

Comparing inclined locomotion in a ground-living and a climbing ant species: sagittal plane kinematics

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Abstract Formicine ants are able to detect slopes in the substrates they crawl on. It was assumed that hair fields between the main segments of the body and between the proximal leg segments contribute to graviception which triggers a change of posture in response to substrate slopes. The sagittal kinematics of two ant species were investigated and compared on different slopes. *Cataglyphis fortis*, a North African desert ant, is well known for its extraordinary sense of orientation in texturally almost uniform habitats, while *Formica pratensis*, a common central-European species, primarily uses landmarks and pheromone traces for orientation. A comparison of these two species reveals differences in postural adaptations during inclined locomotion. Only minor slope-dependent angular adjustments were observed. The largest is a 25° head rotation for *Cataglyphis*, even if the slope is changed by 150°, suggesting dramatic changes in the field of vision. The trunk's pitch adjustment towards the increasing slope is low in both species. On all slopes *Cataglyphis* achieves higher running speeds than *Formica* and displays greater slope-dependent variation in body height. This indicates different strategies for coping with changing slopes. These specific aspects have to be reflected in the ants' respective mode of slope perception.

Keywords Climbing · *Cataglyphis* · *Formica* · Inclined locomotion · Sagittal kinematics

List of symbols

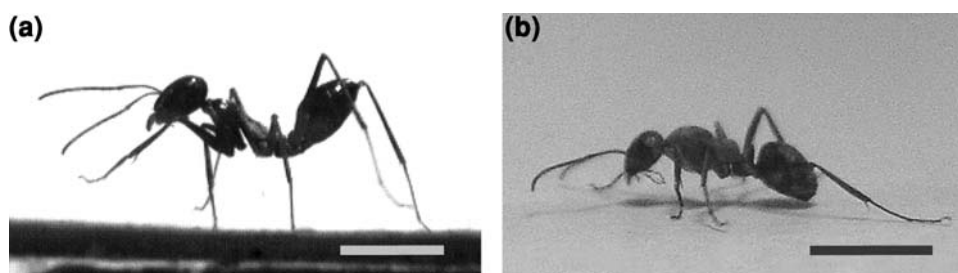
φ	Slope of the substrate
v_{abs}	Speed parallel to the substrate
l_{T}	Individual length of the alitrunk (thorax)
$v_{\text{rel}} = v_{\text{abs}}/l_{\text{T}}$	Relative speed
h_{abs}	Perpendicular distance between substrate and centre of mass (body height)
$h_{\text{COM}} = h_{\text{abs}}/l_{\text{T}}$	Relative distance between substrate and centre of mass
b	Typical fluctuation of the centre of mass perpendicular to the substrate
α	Angle between substrate and alitrunk axis
β	Angle between caput (head) and alitrunk
γ	Angle between caput and substrate
δ	Angle between alitrunk and gaster (abdomen)
ε	Angle between gaster and substrate
g	Gravitational acceleration

Introduction

The ability of *Cataglyphis* desert ants (Fig. 1a) to navigate in largely structureless, plane habitats is primarily a result of their solar compass (Wehner 2003), their step-counting odometer (Wittlinger et al. 2006), and their ability to compensate for inevitable mistakes along their convoluted food searching path (Müller and Wehner 1988; Wolf and Wehner 2005). It has been shown that inclined substrates do not affect their ability to correctly estimate distance to the nest (Wohlgemuth et al. 2001; Grah et al. 2005). For this feature no anatomical correlate has been found yet, but

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Fig. 1 Both species investigated in this study shown on level ground: **a** *Cataglyphis fortis* showing the typical erect gaster, **b** *Formica pratensis*. The bars in the lower right corners approximate 4 mm each



it seems that *Cataglyphis* desert ants use idiothetic mechanisms to estimate distances in their almost unstructured desert habitats. Similar mechanisms might be used to take substrate slopes into account.

Formica pratensis (Fig. 1b) is a taxonomically related species, but in contrast to *C. fortis* it populates quite different habitats in meadows and shrubs of Central Europe. It orients itself almost exclusively by using landmarks and pheromone traces left on the substrate (Graham and Collett 2002; Fukushi and Wehner 2004). Landmark-based orientation with no recourse to celestial cues has already been demonstrated in the closely related species *F. japonica* (Fukushi and Wehner 2004). In richly structured habitats, that are also typical for *F. pratensis*, hundreds of landmarks are available for use in orientation and distance measurement.

Nevertheless, another related species, *Formica polyctena*, is able to orient itself solely by the means of graviception (Markl 1964). Hair fields in the joints between their body segments enable the detection of gravitational deflection and are essential for graviception. These hair fields may also be utilised to detect altered posture and kinematics in *F. pratensis* and *C. fortis*. The position and shape of the hair fields are very similar in the two species (Wittlinger, personal communication), but due to differences in their environments and owing to the resulting reliance on different orientational cues, the level of precision and specific characteristics of the hair fields may differ.

Inside the nests of *Cataglyphis* and *Formica* sensory stimuli that are used in the foraging habitat, such as the position of the sun, are obviously not available. Path-finding abilities inside the nest are probably based on proprioceptive cues and pheromone traces. Therefore, it seems likely that proprioceptive sensing mechanisms, such as graviception, are in regular demand and can also be used during foraging.

