F_V$ | $F_L$ | $F_{H-}$ | $F_{H+}$ |
| Prothoracic | 0.431±0.023 | 0.357±0.022 | 0.301±0.021 | |
| Mesothoracic | 0.404±0.054 | 0.376±0.054 | 0.226±0.036 | 0.640±0.036 |
| Metathoracic | 0.512±0.054 | 0.433±0.051 | | 0.541±0.042 |

Values are equal to the time to peak force divided by the duration of the vertical force.

$F_V$ represents vertical force; $F_L$ represents lateral force; $F_{H-}$ and $F_{H+}$ represent horizontal decelerating and accelerating forces, respectively.

Values are mean ± S.E. $N=9$, 6 and 13 for pro- meso- and metathoracic legs, respectively.

force pattern often showed a broad maximum compared to the patterns found for legs one and three (Fig. 4A). $F_V$ was 52±3 % of body weight (Table 1). The horizontal force component was initially decelerating (i.e. $F_{H-}$, negative) and then became accelerating (i.e. $F_{H+}$, positive). $F_H$, the absolute magnitude of $F_{H-}$ and $F_{H+}$, was 41±6 % of $F_V$. At a constant average velocity of the body, the horizontal force reversed direction at the same time that the vertical force attained a maximum. However, when the average velocity of the animal was not constant, the horizontal force did not pass through the origin at mid-stance. Depending on the amount of whole-body acceleration, $F_H$ changed in magnitude and direction. In contrast to the horizontal force component, the lateral force attained a single maximum at the same time as the maximum vertical force. Lateral force maxima were about half the magnitude of the vertical forces: $F_L=52±4$ % of $F_V$. Again, $F_L$ was significantly correlated with $F_V$ ($F_{(1,9)}=9.5$, $P=0.015$; $r^2=0.54$).

## Direction of forces

The vertical ground reaction forces were directed upwards. Lateral forces were directed towards the coxa as in the first leg ($\theta_1=-23±5°$; Fig. 4B). Horizontal force changed from negative ($\theta_2=-18±3°$; Fig. 4C) to positive ($\theta_2=26±5°$; Fig. 4C) during one step.

## Forces relative to body position

The direction of the force in the lateral projection changed with the motion of the leg and the body. The force vector tended to point towards the coxal region
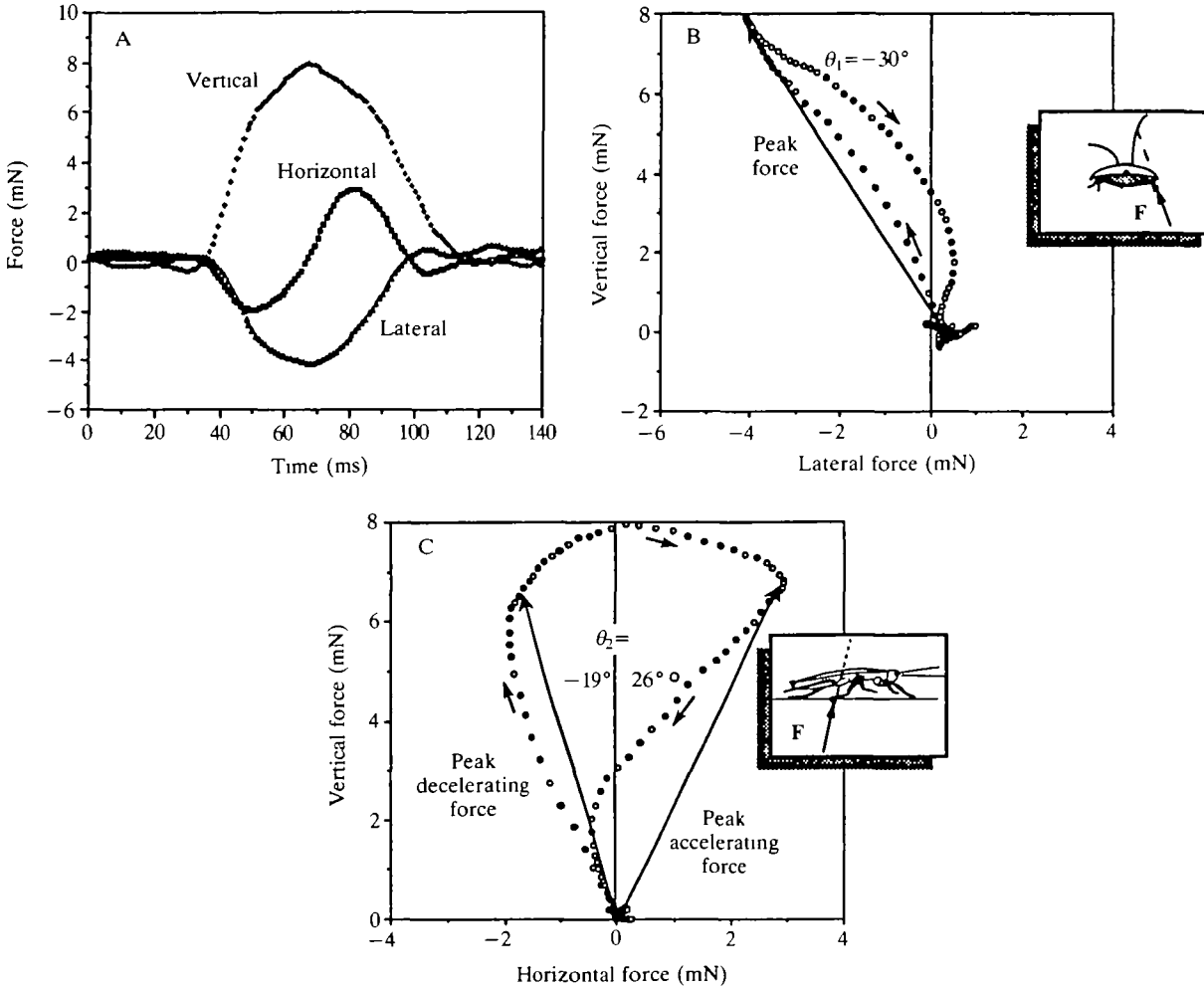
Fig. 4. Mesothoracic leg ground reaction force patterns. See Fig. 2 for further details.

