

Dynamics and kinematics of ant locomotion: do wood ants climb on level surfaces?

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SUMMARY

The biomechanics of running in small animals have remained poorly characterized because of the difficulty of recording three-dimensional ground reaction forces. Available techniques limit investigations to animals with a body mass above 1 g. Here we present, for the first time, single-leg ground reaction forces of ants (body mass 10 mg), measured with a custom-built miniature force plate. We investigated forces and high-speed kinematics for straight level runs (average speed: 8.4 cm s^{-1}) of *Formica polyctena* workers. The major finding was that the time course of ground reaction forces strongly differed from previous observations of larger insects. Maximum vertical force was reached during the first third of the tripod contact phase. During this period the body was decelerated predominantly by the front legs. Subsequently, the front legs pulled and accelerated the body. This ‘climbing’ type of stride may be useful on the bumpy and unstable substrates that the animals face in their natural habitats, and may therefore also occur on level ground. Propulsive forces were generated predominantly by the front and hind legs. Dragging of the gaster on the substrate resulted in a breaking momentum, which was compensated by the legs. Future investigations will reveal, whether the identified pattern is due to specialization.

Key words: *Formica polyctena*, arthropods, ground reaction force, locomotion.

INTRODUCTION

The kinematics of ant locomotion seems to be fairly similar to those observed in other insects, which suggests similarities in the patterns of ground reaction forces. However, ants are much smaller than the insects investigated so far and gravity may no longer be the dominant factor when compared with other forces such as drag and those involved in securing a foothold (Federle et al., 2000; Full and Köhl, 1992). In the light of this, the similarity of locomotory principles among insects is more surprising than it may at first appear. Probing this for a notably small sized class of legged locomotion may reveal rather different dynamical patterns.

Comparatively slow walking insects such as stick insects (Graham and Cruse, 1981), leaf beetles (Pelletier and Caissie, 2001) and locusts (Burns, 1973; Duch and Pflüger, 1995) display an alternating tripod gait. This is also true of cockroaches at higher running speeds (Delcomyn, 1971). To distinguish between the two categories Seidl and Wehner (Seidl and Wehner, 2008) describe two basic forms of insect locomotion. The first mode, largely relying on sensory feedback, is well known from the slow moving stick insect *Carausius morosus* (Cruse, 1979). The second type, known from faster moving cockroaches, is characterized as a dynamically stable bouncing gait (Full and Tu, 1990; Full and Koditschek, 1999). Several studies substantiate the notion that locomotion in arthropods follows the same rules as those observed for a wide range of terrestrial vertebrates. In eight-, six-, four- and two-legged animals ranging in size from cockroaches to humans, the force patterns were found to be consistent with a simple spring loaded inverted pendulum (SLIP) model. This model describes the general mechanics of the centre of mass (COM) during dynamically similar types of locomotion such as running, hopping or trotting, in the sagittal plane (Blickhan and Full, 1993). Schmitt et al. (Schmitt et al., 2002) developed an analogue model for the horizontal plane – the so called lateral leg-spring (LLS) model. This has been validated with experimental data from the cockroach *Blaberus discoidalis*

(Full and Tu, 1990). Both models are based on a typical time course for the resulting ground reaction forces. During a complete stride at slow running speed a sinusoidal pattern is expected, oscillating with the stride period around the net load in both a vertical (body weight) and a lateral direction. At higher speeds of locomotion the animals only remain in contact with the surface for a fraction of the natural period of the system. A sinusoidal trajectory with a negative (braking) momentum at the beginning and a positive (accelerating) one at the end is expected in the fore–aft force (Blickhan and Full, 1993; Schmitt et al., 2002).

As mentioned above, cockroaches use an alternating tripod gait when running or trotting (mean speed: 35 cm s^{-1}). In fact, the sum of the ground reaction force components from the three synchronously acting legs (total force) complies with the conditions of the SLIP and the LLS. All active legs generate rather similar, outwardly directed, forces during one tripod. Consequently, the centre of mass is pushed to the side, where only the middle leg supports the animal. Similar to the lateral force component, the vertical one also describes a roughly parabolic curve progression for each leg. Consequently and in agreement with the SLIP model, the time course of the total force component in this direction is also unimodal. In the direction of motion the negative horizontal force of the front leg is approximately cancelled out by the positive contribution of the hind leg. Only the sinusoidal course of the middle leg remains to constitute the fore–aft component of the whole system (Blickhan and Full, 1993). During running then, the total force equates to the expected sinusoidal pattern. Kinematic analysis of ant locomotion reveals similarities to cockroaches. According to Zollikofer (Zollikofer, 1994) *Formica* ants trot with comparable velocities and the same gait pattern (tripod). *Formica pratensis* for example moves with about $9 \text{ body lengths s}^{-1}$ (Weihmann and Blickhan, 2009). This is exactly the average relative speed reached by *Blaberus discoidalis* in the experiments described by Full and Tu (Full and Tu, 1990). Although similarities in terms of running

velocity and gait pattern are obvious, differences in movement control do seem to occur. Evidence suggests that both types of movement control described above are used within the subfamily Formicinae. There are species adapted to fast running across flat terrain and others that negotiate their rugged habitat mostly by scrambling. Recent kinematic studies have revealed differences between *Cataglyphis* and *Formica pratensis* despite their kinship, similar anatomy and similar sensory configuration (Weihmann and Blickhan, 2009). The high relative velocity of *Formica* ants [according to Sponberg and Full (Sponberg and Full, 2008), the influence of control and feedback loops is limited] and the rhythmic fluctuations of the COM which occur in this species point to a cockroach-like type of locomotion (Seidl and Wehner, 2008; Weihmann and Blickhan, 2009).

Weihmann and Blickhan (T.W. and R.B., submitted) demonstrate that wood ants do not make larger posture adjustments to inclines than the desert ant *Cataglyphis fortis*, and postulate that wood ants always try to find a secure foothold on the substrate, as do chameleons (Higham and Jayne, 2004).

Our aim was to analyze whether the similarities to cockroach locomotion found in the kinematics of ant locomotion are also reflected in the ground reaction forces, or whether a permanent clinging to the substrate can be detected despite higher relative velocities than those reached by chameleons or stick insects. The first experiments were conducted in the horizontal plane to permit a comparison with previous studies (Full et al., 1991). In order to answer the questions we have set ourselves we built a miniature force plate to measure ground reaction forces in the micronewton range. For the first time, we are able to resolve three-dimensional forces during free locomotion of very small insects (body mass *ca.* 10 mg).

MATERIALS AND METHODS

Animals

Workers of a *Formica polyctena* (Förster 1850) colony collected in a forest near Jena, Germany were used as study animals ($N=8$; average mass: 10.3 ± 1.0 mg; \pm s.d.). Depending on the filling of the crop, the length of the gaster is highly variable. Therefore, the length of the thorax (average length: 3.1 ± 0.3 mm; \pm s.d.) from cervix to petiolus was used to scale body length. Only straight runs at a constant speed were selected ($v=8.4 \pm 2.0$ cm s⁻¹; \pm s.d.). On average, the maximum lateral deflection of the straight path during the stepping cycle was 1.0 ± 0.4 mm. The surface of the track and the tread of the force plate were covered with scale paper.