Literature on animals, particularly arthropods, walking on slopes is rare. When humans walk uphill, they bend their trunk slightly forwards in order to bring their centre of gravity above the new point of support. For the same reason they lean slightly backwards when walking downhill (Leroux et al. 2002). Medium-sized quadruped mammals such as cats align the long axis of their trunk parallel to the

slope, but their legs remain almost vertical (Carlson-Kuhta et al. 1998; Smith et al. 1998) indicating an adjustment of the leg–trunk angle. In lizards two different strategies have been observed. Primarily terrestrial species lower their centre of mass and change their global leg angles both on ascents and descents (Jayne and Irschick 1999; Higham and Jayne 2004), while specialist climbers, such as chameleons and geckos, do not alter neither their clearance nor the orientation of their feet relative to the centre of mass at stance (Jayne and Irschick 1999; Zaaf et al. 2001; Higham and Jayne 2004; Autumn et al. 2006). Similarly, insects seem to alter the position of their legs relative to the body axis only to a minor degree during climbing (Cruse 1976; Goldman et al. 2006; Seidl and Wehner 2008). However, it has not been investigated yet, whether or not ants that are specifically adapted to different habitats display deviating strategies in mastering slopes.

In summary, both biomechanical and sensorial demands may cause species-specific kinematic differences. A kinematic analysis may allow conclusions to be drawn on which sensors are responsible for graviception. Depending on taxon and the different sensorial demands of specific environmental adaptation, it is hypothesised that predominantly terrestrial (*Cataglyphis fortis*) and predominantly scrambling (*Formica pratensis*) ants have different ways of adjusting their kinematics to different slopes, similar to the two strategies observed in lizards. Possibly these kinematic adjustments are used to evaluate the influence of substrate slope on the measurement of distance to the nest.

Approving aspects which are meaningful for the comparison of the two species are (1) their close kinship and resultant anatomical and sensorial similarities, and (2) their different environmental adaptations, potential species-specific slope-dependent adjustments, and the resultant kinematic differences. To test these differences we investigated the kinematics of the two species mastering different slopes by using video analysis in the sagittal plane.

Materials and methods

Formica pratensis was investigated using an established colony kept in the C.R. Taylor Motion Lab at the University

of Jena during the first half of October. The animals were taken from a sample site characterised by groves and meadows in the hilly surroundings. *Cataglyphis fortis* was investigated using wild colonies in Maharès, Tunisia, during the second half of June. The investigated colonies of both species sent forth about 70 active foragers a day.

A four-segment aluminium channel (Fig. 2) with an adjustable segment slope connected the formicary with a forage site containing biscuit crumbs soaked with watermelon juice. In a narrowed section of one of the middle segments the aluminium wall was substituted by glass. Thus, movements could be captured with a high-speed camera (Redlake 2000S, 250 fps) in the sagittal plane. The field of vision was about 40 mm wide. Camera resolution was 480×480 pixels, so minimum tracking accuracy was below 0.1 mm. An accuracy of at least 0.05 mm can be assumed since the used software, WINAnalyze[®], is able to compute sub-pixel resolutions via interpolating algorithms (Frischholz and Spinnler 1993). To avoid noise, a low-pass Butterworth filter with a cutoff frequency of 80 Hz was applied to the raw data. Prior to each recording series the setup was calibrated by structures made up of small LEGO[®] blocks (24.0×9.6 mm).

The floor of the channels was coated with sand or sandpaper in the narrowed part, in order to provide surface roughness. The walls of the channel were covered with FluonTM to prevent escape. Crawling on different slopes was captured at similar times of day, similar channel orientation, and with constant lighting. The slopes φ ranged from -60° (descending) to $+60^\circ$ (ascending) in steps of 30° for both species. To account for the limits of postural adaptations, *Cataglyphis* was also tested on slopes of $\pm 75^\circ$ ($n = 10$), which is atypical for its habitat. Similar slopes were reached in recently published orientation experiments (Grah et al. 2005).

The number of digitised runs (*Formica*, $n = 106$; *Cataglyphis*, $n = 89$) varied for the different slopes in *Formica* from 17 to 28 and in *Cataglyphis* from 14 to 27. Only foraging runs starting from the nest of physically intact animals in windless situations were analysed. The animals did not carry food so load and motivational effects were omitted. Sequences with clearly deviating, i.e. curious, explorative or aggressive behaviour were rejected.

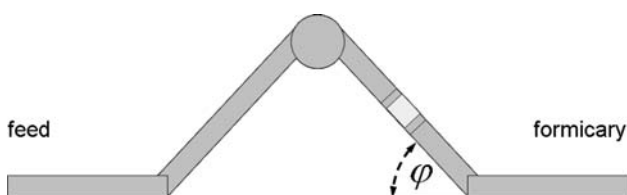


Fig. 2 Experimental setup: adjustable ramp with observation window in the right leg

The following points were digitised in the high-speed films (WINAnalyze[®], Mikromak): mandible, caput–alitrunk joint, petiolus–gaster joint, and the caudal end of the gaster (Fig. 3). The centre of mass position was assumed to be located at $1/8$ thorax length (l_T) from the hind rim of the alitrunk (Zollikofer 1994b). The following kinematic quantities were calculated from the digitised points using MatlabTM 6.5: the absolute (v_{abs}) and the relative (v_{rel}) velocity, the thorax length l_T , the absolute (h_{abs}) and the relative (h_{COM}) body height, typical fluctuations of the centre of mass perpendicular to the substrate b , as well as the angles between substrate and alitrunk α , between head and thorax β , between head and substrate γ , between thorax and abdomen δ , and between abdomen and substrate ε .