during the period between and including the peak horizontal acceleration and deceleration (Fig. 5A). During this time, the force vector was constant in magnitude, but was changing direction.

In the posterior projection, the position of the tarsus with respect to the body did not change appreciably during the step. The positions of the head, abdomen and second leg tarsus were relatively unchanged (Fig. 5B). Throughout the step, the forces were directed through a region between the center of mass of the animal and the coxa joint and changed only in magnitude.

### Metathoracic leg

*Magnitude of forces*

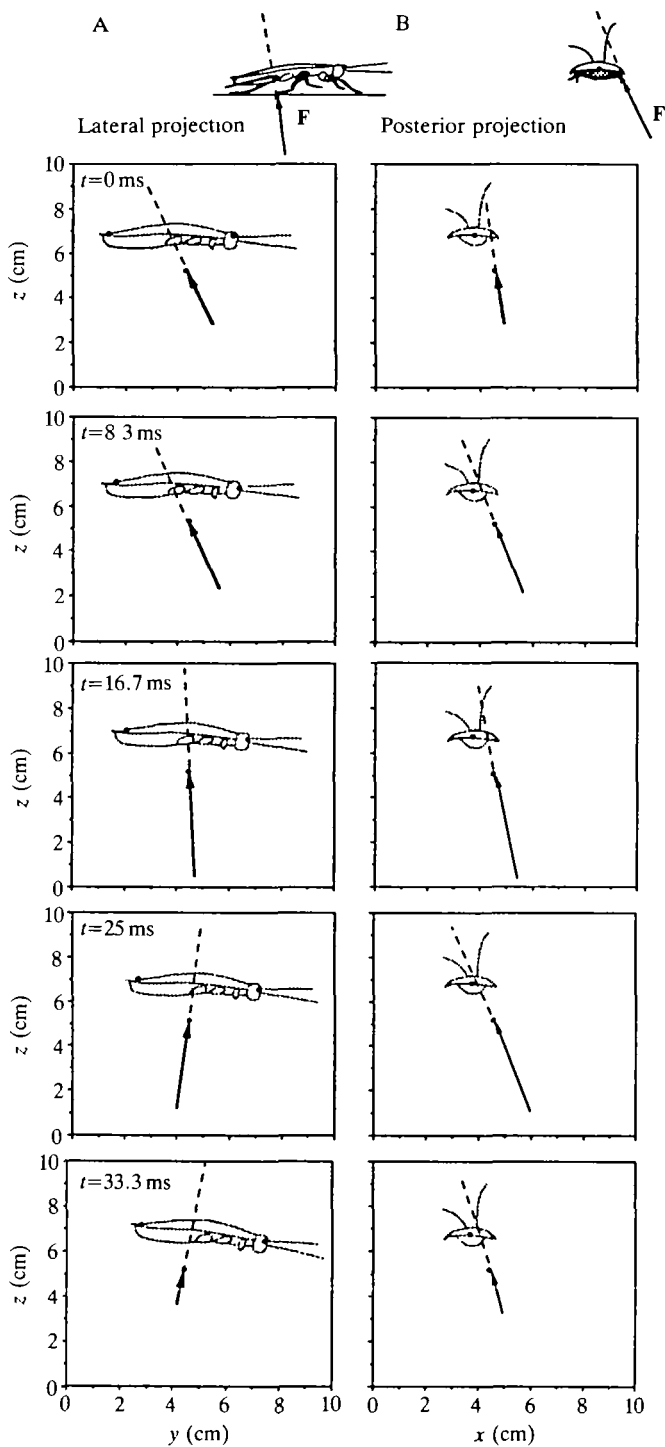The third set of legs are the greatest in both length and mass, and extend behind