Force plate

As no three-dimensional (3-D) force platforms with micronewton resolution are commercially available, the measurements required the development of a custom-built device. This platform consists

of a cross of four horizontal beams fixed to a metal frame (Fig. 1A). These bars (cross) take up the vertical component of the force. In the centre of the cross two orthogonally oriented bars are mounted for transmitting the two horizontal forces (anterior–posterior, lateral). At the end of the beam, a square tread is attached (side length 4 mm). This design minimizes weight and allows for the attachment of small semiconductor strain gauges. Selection of suitable materials (PVC) allows for a sufficiently high natural frequency (lowest component: 280 Hz; critically damped). Contact times of the investigated runs amounted to 61.7 ± 15.2 ms (mean \pm s.d.). The ant's footfall position was measured from a synchronous high-speed video recording of the runs. We analyzed runs in which only a single leg stepped onto the force plate. The unamplified sensitivities of the plate are given in Table 1 together with the residuals of humming and noise remaining after the filter process (analogue 2 pole low pass at 300 Hz). The signals were amplified (factor: 60000) using a commercial amplifier (Vishay 2100, Micro Measurements; Vishay Electronic GmbH, Selb, Germany) and a custom-built amplifier. Forces applied to the plate *via* a needle mounted onto a sensitive bending bar allowed calibration. Owing to the design of the force plate, crosstalk could not be completely eliminated. Without any mathematical corrections this influence could reach values up to 30%. By taking into account the point of force application with an accuracy of 0.1 mm, the maximum crosstalk effect could be reduced to 4–6%.

Video analysis

Runs were recorded using a high-speed video system (HCC-1000, VDS Vosskühler GmbH, Osnabrück, Germany) with a resolution of 1024×512 pixels and a sample rate of 922 frames per second. A mirror provided a side view (Fig. 1B). The camera was mounted perpendicularly at a distance of about 15 cm above the running track. The images were digitized using commercial software (WINalyze v2.1; Mikromak[®]; Berlin, Germany) and were used to select suitable runs (typical movement pattern, straight runs, constant speed). Only trials in which the ants ran straight along the path without touching the walls were evaluated. To ensure that the laboratory animals have to run straight the test canal were very narrow (15 mm; Fig. 1B). Speed was determined by analyzing four consecutive step cycles with the step on the plate in the central segment.

System of coordinates

As we only analyzed straight runs along the direction of the force platform, the animal-fixed system of coordinates was valid for both the kinematic and dynamic investigations (Fig. 1C). The y-axis is parallel to the animal's long axis in walking direction. The x-axis is laterally to the right, parallel to the substrate, and the z-axis is perpendicular to the xy-plane. Positive ground reaction forces in the forward direction (F_y) accelerate the animal. Positive lateral

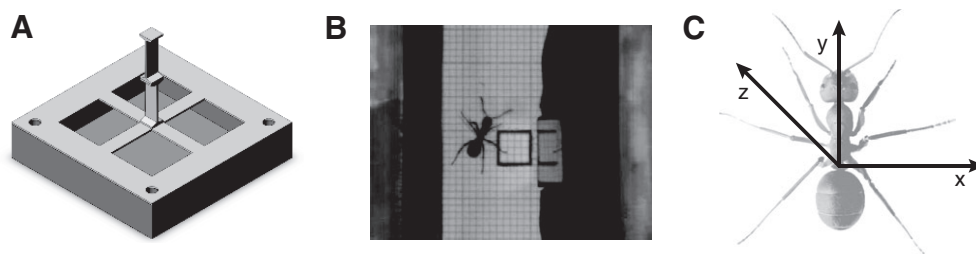


Fig. 1. (A) A drawing of the three-dimensional force plate. (B) Single-leg ground reaction force measurement of a *Formica* ant. The ant is stepping with the second (middle) leg onto the force plate. (C) System of co-ordinates.

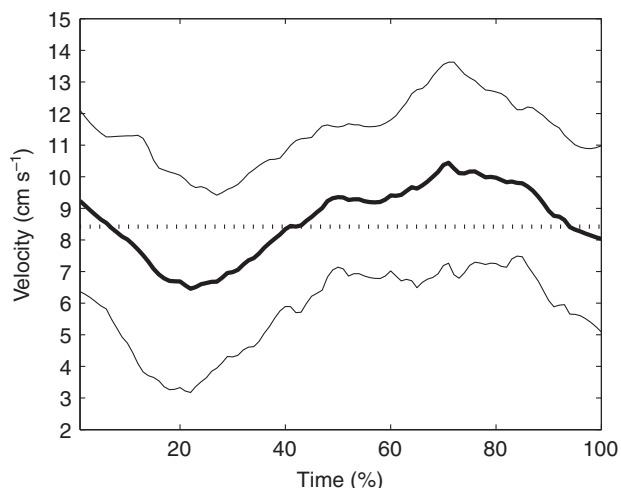


Fig. 2. Average time course of the running speed during the stance phase ($N=27$). Bold line: mean speed (8.4 cm s^{-1}); thin lines: the standard deviation.

forces (F_x) accelerate the animal to the right, and positive vertical forces (F_z) push the animal upwards. We do not distinguish between left and right legs. All results on the left side are mapped to the right. Correspondingly a positive forward force observed for the front leg implies pulling and negative force implies pushing. For the right middle leg a positive lateral force implies pulling, and for the hind leg a positive forward component implies pushing.

RESULTS Kinematics

Time course of running speed

On average, the animals ran at a speed of $8.4 \pm 2.0 \text{ cm s}^{-1}$ ($N=27$ runs; range: $3.6\text{--}13.2 \text{ cm s}^{-1}$). The time course (Fig. 2) was roughly sinusoidal. In the first half of the stance, as detected for the leg under investigation by the force plate, the animals decelerated down to a speed of about 6.6 cm s^{-1} and accelerated thereafter to a speed of up to 10.5 cm s^{-1} .

Points of touchdown of the legs

During contact, the tarsi moved almost parallel to the long axis of the animal's body (Fig. 3). The lateral distance of the start and end values, with respect to the petioles [about centre of mass; see Zollikofer (Zollikofer, 1994)], did not differ (t -test, $P>0.05$; Table 2).

Table 1. Sensitivity of the force plate and the maximum absolute value of the residual noise for the three components

	Lateral	Anterior	Vertical
Sensitivity	213.8 mV N^{-1}	311.7 mV N^{-1}	42.3 mV N^{-1}
Residual noise	$1.6 \mu\text{N}$	$1.1 \mu\text{N}$	$8.2 \mu\text{N}$

Table 2. Leg placement: coordinates of touch down and take off of the tarsi with respect to the petiolus

Leg	Contact time (ms)	Lateral x (mm)		Anterior–posterior y (mm)		
		Touch down	Lift off	Touch down	Lift off	Δy
Front	67.0 ± 11.7	2.21 ± 0.42	2.47 ± 0.56	5.39 ± 0.37	0.72 ± 0.57	4.67 ± 0.54
Middle	60.1 ± 8.9	5.25 ± 0.77	5.02 ± 0.84	3.00 ± 0.43	-1.83 ± 0.73	4.83 ± 0.97
Hind	57.5 ± 20.7	4.03 ± 0.79	3.74 ± 0.61	-2.97 ± 0.38	-6.07 ± 0.35	3.09 ± 0.34

Values are mean \pm s.d.