Locomotion speed is a major factor in ant kinematics (Zollikofer 1994b; Seidl and Wehner 2008), and different velocity ranges were observed for each different substrate slope (Fig. 4c; Table 1). In order to estimate rather the effect of the substrate slope than the effect of speed on a certain kinematic parameter (y_{abs}), the significance of the linear slope in the particular velocity dependency was specified for each species and substrate slope. Significant velocity-dependent changes were found for a few parameters and slopes, but no regularity in the occurrence of these dependencies among the slopes could be identified.

In order to avoid bias in the slope dependencies due to velocity effects the data were linearly corrected

$$y_{cor} = y_{abs} - a(v_{abs} - v_{ref})$$

using a constant Froude number $Fr = 0.25$ as reference value

$$v_{ref}(\varphi) = \sqrt{Fr \cdot g \cdot h_{abs}(\varphi)},$$

with the gravitational acceleration g , the measured velocity values v_{abs} , the slope of the regression line through y_{abs} (v_{abs}) a , and the reference velocity v_{ref} determined for each substrate slope on the basis of the respective median value of the body height $h_{abs}(\varphi)$. This correction was applied only when a certain velocity-dependent slope a was significant. In this case, values y_{abs} measured for a certain

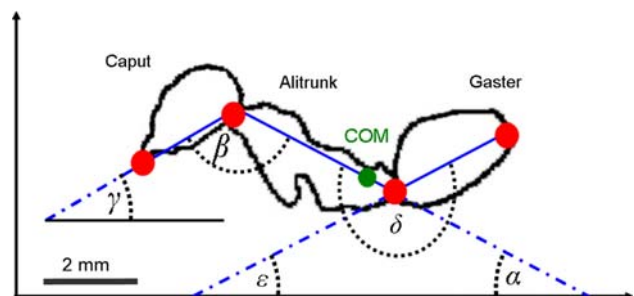
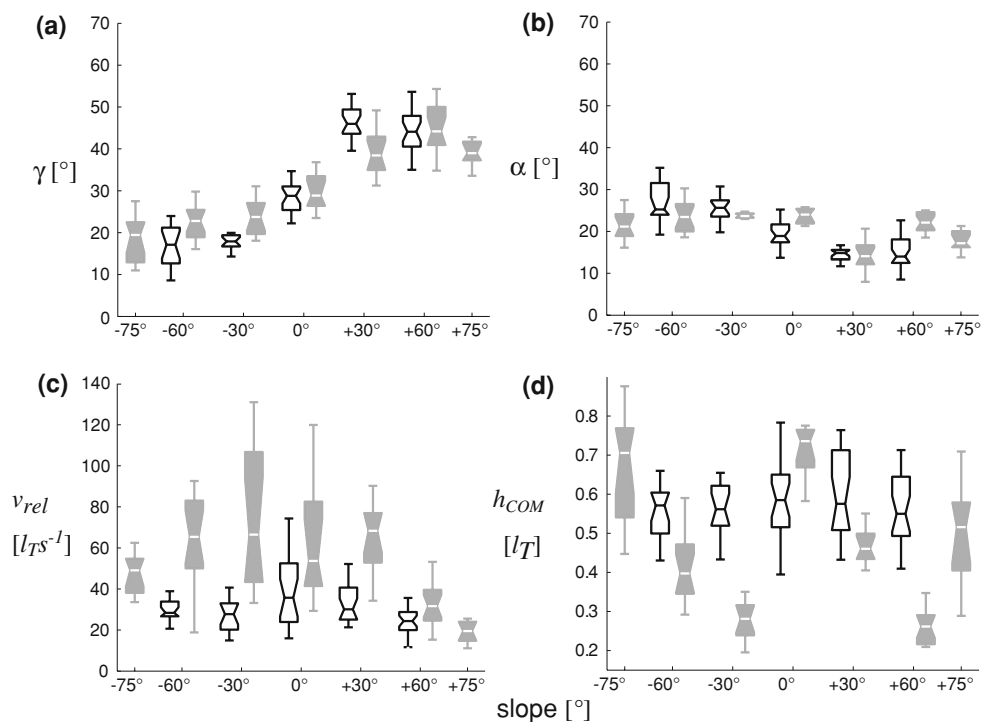


Fig. 3 Silhouette of *Cataglyphis fortis* with α (alitrunk–substrate angle), β (caput–alitrunk angle), γ (caput–substrate angle), δ (gaster–alitrunk angle), ε (gaster–substrate angle)

Fig. 4 **a** The caput–substrate angle changes with the slope of the substrate for both *Cataglyphis* (gray) and *Formica* (white). **b** Alitrunk–substrate angle α ; **c** relative locomotion speed v_{rel} ; **d** relative body height perpendicular to the substrate h_{COM}



substrate slope at different velocities v_{abs} were transformed to the respective corrected values y_{cor} at the reference velocity v_{ref} specific for this substrate slope.