Fig. 5. Ground reaction forces of the mesothoracic leg with respect to body position. See Fig. 3 for further details.
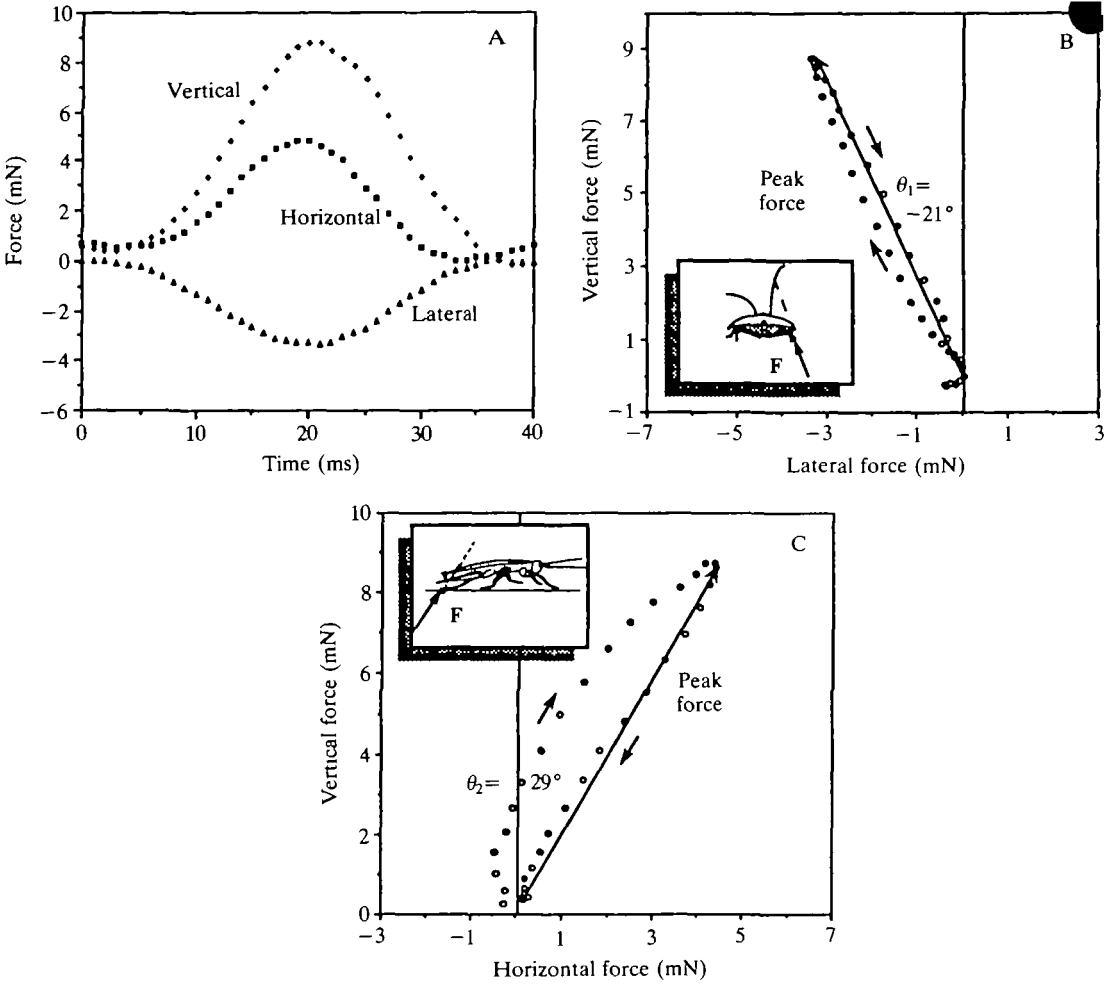
Fig. 6. Metathoracic leg ground reaction force patterns. See Fig. 2 for further details.

the animal's center of mass during a step. Vertical force was the largest force component ($F_V=52\pm2\%$ of body weight; Fig. 6A; Table 1) exerted by this leg. Horizontal forces were positive and $F_H$ was $41\pm5\%$ of $F_V$. Lateral forces were smaller than those measured in the first and second legs ($F_L=35\pm3\%$ of $F_V$). As in the other legs, $F_L$ was correlated with $F_V$ ($F_{(1,14)}=12.0$, $P=0.004$; $r^2=0.48$).

*Direction of forces*

Vertical forces were directed upwards to support weight. Lateral and vertical ground reaction forces varied in direct proportion and therefore maintained a relatively constant direction throughout the step (Fig. 6B). Lateral force was directed towards the body and $\theta_1$ was $-19\pm1°$ from the vertical. In general, horizontal force was accelerating over nearly the entire period of ground contact

and directed towards the center of mass in the direction of motion ($\theta_2=23\pm3°$; Fig. 6C). This leg sometimes exerted a small decelerating force at limb touchdown and lift-off (see Figs 6C and 8).

*Forces relative to body position*

The lateral projection of the force and position data showed that, at maximum magnitude, the force vector was not aligned precisely along the leg, but was directed somewhat posteriorly to the coxa (Fig. 7A). As the magnitude of the force decreased, the force vector was directed more posteriorly through the abdomen. The posterior projection showed a pattern similar to that observed in the first and second legs. Forces were directed towards the center of mass throughout the step (Fig. 7B).

## Comparison of forces among legs

For all legs, $F_V$ was correlated with body weight ($F_{(1,39)}=28$, $P<0.001$) and showed no significant variation with respect to speed ($F_{(2,39)}=1.4$, $P=0.24$). The magnitude of $F_V$ did not differ among the legs ($F_{(1,39)}=1.4$, $P=0.3$; Table 1). Although the force data could not be collected simultaneously for more than one leg in a tripod, trials were acquired during which all three legs stepped upon the force platform in succession while the insects traveled at a uniform average velocity. From such trials, it was evident that $F_V$ was equal in magnitude across the legs in a tripod (Fig. 8). Total vertical force exerted by all legs was 1.5 times body weight. $F_V$ and $F_L$ were not a function of speed ($F_{(1,39)}=1.4$, $P=0.24$ and $F_{(1,39)}=1.7$, $P=0.24$ for $F_V$ and $F_L$, respectively).