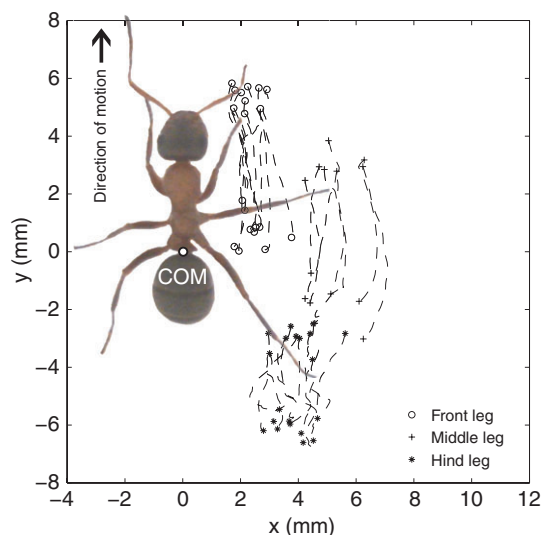


Fig. 3. Position of the tarsi with respect to the petiolus (dashed lines) and the points of touch down and lift off (symbols) in the animal-fixed system of coordinates. In accordance to Zollikofer (Zollikofer, 1994) the petiolus is considered as the COM.

The front legs contacted the ground closer to the body axis ($x_{td}=2.21 \text{ mm}$) than the middle and hind legs (5.25 mm and 4.03 mm). Touchdown occurred anterior to the petiolus for the front and middle legs ($y_{td}=5.39 \text{ mm}$ and 3.00 mm) but posterior for the hind legs (-2.97 mm). Although the front and hind legs stayed anterior or posterior to the petiolus, respectively, the middle leg switched side and was lifted off posterior to the petiolus (-1.83 mm).

The distance covered in direction of the long axis (Δy ; Table 2) was shorter for the hind legs than for the front and middle legs (Tukey's test, $P<0.05$). The high-speed video recordings confirmed that after complete extension, the hind legs were dragged along and did not change their position with respect to the body. This peculiarity is also supported by the force recordings described below. Contact times on average amounted to $61.7 \pm 15.2 \text{ ms}$ (mean \pm s.d.). There was a slight but not significant tendency towards shorter times from the front to the hind legs. In agreement with the findings of Seidl and Wehner (Seidl and Wehner, 2008), all observed ants ran with a tripod gait. Our results can be explained by the function and arrangement of the different legs. Front legs contribute to propulsion largely by flexion, whereas hind legs do this by extension. Middle legs generate thrust by leg rotation.

Dynamics

Ground reaction forces

The force patterns were variable. Nevertheless, a basic pattern emerged that differed from previous findings in other walking and running insects.

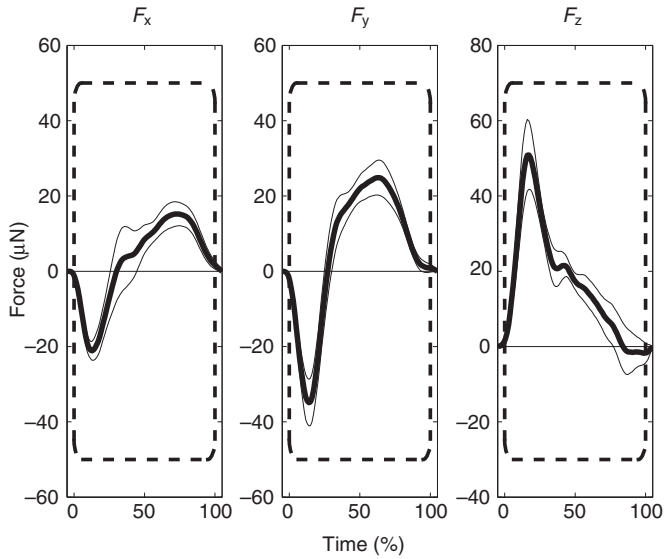


Fig. 4. Components of the ground reaction force of the front leg. Bold lines: mean ($N=10$); thin lines: s.e.m. The dashed rectangle marks stance, without considering the tripod overlap.

Front legs

Surprisingly, both horizontal components of the ground reaction force changed sign. During the first third of the contact, negative forces were observed in the anterior (minima: $F_y = -39.6 \pm 18.6 \mu\text{N}$; mean \pm s.d.) and in the lateral (minima: $F_x = -27.4 \pm 11.2 \mu\text{N}$) direction. The average of the peak forces observed in the individual tracings is higher than the peak of the average time-course depicted in Fig. 4 as this process results in smoothing due to shifts of the instant where the peak occurs. In the second half of the step, forces became positive with maxima of $F_x = 21.8 \pm 8.5 \mu\text{N}$ and $F_y = 29.7 \pm 13.9 \mu\text{N}$, respectively. Similarly, the vertical component of the ground reaction force reached its maximum ($F_z = 58.3 \pm 25.3 \mu\text{N}$) after the initial $27.6 \pm 15.9\%$ of the stance and thereafter decreased continuously.

Middle legs

The lateral component of the ground reaction force (F_x) of the middle leg (Fig. 5) had a sinusoidal time course similar to that observed for the front leg, but forces changed sign at about the middle of the stance. The negative maximum ($-41.4 \pm 20.0 \mu\text{N}$) was reached after about 25% of the contact, the positive maximum ($26.1 \pm 14.6 \mu\text{N}$) was reached after $66.2 \pm 8.0\%$ of contact.

Fore–aft forces were clearly lower for the middle legs as compared with the other legs. The time course varied strongly. Negative as well as positive force peaks in the order of $10 \mu\text{N}$ were observed. The vertical maximum of $57.9 \pm 24.4 \mu\text{N}$ was reached after $35.3 \pm 12.9\%$ of contact, similar to the location of the maximum of the lateral force and those detected for the front leg.

Hind legs

Forces observed for the hind legs were much more reproducible (Fig. 6). All components showed an unimodal time course. Laterally, after $47.1 \pm 12.5\%$, a minimum ($-17.6 \pm 8.2 \mu\text{N}$) was reached. Anteriorly, after $42.5 \pm 10.2\%$ of stance, the animal pushed with $29.1 \pm 6.4 \mu\text{N}$. Within the last third of the ground contact, a small negative force (pulling) of about $-8.8 \pm 5.7 \mu\text{N}$ was observed. It results from dragging the tarsi across the surface (see above). The vertical component (F_z) has its maximum ($44.4 \pm 13.1 \mu\text{N}$) at about $44.1 \pm 11.4\%$ of the contact time.