The Froude number is a dimensionless velocity and therefore a suitable way for comparing animals of different sizes and even different biomechanical design (Alexander 1991; Ruina et al. 2005; Geyer et al. 2006). The value $Fr = 0.25$ was chosen to keep the reference velocities in the range of naturally attained running speeds. In both species the reference velocities v_{ref} over all slopes were about 0.07 m s^{-1} . This value is covered by the velocity ranges of nearly all substrate slopes. However, the reference velocities vary stronger in *Cataglyphis* due to its higher variability in h_{COM} (see below).

Due to the distributional skewness of the data, non-parametric tests were carried out to investigate the effect of slope (non-parametric ANOVA, Kruskal–Wallis with Bonferroni post hoc test; pair-wise test, Man–Whitney U test). If not indicated explicitly significance is given on a level of $P < 0.05$. Data, primarily obtained from kinematics in the horizontal plane, are not considered in the results of this paper. Step frequency, duty factor, and other spatio-temporal parameters were already published in a parallel cooperative project led by Seidl and Wehner (2008).

Results

In both species segment angle adjustments, if observed, are low compared to the changes in slope. Consequently, the

differences in substrate slopes are not compensated by corresponding angular changes with regard to gravity. This is also true for shallow slopes. Most parameters of *Formica* saturate, at least on ascents and descents between 30° and 60°. Pronounced adjustments only occur in the height adaptation of the centre of mass in *Cataglyphis*. The slope-dependent clearance of this species changes a lot more than that of *Formica*.

Speed (v)

Running speed depends on the slope (Fig. 4c; Table 1). Within $\pm 60^\circ$ both the absolute speeds v_{abs} and the relative speeds $v_{rel} = v_{abs}/l_T$ (*Formica*: $l_T = 3.15 \pm 0.25 \text{ mm}$, *Cataglyphis*: $l_T = 3.73 \pm 0.24 \text{ mm}$) of locomotion are significantly ($P < 0.01$) higher in *Cataglyphis* than in *Formica*. The median values range from $31.7 l_T s^{-1}$ at $+60^\circ$ to $68.4 l_T s^{-1}$ at $+30^\circ$ in *Cataglyphis* and from $24.4 l_T s^{-1}$ at $+60^\circ$ to $35.7 l_T s^{-1}$ at 0° in *Formica*. Both species slow down appreciably when running up the steepest slopes. In *Formica*, only the value at $+60^\circ$ differs significantly from those observed on other slopes. In *Cataglyphis* the dependency varies. On level ground this species tends towards lower speeds (skewness: $+0.68$). The values at $+75^\circ$ and $+60^\circ$ lie significantly below the values for all other slopes, but differ from each other. Downwards (-30° , -60°), the median speed tends to increase in *Cataglyphis* to up to $66.5 l_T s^{-1}$. Only on the steepest descent the velocity decreases to a value below the one that was observed on

Table 1 Median values (bold) and quartiles of the investigated parameters (rows) with regard to substrate slope (columns) for both species

	-75°	-60°	-30°	0°	+30°	+60°	+75°							
<i>v_{rel}</i> [<i>l_T</i> s ⁻¹]														
<i>C. fortis</i>	49.1	54.7	65.4	83.1	66.5	106.7	53.7	82.5	68.4	77.0	31.7	39.6	19.5	24.0
		38.1		50.0		43.4		41.4		52.9		24.6		14.8
<i>F. pratensis</i>			28.4	19.5	27.7	19.6	35.7	29.0	30.1	22.3	24.4	16.0		
				14.4		11.7		13.8		14.0		11.5		
<i>h_{COM}</i> [<i>l_T</i>]														
<i>C. fortis</i>	0.71	0.77	0.40	0.47	0.28	0.32	0.74	0.76	0.46	0.50	0.26	0.29	0.52	0.58
		0.54		0.35		0.24		0.67		0.43		0.22		0.40
<i>F. pratensis</i>			0.57	0.60	0.56	0.62	0.59	0.65	0.58	0.71	0.55	0.64		
				0.50		0.52		0.52		0.51		0.49		
<i>b</i> [<i>l_T</i>]														
<i>C. fortis</i>	0.06	0.07	0.04	0.05	0.03	0.04	0.03	0.03	0.04	0.05	0.06	0.07	0.04	0.05
		0.05		0.03		0.02		0.03		0.03		0.04		0.03
<i>F. pratensis</i>			0.05	0.07	0.05	0.05	0.04	0.04	0.05	0.06	0.06	0.07		
				0.04		0.04		0.02		0.04		0.04		
<i>α</i> [°]														
<i>C. fortis</i>	21	24	24	27	24	25	24	25	14	17	22	25	17	20
		19		20		23		22		12		20		16
<i>F. pratensis</i>			25	31	26	27	16	19	15	16	14	18		
				24		24		15		13		11		
<i>β</i> [°]														
<i>C. fortis</i>	140	142	134	136	134	135	129	130	127	128	116	118	123	124
		138		132		130		125		124		113		120
<i>F. pratensis</i>			134	142	137	140	132	135	119	122	122	125		
				133		134		130		118		119		
<i>γ</i> [°]														
<i>C. fortis</i>	20	23	23	25	24	27	29	34	38	43	44	50	39	42
		13		19		20		26		35		41		37
<i>F. pratensis</i>			17	21	18	19	32	35	46	49	45	48		
				13		17		29		44		41		
<i>δ</i> [°]														
<i>C. fortis</i>	220	225	218	227	214	221	233	241	212	217	213	219	207	213
		214		212		212		231		208		208		202
<i>F. pratensis</i>			155	157	161	168	149	157	149	154	155	152		
				150		160		143		145		158		
<i>ε</i> [°]														
<i>C. fortis</i>	21	26	14	26	14	18	31	45	17	28	16	20	11	14
		10		7		9		24		14		8		6
<i>F. pratensis</i>			-53	-49	-43	-36	-41	-33	-46	-41	-38	-37		
				-59		-51		-50		-50		-42		