With respect to the timing of peak force generation, $F_V$ and $F_L$ were attained simultaneously in all three legs of the tripod ($F_{(2,27)}=0.31$, $P=0.31$ and $F_{(2,26)}=0.85$, $P=0.44$ for $F_V$ and $F_L$, respectively; Table 2). Peak horizontal accelerating force ($F_{H+}$) in leg three preceded $F_{H+}$ in the second leg (Scheffe $F$-test, $P<0.05$). Peak horizontal decelerating force ($F_{H-}$) in leg two preceded $F_{H-}$ in the first leg (Scheffe $F$-test, $P<0.05$). Peak horizontal decelerating force ($F_{H-}$) in leg one preceded $F_{H+}$ in the third leg (Scheffe $F$-test, $P<0.05$).

## Discussion

### Gait

The six-legged cockroach *B. discoidalis* used an alternating tripod gait similar to other symmetrical gaits (Delcomyn, 1971, 1981). Kinematic data show that the right front, left middle and right hindlegs contact the ground at nearly the same time and alternate with the left front, right middle and left hindlegs. Even though an aerial phase is absent, this gait has been characterized as a running or bouncing gait (Full and Tu, 1990, 1991). The center of mass of the animal undergoes repeated accelerations and decelerations with each step, even when it travels at a constant average velocity. Horizontal kinetic energy and gravitational potential energy of the center of mass fluctuate in phase, just as they do in running bipeds
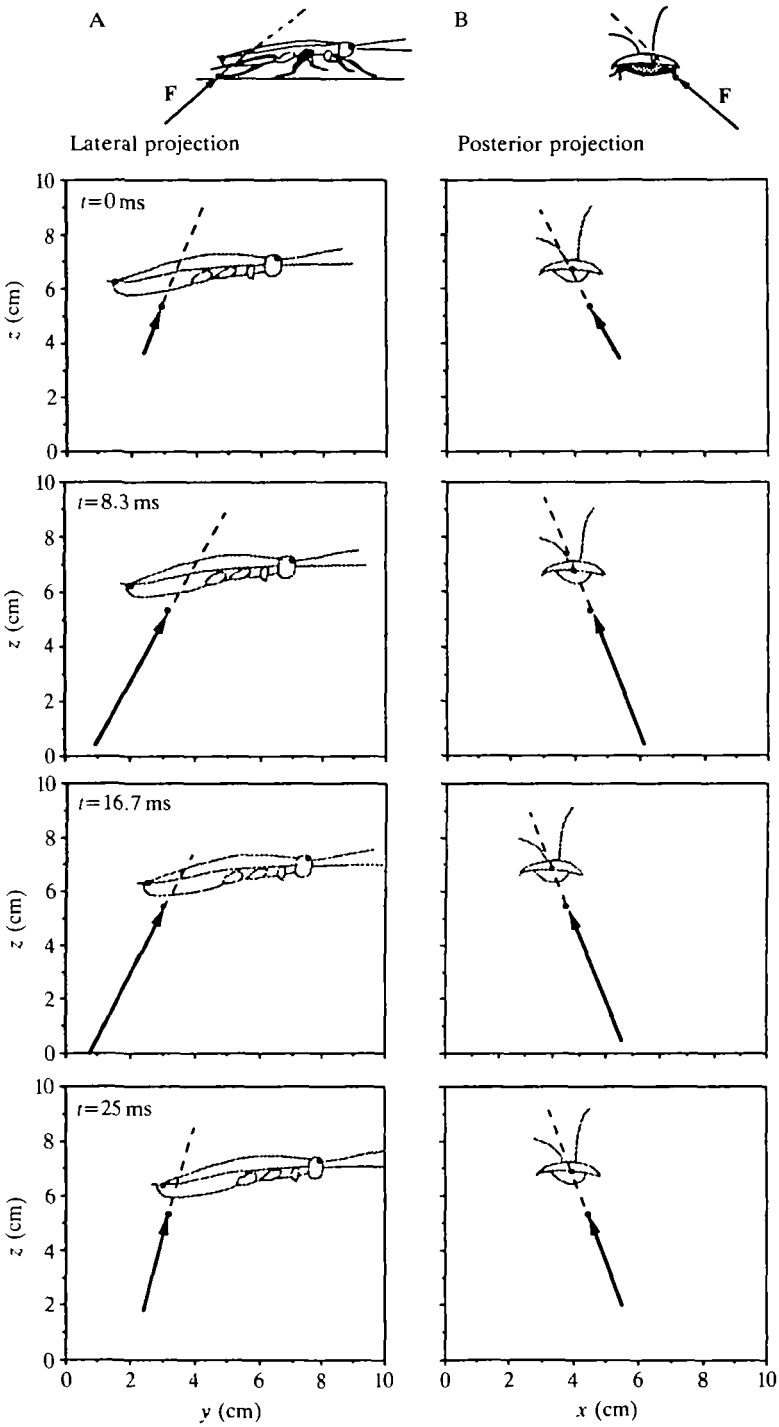
Fig. 7. Ground reaction forces of the metathoracic leg with respect to body position. See Fig. 3 for further details.
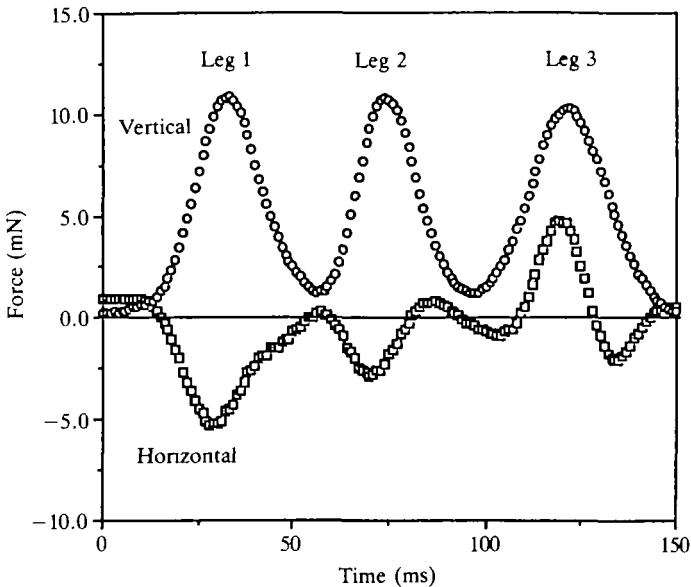
Fig. 8. Ground reaction forces from three legs stepping on the force platform in succession. The forceprint is from a single trial in which the first (prothoracic), second (mesothoracic) and third (metathoracic) legs stepped on the plate in succession. Vertical forces from each of the three legs were the same in magnitude.