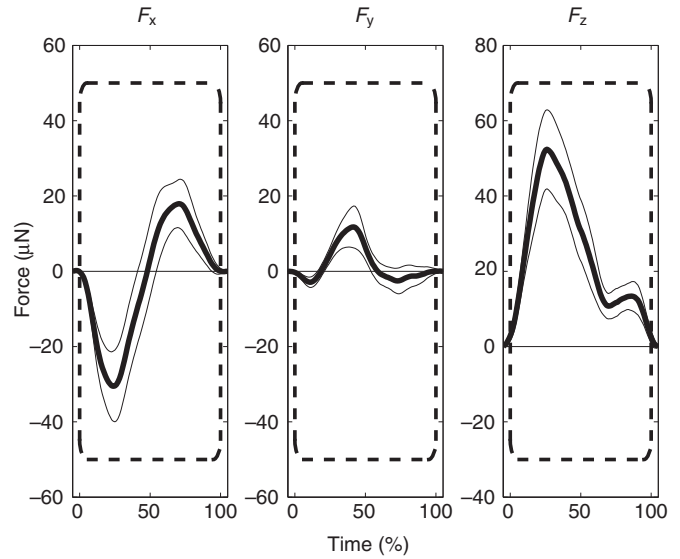


Fig. 5. Components of the ground reaction force of the middle leg. Bold lines: mean ($N=7$); thin lines: s.e.m. The dashed rectangle marks stance, without considering the tripod overlap.

Table 3 shows the average extrema of the ground reaction forces and their relative times during stance phase. In all legs the vertical force component was dominant. Vertical load was about evenly distributed among the legs. There was no significant difference between the legs (ANOVA, $P=0.29$). The anterior forces were lower and less evenly distributed. The highest propulsive forces were generated by front and hind legs. The front legs strongly contributed to braking. Although the hind legs largely pushed outward, the middle and front legs pushed and pulled with about the same magnitude sideways.

More relevant than the peak forces are the net contributions to momentum by each leg (Table 4). In the vertical component there was no net difference with respect to leg number (ANOVA, $P=0.67$). Weight was thus evenly distributed among the legs. In the

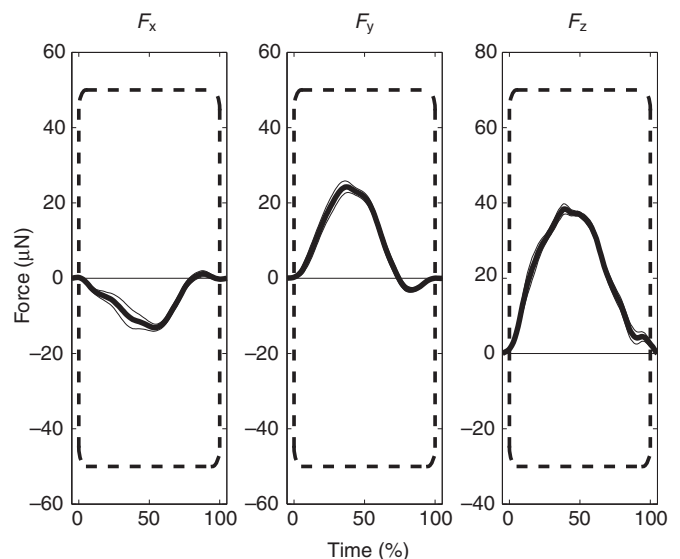


Fig. 6. Components of the ground reaction force of the hind leg. Bold lines: mean ($N=10$); thin lines: s.e.m. The dashed rectangle marks stance, without considering the tripod overlap.

Table 3. Extrema of the ground reaction force and the relative time during stance phase

Leg	Value	F_x (lateral)		F_y (anterior)		F_z (vertical)
		Minimum	Maximum	Minimum	Maximum	Maximum
Front	Force (μN)	-27.4 ± 11.2	21.8 ± 8.5	-39.6 ± 18.6	29.7 ± 13.9	58.3 ± 25.3
	Time (%)	19.8 ± 7.6	62.4 ± 15.9	18.4 ± 3.8	54.0 ± 14.7	27.6 ± 15.9
Middle	Force (μN)	-41.4 ± 20.0	26.1 ± 14.6	-7.8 ± 4.3	14.1 ± 13.5	57.9 ± 24.4
	Time (%)	28.3 ± 6.0	66.2 ± 8.0	54.9 ± 27.4	41.6 ± 23.5	35.3 ± 12.9
Hind	Force (μN)	-17.6 ± 8.2	3.4 ± 2.8	-8.8 ± 5.7	29.1 ± 6.4	44.4 ± 13.1
	Time (%)	47.1 ± 12.5	81.5 ± 6.7	77.4 ± 7.6	42.5 ± 10.2	44.1 ± 11.4

Values are mean \pm s.d.

direction of locomotion, the front and hind leg both contributed considerably to propulsion whereas the contribution of the middle leg was negligible. Here the braking and accelerating segments cancel each other out. With respect to the lateral component the tripodal walking pattern must be taken into account. Above we mapped all forces measured for the left legs to the right legs of the body. Within the tripod the left middle leg generates forces in concert with the right front and hind legs and *vice versa*. The momentum of the right hind leg pushing the animal to the left was largely compensated by the sum of the momentums generated by the right front leg and the left middle leg (Table 4).

Vectors of the ground reaction force

Figs 7–9 show projections of the force vector during stance with respect to the body fixed (petiolus) co-ordinate system (for convention see Fig. 1C). Here too, the forces generated by the tripod are depicted (right front leg, left middle leg, right hind leg). Drawing the vectors in that way helps to visualize the action of the ground reaction forces with respect to the centre of mass.

In the horizontal plane (Fig. 7A,B) it was obvious that at the beginning of the stance, all vectors of the ground reaction force pointed towards the petiolus (centre of mass). Whereas the direction of the force vector (115 deg. with respect to x-axis; maximum at 38% of

Table 4. Mean contributions to momentum

Leg	Lateral (nN s^{-1})	Anterior (nN s^{-1})	Vertical (nN s^{-1})
Front	226 ± 507	417 ± 453	1158 ± 496
Middle	127 ± 707	-2 ± 281	1447 ± 453
Hind	-368 ± 315	589 ± 194	1354 ± 926
Σ_{tripod}	-15	1004	3959

The lateral components measured at the right middle leg are mapped to the left assuming a tripod consisting of the right front leg, the left middle leg and the right hind leg. For convention of the sign see Fig. 1C. The lateral component of the mean momentum right front leg is pointing outwards whereas those of the middle and hind leg are pointing inwards (compare Fig. 1A). The values were calculated as means of the single measurements, hence differences with Figs 4–6 may result.