The abbreviations and symbols follow the list given in the “List of symbols”: *v_{rel}* relative speed, *h_{COM}* relative height of the centre of mass, *b* vertical fluctuation of the centre of mass, *α* alitrunk–substrate angle, *β* caput–alitrunk angle, *γ* caput–substrate angle, *δ* gaster–alitrunk angle, *ε* gaster–substrate angle

level ground. On slight to medium ascents (+30°) locomotion velocity in *Cataglyphis* increases. Velocity tends to decrease in *Formica* in both increasing and decreasing slopes.

Body height (*h_{COM}*) and its oscillations (*b*)

On level ground the relative body heights of the two species (Figs. 4d, 5; Table 1) are in a similar range, although the leg

lengths normalised to l_T differ considerably. Estimated from Wehner and Sommer (personal communication), and Zollikofer (1994a) *C. fortis* has legs that are approx. 1.5 times longer than those of *Formica*. However, height differences are significant on all slopes. In *Formica*, the medians range from 0.55 l_T at $+60^\circ$ to 0.59 l_T at 0° , indicating almost no slope-dependent changes. *Cataglyphis*, on the other hand, clearly reduces body height on intermediate slopes ($\pm 30^\circ$ and $\pm 60^\circ$; Fig. 4d; Table 1). Despite its longer legs, its normalised body height then is lower as in *Formica*. On the steepest slopes ($\pm 75^\circ$) the centre of mass is elevated again (range 0.26 l_T at $+60^\circ$; 0.74 l_T at 0°). At $+75^\circ$ values are similar to those at $+30^\circ$ and at -75° even values similar to 0° are reached. Consequently, in *Cataglyphis* a more pronounced height adjustment can be observed.

The oscillation of the centre of mass perpendicular to the substrate differs slightly in the two species (Table 1). In *Formica* typical oscillation values range from 0.04 l_T to 0.06 l_T with no significant changes between the substrate slopes. On steeper slopes the oscillations seem to increase. In *Cataglyphis* oscillation amplitudes adapt to steeper slopes, but only oscillation values at steep slopes (-75° and $+60^\circ$) differ significantly from level values. The highest amplitudes are reached at -75° while the oscillations at $+75^\circ$ are similar to those on shallow slopes. Both species reach amplitudes of the same magnitude. When it comes to descents, oscillations are significantly higher in *Formica*.

Angles (α , β , γ , δ , ε)

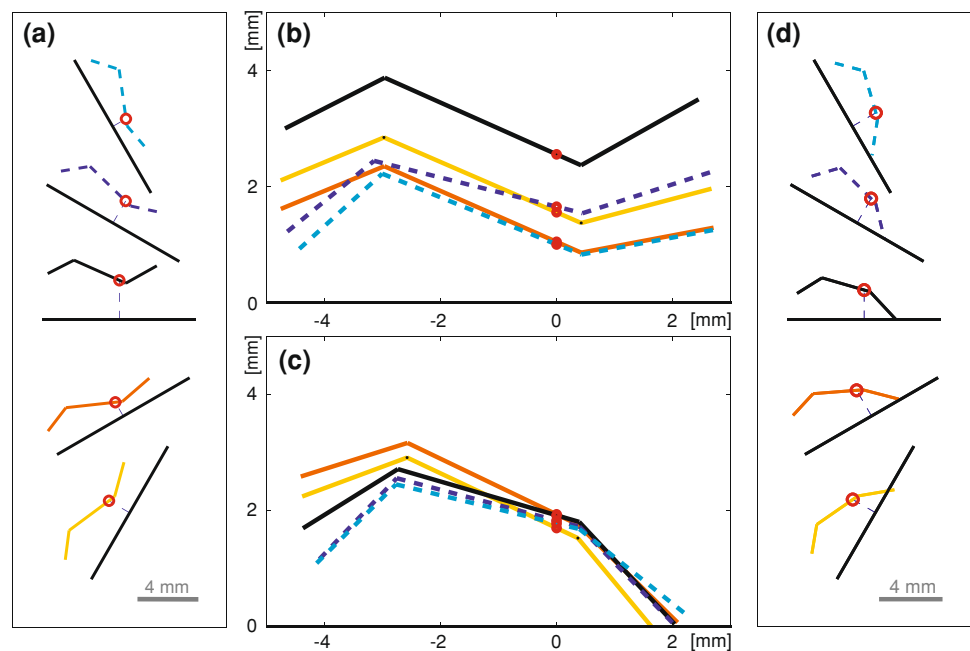
In general segment angles follow the slope of the substrate with minor adaptations (e.g. alitrunk–substrate angle α ;

Figs. 4b, 5; Table 1). The alitrunk–substrate angle (median at 0° ; *Formica* 16° , *Cataglyphis* 24°) is slightly reduced in *Formica* during ascents (14°) and significantly increased (26°) on descents. While slope dependency in *Formica* displays a roughly sigmoid shape no such pattern is observed in *Cataglyphis*, where the values are similar for most slopes, except $+30^\circ$ and $+75^\circ$ which are significantly lower than all the other values. All adjustments are virtually negligible compared to the angular changes in the substrate. Significant differences between the species occur at 0° and $\pm 60^\circ$.