and in trotting quadrupedal mammals (Cavagna *et al.* 1964, 1977; Heglund *et al.* 1982) and crabs (Blickhan and Full, 1987). Although cockroaches moved their center of mass with two sets of alternating tripods, the present data clearly show that six-legged runners cannot be characterized as merely quadrupeds with an additional set of legs. Each leg in the cockroach generated a unique ground reaction force pattern.

### Magnitude and direction of single leg forces

The prothoracic leg of *B. discoidalis* acted as a brake in the horizontal direction (Figs 2 and 3). Accelerating or pulling forces were not observed. At the same time, the first leg generated a vertical force comparable to that measured in the other two legs (Table 1). The line of action of the three-dimensional ground reaction force vector pointed from the tarsus on the ground posteriorly towards the coxa. Contrary to the hypothesis of Hughes (1952), the leg functioned more as an inclined strut than as a lever.

The prothoracic leg's vertical force pattern was similar to that produced by the leg of a running biped or trotting quadruped. The shape of the vertical force pattern can be described by a modified Fourier series with a shape factor designated as $q$, where vertical force$=a[\cos(\pi t/T)-q\cos(3\pi t/T)]$ from the time a leg is set down $(-T/2)$ to when it is lifted $(+T/2)$ (Alexander and Jayes, 1978), where $a$ is a constant and $t$ is time. The shape factor describing the prothoracic

leg's vertical force pattern ($q=-0.1$ to 0; duty factor$=0.5$) corresponds to a run or trot when compared with two- and four-legged mammals. Shape factors of 0.2–0.5 describe a walk, which is characterized by a minimum approximately half-way through ground contact time with maxima both before and after.

The prothoracic leg's horizontal force pattern was different from that seen in the foreleg of a trotting quadruped, such as a dog, despite the fact that whole-body ground reaction force patterns can be similar in six- and four-legged runners (Alexander, 1977a; Full and Tu, 1990, 1991). The foreleg of a dog generates a decelerating horizontal force followed by an accelerating force. Only during a gallop or bound do the dog's forelegs function as in the cockroach, producing primarily decelerating forces (Cavagna et al. 1977; Heglund et al. 1982). Blickhan and Full (1987) found that the leading legs of sideways-running crabs also generate decelerating forces only.

Previous studies on arthropods have only measured single-leg ground reaction forces during slow locomotion. In contrast to B. discoidalis, the first leg in walking stick insects (Cruse, 1976), crickets (Harris and Ghiradella, 1980) and spiders (Blickhan and Barth, 1985) has been described as performing a 'feeler' function, resulting in vertical forces that vary greatly. Nevertheless, the first leg in stick insects was also found to decelerate the center of mass during slow walking (Cruse, 1976). Although the first leg in B. discoidalis may perform a sensory function at very low speeds, when locomotion is intermittent, the forces recorded in the present study were very consistent during running.

Forces in the mesothoracic legs of B. discoidalis were similar to the ground reaction forces generated by the leg of a running biped or trotting quadruped (Fig. 4). Vertical forces attained a maximum at mid-stance and were the largest force component (Table 1). Horizontal forces acted first to decelerate and subsequently to accelerate the body (i.e. force changed direction from negative to positive at mid-stance; Fig. 5). Although the mesothoracic legs are acting as inclined struts, the present results do not support the hypothesis that the mesothoracic legs always assist forward movement (Hughes, 1952).

The mesothoracic leg's vertical force pattern had a single maximum and a shape factor similar to or somewhat greater than that of the prothoracic leg and that produced by the leg of a running biped or trotting quadruped ($q=0$ to 0.1). The vertical force pattern was not similar to that found in a stiff-legged walking gait, in which two maxima have been measured (Cavagna et al. 1977). By contrast, crickets may employ a stiff-legged walk, since the vertical force pattern of the mesothoracic leg shows a distinct 'dip' at mid-stance ($q=0.2$–0.3; Harris and Ghiradella, 1980). However, not all the legs of the cricket show this pattern. Moreover, slowly walking stick insects generate vertical force patterns with a single maximum (Cruse, 1976).

Metathoracic legs of B. discoidalis tended to accelerate the center of mass, because horizontal ground reaction forces were directed towards the body (Figs 6 and 7). A comparable action for hindlegs has been described for a wide variety of animals, such as stick insects (Cruse, 1976) and spiders during slow walking

(Blickhan and Barth, 1985), crabs running (Blickhan and Full, 1987) and many quadrupedal mammals bounding (Cavagna *et al.* 1977; Heglund *et al.* 1982). The third leg of *B. discoidalis* also generated a vertical force comparable to that measured in legs one and two (Table 1). The metathoracic leg's vertical force pattern had a single maximum and a shape factor similar to that produced by the leg of a running biped or trotting quadruped. The third leg functioned as an inclined strut, but, as pointed out by Hughes (1952), it was also capable of actively developing axial forces.