Values are mean \pm s.d.

contact time; time III, Fig. 7A) changed only a little for the hind leg, the force vectors changed orientation of the front and middle legs. After 14% of the stance phase (just before time I, Fig. 7A), the front leg generated a maximum pushing force vector with an angle of 234 deg. with respect to the x-axis. In the middle leg a corresponding maximum was observed at 24% of contact time (orientation: 3 deg. with respect to the x-axis). The largest horizontal forces after the

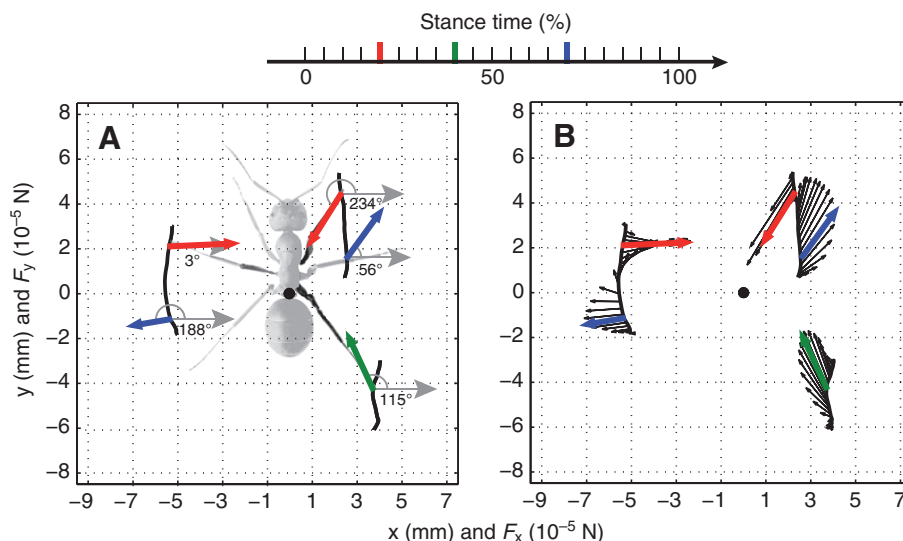


Fig. 7. Horizontal projections of the ground reaction force generated by a tripod consisting of the right front leg, the left middle leg and the right hind leg. (A) Selected vectors and angles with respect to the x-axis at instant I (red), II (green) and III (blue). (B) Force vectors mapped onto the position of the tarsi in the body coordinate system (the petiolus is marked as a black dot at the point of origin). The lines at the vector bases mark the mean path of the leg tips with respect to the petioles during stance (compare with Fig. 3). The animal is assumed to walk upwards in the diagram, i.e. while fixing the coordinate system at the petioles the tips move from above (anterior) to below (posterior) during stance. Correspondingly, the bases of the vectors of the ground reaction force move in this direction with respect to time.

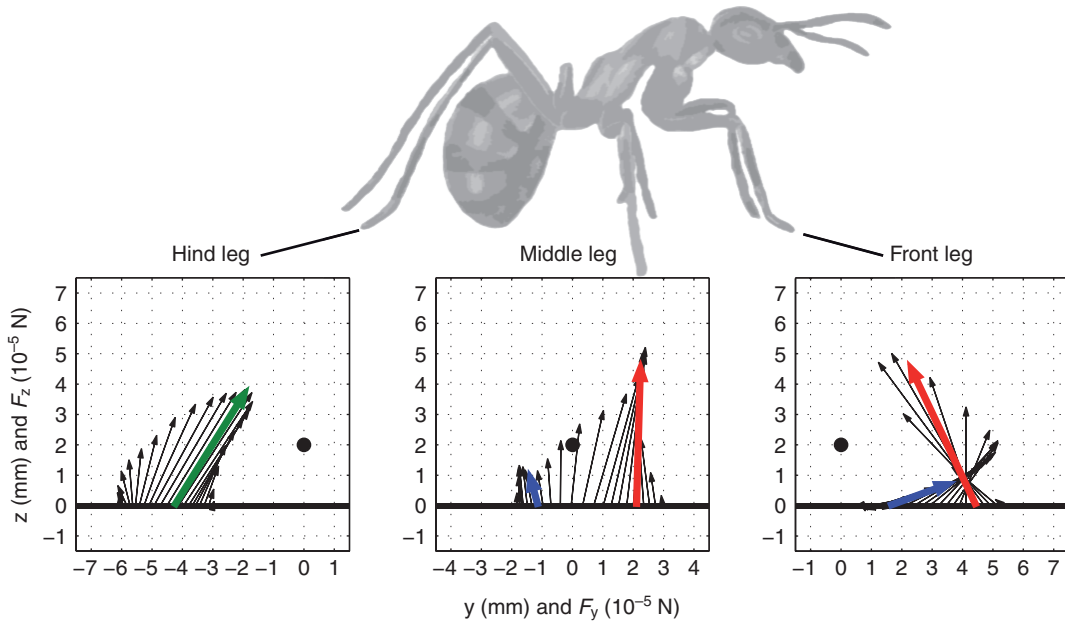


Fig. 8. Projection of the ground reaction force vectors into the sagittal plane. Black dot: petiolus at (0, 2). The animal moves from left to right and the leg tips (bases of the vectors at the y-axis in the xy-plane) from right to left. The colouring of the force arrows are the same as in Fig. 7.

orientation change occurred at about 70% of contact time (time II, Fig. 7A). The pulling forces were directed at 56 deg. for the front leg and at 188 deg. for the middle leg with respect to the x-axis.

In the sagittal plane the projection of the ground reaction force of the hind leg reached a maximum value at 39% of contact time (time III, Fig. 8). Its orientation of 58 deg. with respect to the y-axis was largely maintained during stance. The vector of the ground reaction force of the middle leg roughly remained perpendicular to the substrate (y-axis) or parallel to the z-axis. In the first leg,

orientation changed from braking to forward acceleration, as observed in the horizontal plane. The angle with respect to the y-axis shifted continuously during stance from 145 deg. to 0 deg. at the end of the stance phase.

In the projection into the transverse plane, again, the orientation of the vector of the ground reaction force of the hind leg shifted only little. At the instant of maximum force development (39% of contact time; time III, Fig. 9), the angle with respect to the x-axis amounted to 106 deg. and the vector clearly pointed above the centre

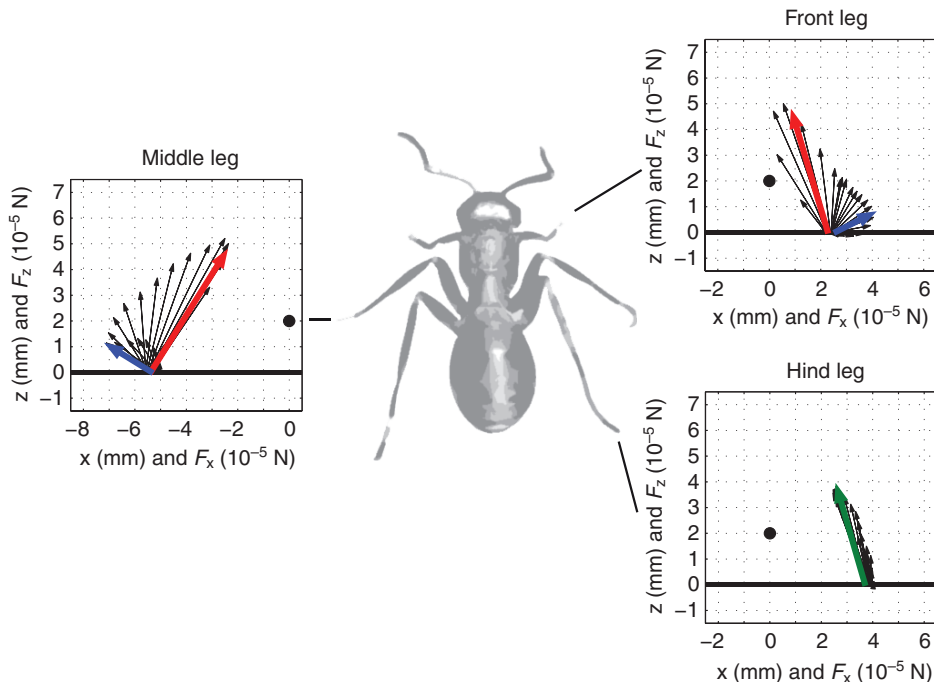


Fig. 9. Projection of the ground reaction force vectors into the transverse plane. Black dot: petiolus at (0, 2). The animal moves 'into' the page. In the projection the leg tips follow a complicated time course (compare with Fig. 3). The colouring of the force arrows are the same as in Fig. 7.