Further adjustments may occur in the caput–alitrunk joint (angle β ; Table 1). This joint adapts to slope changes almost continually. In both species this adaptation has a roughly sigmoid character. The differences of the median values do not exceed 25° in the tested range of slopes. The angle of the caput with respect to the substrate is $\gamma = 180^\circ - \alpha - \beta$. Here, too, slope adjustment seems to be sigmoid, but the angle comprised is about 30° (Fig. 4a). Levelling off occurs in *Formica* at $\pm 30^\circ$, in *Cataglyphis* at $\pm 60^\circ$. The caput–substrate angle changes from high values at $+60^\circ$ (44° *Cataglyphis*) and $+30^\circ$ (46° *Formica*) to low values at -60° (22° *Cataglyphis*; 17° *Formica*). Reacting to decreasing slopes the caput is held increasingly parallel to the substrate.

In both species the gaster orientation relative to the alitrunk (δ) is almost constant (Table 1). In *Formica* this angle decreases slightly on lower slopes. At -30° , as an exception, the angle is significantly higher (161°) than on most of the other slopes (-60° , 0° , $+30^\circ$). Here the distal gaster tip often touches the substrate passively widening the angle. In *Cataglyphis* a clear exception occurs at 0°

Fig. 5 Median posture of ants while walking on different slopes. Left and top middle (a, b): *Cataglyphis*; right and bottom middle (c, d): *Formica*. Left and right (a, d): with slopes; middle (b, c): posture relative to the walking surface. The centre of mass is represented by red circles. Slopes 0° solid black, $+30^\circ$ dashed blue, $+60^\circ$ dashed cyan, -30° solid red, -60° solid yellow (colour figure online)



where the angle $\delta = 233^\circ$ is significantly ($P < 0.001$) higher than on all other slopes. In level locomotion the range covered by the other slopes is clearly exceeded. On these slopes angles from $207^\circ (+75^\circ)$ to $220^\circ (-75^\circ)$ are reached (Table 1). In *Formica* the gaster ($\varepsilon = \delta - \alpha - 180^\circ$) always points towards the substrate whereas in *Cataglyphis* it points away. In *Cataglyphis* the slope dependency of the gaster–substrate angle matches that of the gaster–alitrunk angle δ . Accordingly $\varepsilon = 30.5^\circ$ ($P \leq 0.02$) is exceptionally high on level ground. Otherwise the values are almost constant, ranging between $11^\circ (+75^\circ)$ and $21^\circ (-75^\circ)$. In *Formica* the slope-dependent adjustment of the gaster angle is small, the median values range from $-38^\circ (+60^\circ)$ to $-53^\circ (-60^\circ)$. The values at -60° differ from all other slopes ($P < 0.01$). The difference between $+60^\circ$ and -30° is also significant.

Discussion

While walking on different slopes, the species examined (*C. fortis*, *F. pratensis*) only make minor postural changes. Despite differences in morphology, and in particular the greater leg length in *Cataglyphis*, kinematics is surprisingly similar in the two species. According to Seidl and Wehner (2008), spatio-temporal parameters such as phase shift between individual legs and duty factor are fairly constant over all slopes. Both species use a tripod gait in which stance phases are slightly longer than swing phases. The running speeds reached by *Cataglyphis* are higher on all slopes. Apart from this, the following differences in sagittal kinematics are substantial:

- greater slope-dependent variation in body height in *Cataglyphis* compared to *Formica*;
- the degree to which the gaster is raised in *Cataglyphis* as compared to the gaster in *Formica*, that points towards the substrate in a fairly fixed position.

Assuming that locomotion velocity is a measure of bio-mechanical adaptation to slope and specific substrate, e.g. the degree of static stability (see below), it can be concluded that *Cataglyphis* and *Formica* use different strategies (Seidl and Wehner 2008). Reduced running speed on steep ascents might be an energy saving strategy since increasing speed raises energy consumption on inclines (Full and Tullis 1990). Wohlgemuth et al. (2002) demonstrated lower velocities in *Cataglyphis* on inclines and declines. But they investigated only home bound runs of specimens loaded by carrying pieces of food differing in weight and size. Hence, their results cannot reasonably be compared with our findings. The presence of food presumably significantly affected both the position of the centre of mass and the motivation of the ants to move at speed.

Adjustment of body height (h_{COM})

On level ground, clearance in *Cataglyphis* is not much higher than in *Formica*. In particular on moderate slopes the height of the centre of mass is significantly smaller in *Cataglyphis*. The more pronounced slope-dependent changes in *Cataglyphis* may indicate that the animals are less adapted to climbing on inclined substrates than *Formica*.