*Implications for leg design*

Examination of the ground reaction force patterns of the six-legged *B. discoidalis* raises two fundamental mechanistic questions dealing with leg design for terrestrial locomotion. First, why do animals traveling at a constant average speed generate significant horizontal ground reaction forces? Energy fluctuations of the center of mass could be reduced considerably if horizontal ground reaction forces were decreased. Full and Tu (1991) found that 60–80 % of the mechanical energy of the center mass in the rapid running cockroach *Periplaneta americana* can be accounted for by accelerations of the center of mass in the horizontal direction. The horizontal ground reaction forces generated by *B. discoidalis*, relative to $F_V$, are 2–4 times that measured in terrestrial birds and mammals (Alexander, 1977*a*; Biewener, 1983; Biewener *et al.* 1988; Cavagna *et al.* 1977; Heglund *et al.* 1982). Lateral ground reaction forces are even greater in magnitude relative to $F_V$ (Alexander, 1977*a*). Second, why do the legs of cockroaches, and probably other arthropods with sprawled postures, operate against one another during ground contact? Leg forces that oppose each other would appear to increase the total force required from leg muscles.

Alexander (1977*b*) has argued that for bipeds inclusion of horizontal forces actually decreases mechanical work and metabolic cost. We propose that horizontal ground reaction force production can minimize joint moments and muscle forces in a leg. More importantly, we suggest that total force can be minimized, even when legs push against one another.

Consider a simple planar model of *B. discoidalis* in a lateral projection (Fig. 9). Musculo-skeletal forces at the joints will be decreased if the moments around the joints are minimized. A moment is defined by the product of the lever arm, or distance vector, and the resultant force vector. Thus, to decrease the moment, either the magnitude of the ground reaction force can be decreased or the direction of the force can be altered. In *B. discoidalis*, the largest force component produced by each leg was in the vertical direction. Despite the disparity in leg size and position, $F_V$ at each leg was the same (Table 1). The large forces imposed upon the legs for the support of weight create large moments about the joints, because the vertical forces are exerted at the most distal point of legs which radiate out from underneath the thorax. Fig. 9 shows the long moment arm associated with the vertical ground reaction force for the joints of the third leg. The moment generated about each joint must be balanced by an opposing musculo-skeletal
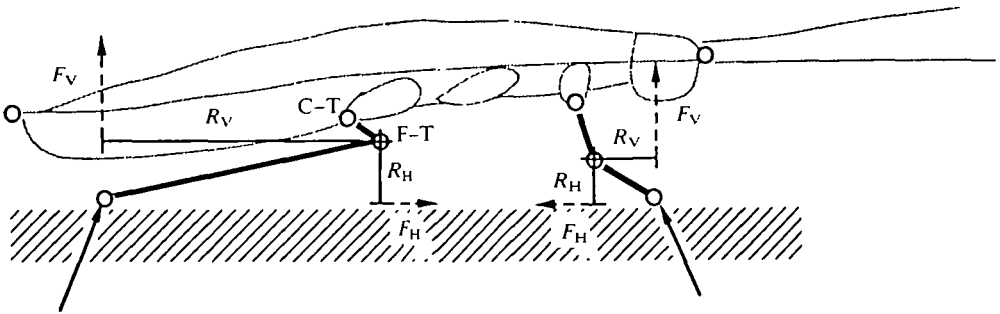
Fig. 9. Diagram of a lateral projection representing the relationship of ground reaction forces, joint positions and lever arms for the prothoracic and metathoracic legs of a cockroach during ground contact. Ground reaction forces (solid arrows) and moment arms ($R$) are resolved into vertical (V) and horizontal (H) components. Vertically directed forces ($F_V$) without horizontal components generate large moments ($F_V \times R_V$) about each joint, which must be balanced with large muscle forces owing to the small muscle lever arms. Moments become zero when the force vector is directed through the joint. This simple planar model only considers the joint motion in the plane of the lateral projection. Future three-dimensional quantitative models should include the major axis of rotation for each joint and the contribution of passive forces. C–T and F–T represent coxa–trochanter and femur–tibia, respectively.

force 20–30 times that of the body weight because the muscle levers arms are relatively short. Fig. 10A shows estimated moments about the coxa–trochanter and femur–tibia joint for the third and first legs in a lateral projection.

If we assume that the vertical force component ($F_V$) is constant, then the ground reaction force vector will be more in line with the joint when a horizontal force ($F_H$) is applied (Fig. 9). Joint moments and muscle forces will decrease as horizontal force increases from zero (Fig. 10A). The higher the joint is off the ground, the lower the magnitude of the horizontal force required, because the moment arm associated with the horizontal force (i.e. $R_H$) is simply the distance from the ground to the joint. Joint moments will attain a minimum when the