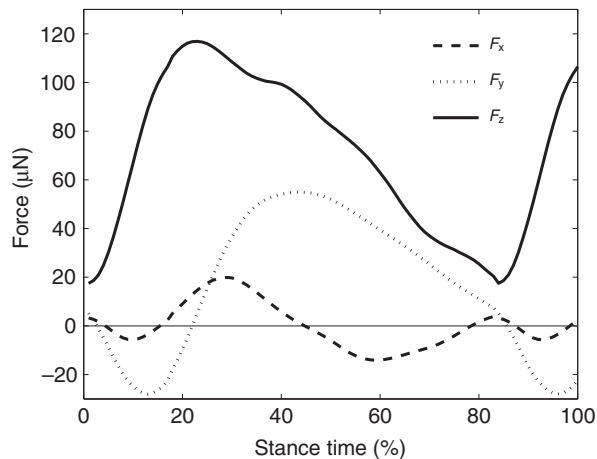


Fig. 10. Components of leg-generated force acting on the COM, calculated as the sum of the single leg forces during the stance phase of one tripod, taking into consideration the initial and final stance overlap of 17%. The lateral force (F_x) oscillates around zero with a zero net momentum. The fore-aft force (F_y) also oscillates around zero but the initial braking momentum is followed by an accelerating momentum, which exceeds the former by a factor of five (maximum of the mean force $53 \mu\text{N}$). Vertical force (F_z) is positive throughout the stance and reaches a maximum ($121 \mu\text{N}$) early, at 25% contact time.

of mass. For the front and middle legs, the pattern observed in the horizontal perspective was visible again. The vectors of the ground reaction force were close to mirror-image symmetrical with respect to the zy -plane. At the beginning of stance they pointed towards the centre of mass and then the directions reversed. Although the angle included with the x -axis decreases from approximately 120° to 30° for the front leg, this angle increases about the same amount ($\sim 90^\circ$ from 60° to 150° for the middle leg). For both legs the instant of the force maximum was observed again at about 20% of stance (time I, Fig. 9).

DISCUSSION

Ground reaction force during one tripod

Red wood ants display a typical tripod gait pattern in which all legs of a tripod have ground contact in phase with each other (Seidl and Wehner, 2008). The front and the hind legs of one side and the middle leg of the other side contact the ground simultaneously while the other legs are in the swing phase. All statements in our discussion refer to the combination of right front leg, left middle leg and right hind leg. We observed a stance-phase overlap of $17 \pm 3\%$ between subsequent tripods which entailed a higher duty factor than that found by Seidl and Wehner (Seidl and Wehner, 2008). As mentioned above we used scale paper as a substrate. Sand paper, as used by Seidl and Wehner, is rougher. The time required to obtain and release footholds (Federle and Endlein, 2004; Larsen et al., 1995) should thus have been greater in our experiments. Under the assumption of the double support, the total force (Fig. 10) acting on the animal's centre of mass can be calculated, and with it the acceleration of the ant.

As mentioned above, the net momentum in the lateral direction was zero, i.e. the animal maintained its straight path. As we had selected runs in which the animals maintained a constant speed, we would have expected the net anterior component of momentum to be very small, generating just sufficient thrust to overcome aerodynamic drag. However, air drag is negligible, because even with an overestimated drag coefficient of 4 and a frontal area of

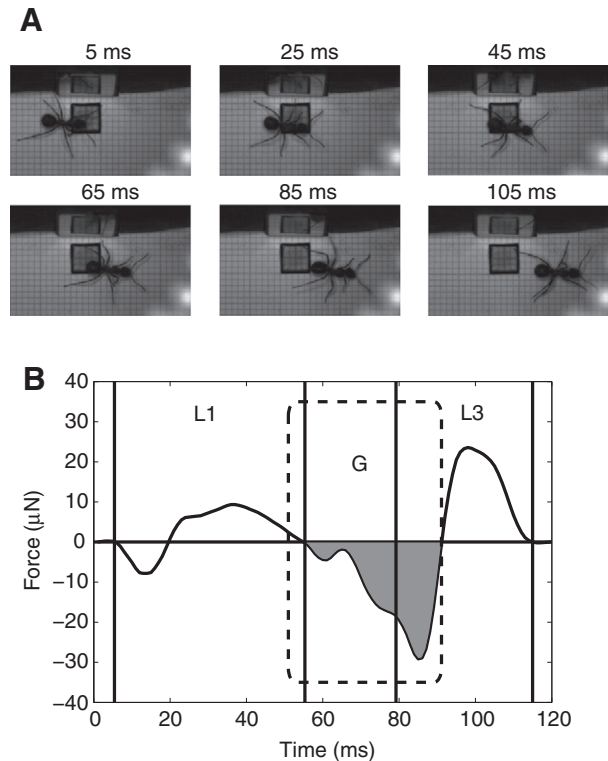


Fig. 11. Braking effect of the gaster in running *Formica* ants. (A) Video recording of ant worker running across the 3-D force plate. (B) Time course of the fore-aft component of the ground reaction force. The animal stepped onto the plate first with the left front leg (L1), then dragged the tip of the gaster (G) across the plate (dashed rectangle), and then stepped onto the plate with the hind leg (L3). Vertical lines indicate the contact and lift-off times for both legs.

12 mm^2 , the estimated drag force is only $0.3 \mu\text{N}$. Thus, the measured forward momentum (1000 nN s^{-1} , Table 4) is much larger than the braking momentum because of air drag ($0.3 \mu\text{N} \times 60 \text{ ms} = 18 \text{ nN s}^{-1}$).