In the sandy and at least in part structurally unstable substrate of the typical desert habitats of *Cataglyphis*, clinging with claws or even wet adhesion via adhesive pads is barely useful. It is likely that the ants attempt to keep their centre of mass inside the supporting polygon in order to avoid instabilities when surmounting slopes. At least on gentle slopes the best strategy for achieving this is to lower the clearance. Elongating the legs to increase abduction would also cause an increase in the supporting polygon. In fact, *Cataglyphis* does not use this strategy (Seidl and Wehner 2008), since it is much less effective. Furthermore, the height adjustment allows the odometer to remain unaffected, as it is based on constant step length (Wittlinger et al. 2007a).

In *Formica* lowering the centre of mass is limited by the gaster. Its position causes the caudal tip to touch the substrate during level locomotion (Figs. 1b, 5c, d). The gaster of *Cataglyphis* points upwards, thus permitting greater range of height adjustments. *Cataglyphis* makes use of the strategy to lower its centre of mass significantly below level values on small and moderate slopes in particular, but re-increases its body height on steeper slopes.

Lizard species also adopt a rather crouched posture during locomotion which is considered, among others, to be an adaptation to climbing. The chameleon *Chamaeleo calypttratus* does not change its body height in relation to the ground (clearance) neither when moving uphill nor when moving downhill ($\pm 30^\circ$). In contrast, the mainly ground-dwelling species *Dipsosaurus dorsalis* significantly reduces clearance in both cases (Jayne and Irschick 1999; Higham and Jayne 2004). These differences may be related to differences with respect to substrate contact. Similarities are observed in the two ant species investigated here.

The unexpected increase of clearance in *Cataglyphis* at higher slopes may be related to the limited ability to cling onto the substrate. With respect to the climbing direction on rough substrate the generation of friction by means of claws is limited in the lower legs, whereas that of the upper legs can be assumed as being uncritical. For details considering the use of claws in ants and other insects see for instance (Larsen et al. 1995; Frazier et al. 1999; Dai et al. 2002; Frantsevich and Gorb 2004; Ridgel and Ritzmann 2005; Clemente and Federle 2008; Endlein and Federle 2008).

The limited friction of the lower legs can be increased by higher clearance. If the lower legs are considered to be the counter-bearing of a pendulum, consisting of the centre of mass pivoting around the point of attachment of the upper limbs, an increase in body height results in higher normal forces (*Load*) on the tarsi of the lower legs. Since critical friction results from $F_{\text{friction}} = \mu_s \cdot \text{Load}$ with the critical friction coefficient μ_s being a material constant, the critical friction increases as well (Cartmill 1985). Presumably, this comes at the cost of reduced normal forces on the upper appendages (Günther and Weihmann 2009). However, with given friction coefficients starting at a certain slope, this is the only way to generate thrust with the lower legs. Indeed, *Cataglyphis* re-increases its clearance after a minimum of $0.26 l_T$ at $+60^\circ$ to $0.52 l_T$ at $+75^\circ$ ($P < 0.001$; Table 1; Fig. 3d).

Moving downhill, the ants significantly reduce their body height already at slopes of -30° ($P < 0.001$). As slopes decrease further, they gradually re-increase the clearance. During steep descents, *Cataglyphis* mostly brachiates down on its hind legs (upper legs in this case) utilising its claws and using the forelegs to strut on the substrate. The steep orientation of the foreleg axes causes a maximum dorsal flexion of the loaded tarsal claws. In this position the terminal tarsomere provides a definite block (Endlein and Federle 2008) which may allow the foreleg claws to contribute to breaking forces. The high clearance at steep descents (Fig. 4d) results in a steeper orientation in the distal segments of the hind legs. This may result in a steep angle of attack of the claws using the lowest curve radius at their tips for contact with the substrate, thus friction is optimized (Dai et al. 2002).

Like chameleons, *Formica* is usually not limited in its ability to generate friction forces within its natural habitat (Gladun and Gorb 2007) and shows almost no kinematic adaptation to changing slopes. Even on marginal slopes these ants apparently use the laterally directed reaction forces (Reinhardt et al. 2009) typical for vertical climbing in geckos and cockroaches (Autumn et al. 2006; Goldman et al. 2006) in order to seek strong adhesion while clamping their legs against each other. This strategy guarantees secure ground contact in all situations and makes slope-dependent postural adaptations dispensable. The relative and absolute velocities of *Formica* observed in this study are much lower than those of *Cataglyphis*. Accordingly, the increased stance durations give them sufficient time to achieve and break firmer attachments (Larsen et al. 1995; Federle and Endlein 2004). To improve the evidence for this conclusion reaction forces on slopes need to be measured in more detail.

Slope-dependent changes in the fluctuations of the centre of mass perpendicular to the substrate (Table 1) probably result from changing strategies of using the tarsi

and adapting the body height. Furthermore, both species stumble more often on higher slopes. That may also increase the amplitudes of the centre of mass.

In conclusion, the differences in height adjustment in *C. fortis* and *F. pratensis* seem to be determined by differences in morphology related to substrate contact.

Adjustment of angles and field of vision

Both *Cataglyphis* and *Formica* moderately adjust their body segments to different slopes. For instance, the pitch adjustment of the thorax to the increasing slope is small and does not exceed 24° . Thus, ants keep their body largely parallel to the substrate, just like other climbing animals (Cruse 1976; Carlson-Kuhta et al. 1998; Higham and Jayne 2004).