Fig. 10. Estimated joint moments and musculo-skeletal forces for the prothoracic and metathoracic legs of a cockroach during ground contact as a function of the magnitude of the horizontal component of ground reaction force. (A) Joint moments generated by the ground reaction force at the tarsus around the coxa–trochanter (C–T, solid line) and femur–tibia (F–T, dashed line) joints of the prothoracic leg and the coxa–tro-chanter (dash–dot line) and femur–tibia (dashed–double–dot line) joints of the metathoracic leg. (B) Summed joint moments around the coxal and femur joints of the prothoracic and metathoracic legs generated by the ground reaction force at the tarsus. (C) Total muscle force necessary to balance the moments around the coxa–trochanter and femur–tibia joints of the prothoracic and metathoracic leg generated by the ground reaction force at the tarsus. Muscle lever arms were estimated for each joint by measurement with a dissecting microscope. Note that the total muscle force function differs from the summed moment curve because the extensor and flexor muscle lever arms differ in each joint. Joints with small muscle lever arms require greater muscle force production than those with large lever arms.

ground reaction force vector is directed through the joint's center. If horizontal force is increased further, then the vector will be directed to the opposite side of the joint and the moment will increase. In general, horizontal forces resulted in the ground reaction force vector pointing towards the coxa of the animal when the force attained a maximum (Figs 3A, 5A and 7A). At the beginning and end of each step, when the force was directed furthest away from the coxa joint, moments were quite small because the forces generated at this time were small. In many birds and mammals the ground reaction force vector of the lateral projection tends to remain aligned with the leg, passing close to the hip to minimize the moment
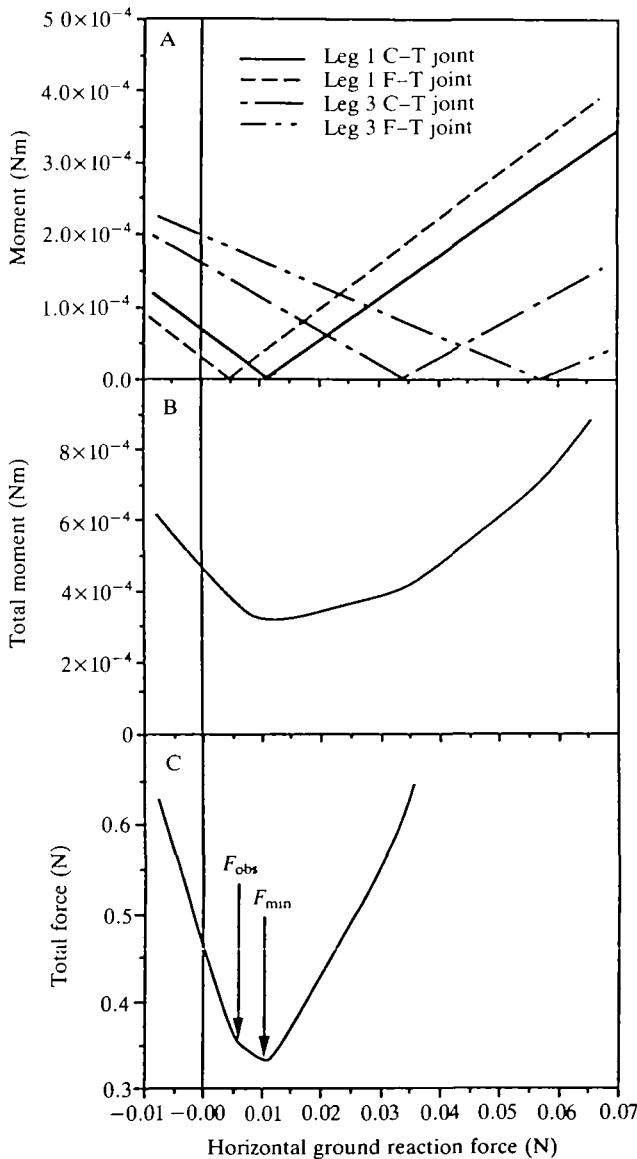


Fig. 10

developed at the limb joints (Alexander, 1977a; Biewener, 1983; Biewener *et al.* 1988).

Because the legs of birds and mammals are placed underneath the body, the ground reaction force vector is oriented near the vertical in the posterior projection. By contrast, the legs of a cockroach are positioned laterally. A ground reaction force vector oriented near the vertical without corresponding lateral forces directed towards the body would result in large moments being developed at the coxal joints. In *B. discoidalis*, moments are minimized with respect to the posterior projection (Figs 3B, 5B and 7B). Addition of a significant lateral force caused the resultant force to be directed along the leg in this projection as well. This dependence of $F_L$ on $F_V$ reduced the moments around the joints and decreased muscle forces. Compared to the generation of strictly vertical ground reaction forces, the production of horizontal and lateral forces by *B. discoidalis* actually reduces joint moments and total muscle force.

Although the resultant force vectors are generally directed towards the coxa, we found significant deviations from this position. The resultant force vector in the lateral projection for the metathoracic leg was directed above and behind the joints (Figs 7A, 9). Horizontal ground reaction forces were smaller in magnitude than predicted for the resultant to be simply oriented to minimize joint moments of the hindleg alone. Horizontal forces 5–10 times higher than observed would be required to minimize metathoracic leg joint moments. For an animal traveling at a constant speed, these large accelerating forces must be balanced to some extent by comparable horizontal decelerating forces of the prothoracic leg. Because the metathoracic and prothoracic legs of *B. discoidalis* are not equidistant from the point of ground contact, large decelerating forces of the prothoracic leg would, in turn, cause greatly elevated moments and muscle forces in the prothoracic leg joints. Closer examination of the joint moments shows that the magnitude of the horizontal ground reaction force corresponding to the minimum joint moment differs among individual joints and legs (Fig. 10A). Perhaps the summed moment of all joints in the metathoracic and prothoracic legs is minimized rather than the moment of individual leg joints. Fig. 10B shows that the total or summed moment ($M_{tot} = \Sigma |M_i|$, where $M_i$ represents the moments of the individual joints) balanced by muscle force attained a minimum at 0.01 N. To make a better estimate of the total muscle force production for the coxa–trochanter and femur–tibia joints of the metathoracic and prothoracic legs, we used approximations of muscle lever arms, since extensor and flexor lever arms vary for each joint (Fig. 10C). Remarkably, the measured horizontal forces would require muscle forces only 12 % greater than the predicted minimum value. Depending on the leg design, legs that push against one another and generate accelerating and decelerating ground reaction forces can actually result in a lower total muscle force production than if only vertical ground reaction forces are generated.