The fact that contrary to expectations a significant positive net impulse in walking direction was observed can be explained by a behavioural trait that occurs under particular, e.g. recruiting circumstances. During locomotion, *Formica* ants hold the tip of their gaster close to the surface (T.W. and R.B., submitted). Consequently ground contact frequently occurs. This was shown by Horstmann (Horstmann, 1976) in experiments on smoked glass. Secretions from the gaster are used to mark the path for their nestmates during foraging (Hölldobler, 1995). Fig. 11 shows a video sequence of an ant crossing the force plate, together with the synchronously registered fore-aft component of the ground reaction force. In the beginning, the animal stepped onto the force plate with the left front leg (L1), which first decelerates and then accelerates. At about 55 ms, the front leg was lifted off the ground but at the same time the tip of the gaster (G) was dragged across the plate, resulting in a braking force. While the gaster was still sliding, the left hind leg (L3) stepped onto the plate and, after the gaster had slipped off the platform, the remaining left hind leg produced a propulsive force until it was lifted off the ground. The net forward thrust generated by the legs could not have been deduced from kinematics alone (Seidl and Wehner, 2008) (T.W. and R.B., submitted); it became visible only through the registration of ground reaction forces. In our setup a continuous registration of the drag force generated by the gaster was not possible. In addition to Horstmann's results, the vertical oscillations

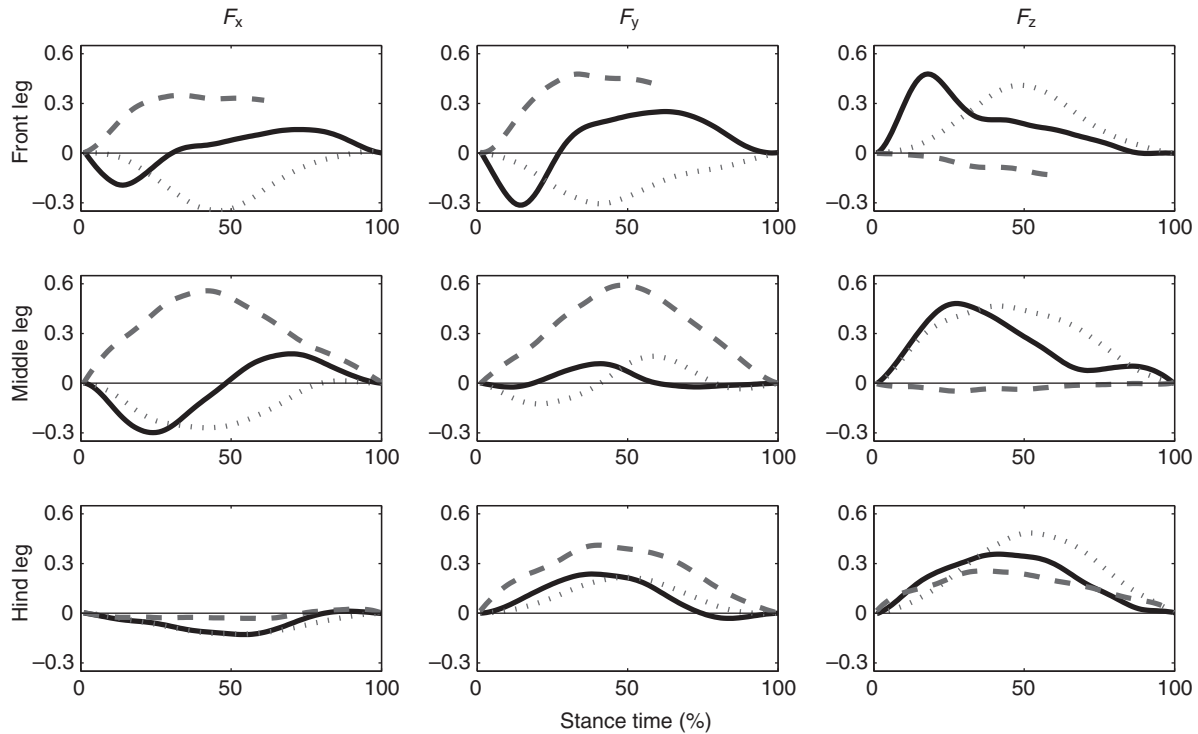


Fig. 12. Comparison of the normalized (to body weight) ground reaction forces in wood ants (solid, black line) and running (dotted, grey line) and climbing cockroaches (dashed, grey line). The cockroach data are taken from the work of Full et al. (Full et al., 1991) and Goldman et al. (Goldman et al., 2006).

of the centre of mass (T.W. and R.B., submitted) confirm the possibility of a more or less cyclical ground contact of the gaster. The calculated vertical component (Fig. 10) of the tripod force – considering the overlap – averages about $70 \mu\text{N}$ which amounts to a contribution of only 70% to the support of the body weight. Since the strong effect of the gaster was unexpected, no systematic force measurements were taken in this study. This will be explored in further studies.

The time course of the ground reaction forces (Fig. 6) and the total vertical force (Fig. 10) indicate that in the initial stance phase, the legs of the tripod carry a proportion of the body weight. Towards the end of the step, the gaster takes more and more load. At the same time the hind leg ceases to generate propulsion forces. This is also the phase when the front leg generates the highest forward thrust. We infer from this context that the increasing load on the gaster brings with it increasing friction in the direction of motion. The resulting deficit is compensated by the positive force production of the front legs. As we did not find a significant difference between the legs in terms of vertical momentum, this issue requires further investigation. Similarly, future research will consider body rotations and torque which can, in principle, be calculated from the data presented.

So far, comparable measurements in other ant species are not available. The most direct comparison is possible with data on the cockroach *Blaberus discoidalis* (Full et al., 1991). This insect also runs with an alternating tripod gait, but it is about 250 times heavier (body mass $\sim 2\text{ g}$) and runs about four times faster than our ants (average speed 37.8 cm s^{-1}).

The ground reaction forces in *B. discoidalis* differ from our findings in several aspects (Fig. 12). With the exception of the fore–aft component (F_y) of the middle leg, all forces were found to be unimodal (Full et al., 1991). As in our study, the vertical forces were evenly distributed among cockroach legs. However, the time

course of the frontal and lateral components was much simpler. Laterally all legs continuously pushed outwards. The front legs were found to mainly decelerate, compensated by the propulsion generated by the hind legs. In contrast to *Formica* ants, the abdomen of *B. discoidalis* did not generate significant braking forces.

Although the relative speed was similar to our experiments with *F. polyctena*, Kram et al. (Kram et al., 1997) found a significantly lower duty factor of 0.53 in *Blaberus discoidalis*. This results in a negligible tripod overlap. The sum of the single leg forces of one tripod could be considered to be the total force acting on the centre of mass. Full et al. (Full et al., 1991) (Fig. 8) present a single measurement in which a cockroach steps onto the platform with all three legs in succession. These data were used to estimate that the sum of the mean vertical force of one tripod only amounts to approximately 70% of the average body weight. Assuming that these cockroaches do not drag their abdomen above the ground, the subject's body weight in this single registration was clearly lower than the specified mean value of 2.1 g.

The net pattern of ground reaction forces of the cockroach very much resembles that observed for running, hopping and trotting vertebrates. This can be described by a lumped parameter model, the spring loaded inverted pendulum model (SLIP) (Blickhan, 1989; Blickhan and Full, 1993; Full and Koditschek, 1999; McMahon and Cheng, 1990). A planar version of the spring mass system can also be used to describe the kinetics of locomotion of cockroaches in the horizontal plane (Schmitt and Holmes, 2000; Seipel et al., 2004). In *Formica* the pattern of the lateral component of the ground reaction force revealed small oscillations of higher frequency (Fig. 10), which may represent higher modes of oscillation of a spring mass model (cp. Geyer et al., 2006), but it clearly differs from the observations in cockroaches. As pointed out above, vertical oscillations take place in the ant. However, due to the influence of the abdomen, the lumped parameter model may not be applicable

to our present data. The kinetics of many gaits is not sufficiently described by the spring mass system (Blickhan and Full, 1993). Examples are creeping, galloping and climbing. *Formica pratensis* seems to adapt its kinematics only slightly when walking across different slopes (T.W. and R.B., submitted). Wood ants adapted to structurally complex substrates (e.g. forest floor, vegetation) may always tend to cling to their substrate, in agreement with our measurements. After a short period of deceleration, the ants pulled inward with both front and middle legs. This allows secure attachment to the substrate with the aid of adhesive pads or claws (Federle et al., 2001; Frantsevich and Gorb, 2004). On smooth surfaces, ants stick with their pretarsal arolium (Federle et al., 2001). In *Formica* these pads are well developed (Gladun and Gorb, 2007). They unfold on smooth substrates when the leg is pulling proximally. The thin fluid film between arolium and substrate can compensate for small-scale surface roughness and ensures an intimate contact between the viscoelastic cuticle of the arolium and the substrate (Drechsler and Federle, 2006). Adhesive pads can achieve very high friction forces (Federle and Endlein, 2004; Federle et al., 2002).