It is conceivable that the ants strive to maintain their visual field and the mapping of the polarisation vectors. Indeed a systematic correction of head posture is observed (*Formica* 30° ; *Cataglyphis* 25°). However, this change is still small compared to the change in slope (120° and 150°) and not sufficient to stabilise the sky segment. One possible slope sensor is the proprioceptive hair field complex on the neck (Markl 1964). The change in the observed sky segment might itself be taken as a correction signal, but as inside the nest all slope perception relies on proprioceptive cues, the animals should also be able to use such cues in an illuminated environment and may not depend on skylight vision to detect substrate slopes at all. Despite this, the systematic sigmoid adjustment of the head requires information about the substrate angle.

Position of the gaster

The erect position of the gaster has been considered a typical attribute of *C. fortis* (Wittlinger et al. 2007b). It was assumed that the erect position was related to an increased manoeuvrability. In the present study we demonstrate that under almost natural conditions the normal position of the gaster relative to the substrate is almost flat on all slopes. The high level of variability (Table 1) indicates that more or less pronounced erection may occur on all slopes. In fact, particularly on level ground, a heavily bent gaster was identified in some trials. In these sequences the animals always seemed to be curious or alarmed. Gaster erection seems to occur during explorative behaviour, but not in normal target-oriented locomotion. However, the few trials with a largely erect gaster, representing aggressive or curious episodes, were excluded from our analysis (see “Methods”). Runs on level ground might not be as target-oriented as the presumably more energy-intensive inclined runs (Full and Tullis 1990; Snyder and Carello 2008) and may thus be

accompanied by an erect gaster more frequently (Table 1; Fig. 5b).

As mentioned above in *Formica* the normal position of the gaster causes its caudal tip to contact the substrate even during level locomotion (Figs. 1b, 5c, d). Since orientation and communication in this genus strongly depends on pheromone traces (Hölldobler 1995), the typical tracing behaviour forces the gaster to point to the ground.

Relevance with respect to slope perception

It has been demonstrated that ants are highly capable of detecting substrate slopes (Markl 1964) and that desert ants of the genus *Cataglyphis* use this information for reckoning the correct distance to their nests (Wohlgemuth et al. 2001, 2002; Grah et al. 2005; Wittlinger et al. 2007b). The results obtained by Markl (1964) suggest that there is no unique sensor for the detection of substrate slopes in hymenoptera but that sensors between the various body segments, on the antennae, and between the alitrunk and the coxae cooperate with each other. However, Markl proposed that the hair fields located at these joints may not be the actual sensor elements but that their function is to permit the ants to keep the angular configuration of their body segments almost constant.

Similarly, we argue here, that adjustment of body height to the slope requires its sensation. Neither clearance nor changes in joint angles are used as a measure for the slope. The relatively pronounced slope-dependent adjustments of body height in *Cataglyphis* amount to less than $0.5 l_T$. Based on anatomical data (estimated from Zollikofer 1994a) and the adopted posture a change in the femur–tibia angle of about 10° can be estimated during this adjustment. In contrast, the respective femur–substrate angle alters by about 30° . This femur deflection is transmitted to the proximal joints (trunk–coxa, coxa–trochanter), possibly sensed by hair fields and may be taken into account in the determination of ground distance when travelling over hills.

Much more plausible with respect to slope detection is the use of “stress gauges” in the muscles (Markl 1964) which in turn are activated to maintain posture at the different slopes. Related feedback loops might include campaniform sensillae, the strain detectors in cuticular structures. Specialised groups of these sensors concentrated in the trochanter allow cockroaches to detect the directions of external and internal forces (Zill et al. 2004; Kaliyamoorthy et al. 2005); hence, they possibly also provide the direction of the gravity vector.

In principle also gravity-induced deflection of the gaster with respect to the alitrunk could be perceived and used to measure inclination. Markl (1964) showed that disabling single sensor complexes by gluing segments together and even cutting off the gaster has little impact on the

graviception of *F. polyctena*. However, gluing the petiolus and gaster joints in a rotated position causes permanent afferent deviations. In this situation the slope perception is strongly impaired. It has also been shown that a dorsal fixation of the gaster onto the thorax can reduce the perceived walking distance significantly (Wittlinger et al. 2007b). However, behavioural fixation experiments remained inconclusive.

As the arrangement and size of the hair plates are very similar in *Formica* and *Cataglyphis* (Wittlinger, personal communication) a comparison between experiments carried out by Markl (1964) and Wittlinger et al. (2007b) is permitted. In Wittlinger’s experiments the gaster is bent anteriorly and glued dorsally onto the alitrunk. Not only does this affect the joints between alitrunk and gaster, it also shifts the centre of mass upward and forward and causes erroneous afferent signals in the coxal joints. This causes a disturbance in the majority of the slope sensors including campaniform sensillae in the legs, which makes it potentially impossible to calculate the real slope. As slope ratio is necessary information to assess the projected distance correctly, the insects are unable to estimate the distance they have to cover in order to reach the nest on level ground.

In short, all slope-dependent complex postural adaptations within the body seem to be primarily caused by the mechanical properties of the ants, e.g., foot anatomy or leg length. These properties, in turn, are adjusted to external conditions, such as substrate roughness or hardness, typical of the specific habitats.

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