*Single-leg forces compared to whole-body ground reaction forces*

When the ground reaction forces from single legs in the alternating tripods of

*B. discoidalis* are summed, the resultant is consistent with whole-body force recordings (Full and Tu, 1990). Lateral forces cancel in such a manner that the resultant force is smaller than any single-leg force component and points towards the side of the second leg of the tripod. Kinematics alone would suggest that the second leg accelerates and decelerates the center of mass, since the horizontal forces of the first and third legs would cancel. However, the kinetics revealed a somewhat different picture. The peak decelerating horizontal force ($F_{H-}$) of the first leg occurs earlier in the step than the peak accelerating horizontal force ($F_{H+}$) of the third leg (Table 2). Therefore, the first, second and third legs all play a role in moving the center of mass in the horizontal direction.

Each leg pair of a hexapedal runner performs a unique function during terrestrial locomotion. Horizontal accelerating and decelerating ground reaction forces can minimize muscle force production while significantly increasing the mechanical power used to move the center of mass. Legs are not constrained to operate in a mechanically identical fashion when using a symmetrical gait. Whole-body dynamics common to two-, four-, six- and eight-legged runners (Full, 1989, 1990) is produced in six-legged runners by a set of three legs that differ in design from, but function in the same way as, one leg of a biped.

### References

ALEXANDER, R. McN. (1977*a*). Terrestrial locomotion. In *Mechanics and Energetics of Animal Locomotion* (ed. R. McN. Alexander and T. Goldspink), pp. 168–203. New York: Wiley & Sons.

ALEXANDER, R. McN. (1977*b*). Mechanics and scaling of terrestrial locomotion. In *Scale Effects in Animal Locomotion* (ed. T. J. Pedley), pp. 93–110. London: Academic Press.

ALEXANDER, R. AND JAYES, A. S. (1978). Vertical movements in walking and running. *J. Zool., Lond.* **185**, 27–40.

BIEWENER, A. A. (1983). Locomotory stresses in the limb bones of two small mammals: the ground squirrel and the chipmunk. *J. exp. Biol.* **103**, 131–154.

BIEWENER, A. A., THOMPSON, J. J. AND LANYON, L. E. (1988). Mechanics of locomotion and jumping in the horse (*Equus*): *in vivo* stress in the tibia and metatarsus. *J. Zool., Lond.* **214**, 547–565.

BLICKHAN, R. AND BARTH, F. G. (1985). Strains in the exoskeletons of spiders. *J. comp. Physiol.* **157**, 115–147.

BLICKHAN, R. AND FULL, R. J. (1987). Locomotion energetics of the ghost crab. II. Mechanics of the center of mass during walking and running. *J. exp. Biol.* **130**, 155–174.

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.

CLARAC, F. AND CRUSE, H. (1982). Comparison of forces developed by the leg of the rock lobster when walking free or on a treadmill. *Biol. Cybernetics* **43**, 109–114.

CRUSE, H. (1976). The function of legs in the free walking stick insect, *Carausius morosus*. *J. comp. Physiol.* **112**, 135–162.

CRUSE, H., CLARAC, F. AND CHASSERAT, C. (1983). The control of walking movements in the leg of the rock lobster. *Biol. Cybernetics* **47**, 87–94.

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.

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.

FULL, R. J. (1990). Concepts of efficiency and economy in land locomotion. In *Efficiency and Economy in Animal Physiology* (ed. R. W. Blake). New York: Cambridge University Press (in press).

FULL, R. J. AND TU, M. S. (1990). The mechanics of six-legged runners. *J. exp. Biol.* **148**, 129–146.

FULL, R. J. AND TU, M. S. (1991). Mechanics of rapid running insects: two-, four-, and six-legged locomotion. *J. exp Biol.* **156**, 215–231.

GRAHAM, D. (1983). Insects are both impeded and propelled by their legs during walking. *J. exp. Biol.* **104**, 129–137.

HARRIS, J. AND GHIRADELLA, H. (1980). The forces exerted on the substrate by walking and stationary crickets. *J. exp. Biol.* **85**, 263–270.

HEGLUND, N. C., CAVAGNA, G. A. AND TAYLOR, C. R. (1982). 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.

HUGHES, G. M. (1952). The co-ordination of insect movements. I. The walking movements of insects. *J. exp. Biol.* **29**, 267–285.

KLÄRNER, D. AND BARNES, J. P. (1986). The cuticular stress detector (CSD2) of the crayfish. II. Activity during walking and influences on leg coordination. *J. exp. Biol.* **122**, 161–175.

RAIBERT, M. H., CHEPPONIS, M. AND BROWN, B., JR (1986). Running on four legs as though they were one. *IEEE J. Rob. Auto.* **RA-2**, 70–82.