Goldman et al. (Goldman et al., 2006) published single-leg force measurements for vertically climbing *Blaberus discoidalis*. As expected, the force patterns differed from those observed during locomotion on level ground (compare Fig. 12), whereas the kinematics did not. In contrast to level running, all legs generated exclusively positive forces in the fore–aft direction to overcome gravity. Additionally, the two forelegs pulled laterally towards the midline to cling to the substrate. While the front legs pulled the head towards the wall, the hind legs pushed the abdomen away from it. Our results for the later stance phase of ants running on level ground show similarities to these force patterns, which are mainly indicated by the positive F_x values of the front and middle legs and the positive F_y value of the front leg. Although differences are observable in the initial stance phase and in the absolute values, the qualitative similarities to cockroach climbing forces are greater than to those reaction forces generated during level running (for a comparison, see above). We assume that the dominating factor in the similar vertical force patterns is the direction of the gravity vector, which also affects the other force components.

The activity of the hind legs seems to be independent of slopes and other influences. On upward slopes it always pushes against the substrate, generates propulsion and determinates the clearance. The only difference between hind leg activity in level and vertical locomotion in cockroaches is that the extrema of F_y and F_z are interchanged because of weight bearing caused by the directional change of the gravity vector.

Pelletier and Caissie (Pelletier and Caissie, 2001) provided evidence that pulling a load during horizontal locomotion influences the speed of operation in a similar way to the angle of the gravity vector during running on slopes. We therefore suppose that the ant's gaster serves a similar role in the fore–aft direction as gravity does during climbing.

As pointed out by Seidl and Wehner (Seidl and Wehner, 2008), insects display two basic forms of locomotion: (i) slow locomotion largely relying on sensory feedback, as in the stick insect *Carausius morosus* (Cruse, 1976), and (ii) dynamically stable bouncing gaits, as in cockroaches (Full and Tu, 1990). Based on kinematic observations, Seidl and Wehner assumed the latter for ants. This may well be valid for the desert ant *Cataglyphis*. *Formica polyctena* seems to bounce too, but the general dynamics are more complicated and no longer described sufficiently by a simple spring mass model. To what extent this gait is controlled by sensory feedback is not known and requires further investigation. *Formica* employs a much

higher cycle frequency (5 Hz at 9 cm s^{-1}) than *Carausius morosus* (~ 2 Hz) (Wendler, 1964), but neuromuscular signal transmission in the ant may be facilitated by short legs. However, the mean speed reached by the ants in our investigation was $12 \text{ body lengths s}^{-1}$ higher than that observed for the cockroach ($9 \text{ body lengths s}^{-1}$) in the force analysis (Full and Tu, 1990; Ting et al., 1994) but lower than the peak values observed for a cockroach running on two legs (Full and Tu, 1991). Compared with the stick insect, the wood ant may be adapted to fast locomotion on a variable and unstable substrate. This may be because of the relatively more muscular coxae of the ants, which enable them to generate the necessary propulsion forces.

The mechanical (non-neuronal) feedback available in spring-like musculo–skeletal systems (Blickhan et al., 2007; Daley and Biewener, 2006; Daley et al., 2007; Grimmer et al., 2008; Seyfarth et al., 2002; Sponberg and Full, 2008) provides further stability and permits the unloading of the neuronal control system during planar locomotion across rough terrain. Other environments may require different measures to achieve a similar goal. Sponberg and Full (Sponberg and Full, 2008) proved the existence of self-stabilising mechanisms that are independent of classical spring mass models (SLIP, LLS) in insects. For example, no adaptations in leg kinematics or muscle activation could be detected. It is probable, therefore, that certain habitat-specific mechanisms lead to a dynamic stabilization of the locomotive system, as defined by Grimmer et al. (Grimmer et al., 2008). The spiny legs of spiders and cockroaches, for example, help to transfer forces and energy on a ‘gap-filled’ terrain with rather sparse footholds (Spagna et al., 2007) and enable the animals to uphold their motion pattern. It remains to be shown in future studies whether the strategy of initial pushing with the front legs offers an advantage for the species investigated within an environment where slopes, solidity and roughness may differ considerably from step to step.

The locomotion of ants is also relevant in the context of orientation. Excellent and extensive information about ant orientation has been gathered by Wehner and his co-workers. Experiments with *Cataglyphis fortis* proved the existence of an internal navigation system (Wittlinger et al., 2007; Müller and Wehner, 1988; Seidl and Wehner, 2008; Sommer and Wehner, 2004). This so-called path integrator performs some kind of vector analysis. Wohlgemuth et al. (Wohlgemuth et al., 2002) demonstrated that this mechanism is used on flat surfaces and works just as well for three-dimensional paths. However, Grah et al. (Grah et al., 2007) concluded that *Cataglyphis* essentially represents its environment in a simplified, two-dimensional fashion. Therefore, the ants must be able to monitor and recalculate the influence of slopes. Here, the animals may make use of graviception. Primarily the hair field mechanoreceptors at nearly all joints of the insects provide this information (Markl, 1974) and their stimulation depends on changes in segment angles. Similar information is provided by chordotonal organs. In addition the campaniform sensilla are used in this context as they detect strains in the exoskeleton of the legs and may be important for slope detection. These sensors are affected by and depend on changing load distribution among the legs (Ehmer and Gronenberg, 1997; Weidner, 1982).

This study provides the first ever information about force patterns during planar locomotion in wood ants. Contrary to expectations formed on the basis of other arthropod studies, the dynamics do not reflect the pure spring-like mechanisms suggested by the rhythmic oscillating type of COM kinematics. Although gravity presses the animal onto its support during level locomotion, the ground reaction forces have significant similarities to those involved in climbing

and less to those at work in cockroaches running on a horizontal surface. There is evidence that the locomotion of wood ants is in fact a 'climbing' style characterized by a permanent clinging to the substrate. Even though the ant's force patterns resemble those of both horizontal and vertical cockroach locomotion, we have to answer the question posed in the title with 'yes'. Wood ants obviously climb on level surfaces. Similarities to horizontal cockroach locomotion, particularly remarkable in the vertical component of the ground reaction force, are probably caused predominantly by the formative direction of the gravity vector. Our results could be the starting point for future comparisons under variable loading and sloped regimes.

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