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Franklin, Elizabeth L, Richardson, Thomas O, Sendova-Franks, Ana B et al. (2011) Blinkered teaching: Tandem running by visually impaired ants. Behavioral Ecology and Sociobiology. pp. 569-579. ISSN: 1432-0762

https://doi.org/10.1007/s00265-010-1057-2

Behav Ecol Sociobiol (2011) 65:569–579
DOI 10.1007/s00265-010-1057-2

ORIGINAL PAPER

Blinkered teaching: tandem running by visually impaired ants

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Received: 20 March 2010 / Revised: 30 July 2010 / Accepted: 25 August 2010 / Published online: 10 September 2010

Abstract During tandem runs, one ant worker recruits another to an important resource. Here, we begin to investigate how dependent are tandem leaders and followers on visual cues by painting over their compound eyes to impair their vision. There are two ways in which *Temnothorax albipennis* might use vision during tandem running. First, the follower might track the movements of the leader by keeping it in sight. Our results suggest that the ants do not use vision in this way. For example, in all four classes of tandem run (those with either leader or follower, both, or neither of their participants with visual impairments) progress was most smooth at about 3 mm/s. This suggests that communication between leaders and followers during tandem runs is not based on vision and is purely tactile and pheromonal. Second, the leader and the follower might be using vision to navigate and our results support this possibility but also suggest that these ants have other methods of navigation. Ants with visual impairments were more likely to follow than to lead, but could occupy either role, even though they had many fully sighted nestmates. This might help to explain why the ants did not focus grooming on their most visually impaired nestmates. Wild-type tandem runs, with both participants fully sighted and presumably taking time to learn landmarks, were overall significantly slower, smoother, and a little less tortuous, than the other treatments. All four classes of tandem run significantly increased mean instantaneous speeds and mean absolute changes in instantaneous acceleration over their journeys. Moreover, tandems with sighted followers increased their speed with time more than the other treatments. In general, our findings suggest that eyesight is used for navigation during tandem running but that these ants also probably use other orientation systems during such recruitment and to learn how to get to new nest sites. Our results suggest that the ants' methods of teaching and learning are very robust and flexible.

Keywords Communication · Teaching · *Temnothorax albipennis* · Navigation

Introduction

Tandem running in ants, a recruitment method in which one ant leads another to a resource, has recently attracted much

Communicated by M. Giurfa

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Electronic supplementary material The online version of this article (doi:10.1007/s00265-010-1057-2) contains supplementary material, which is available to authorized users.

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attention because it qualifies as a form of teaching (Franks and Richardson 2006; Richardson et al. 2007). However, as followers often later become leaders of subsequent tandem runs (Möglich 1978), this begs the question: which sensory systems do the ants use to learn the route of the tandem run so that they can teach it to others? Learning of visual landmarks is an obvious candidate and indeed *Temnothorax albipennis* has been shown both to use small landmarks as beacons (Mcleman et al. 2002) and long horizontal landmarks as cues to their position (Pratt et al. 2001). Other closely related *Temnothorax* species have been shown to use visual cues, individually specific pheromone trails or (in the absence of the former two) the pheromone trails of nest mates (Maschwitz et al. 1986; Aron et al. 1988). Moreover, ants from other genera have been shown to use many other methods to facilitate their impressive feats of navigation: these include pheromone trails (Hölldobler and Wilson 1990), piloting on visual landmarks (see references in Pratt et al. 2001 and Mcleman et al. 2002) and path integration (Müller and Wehner 1988).

Here, we determine to what extent *T. albipennis* ants are dependent on vision during tandem runs by impairing their eyesight. There are two separate issues here: do tandem leaders and followers use eyesight to help them navigate and to learn landmarks and do followers use it to help track the movements of their leader? We painted over one or both of the workers' compound eyes and recorded if they participate in tandem runs as leaders or followers and, if so, how their performance was affected by their reduced visual acuity. We measured this effect through changes in speed, acceleration, and path tortuosity. For example, an increase in path tortuosity or a decrease in speed, with either blinkered leaders or followers, compared to fully sighted wild types, might indicate that visually impaired ants struggle to navigate and to maintain contact with one another. Furthermore, increasing changes in acceleration might suggest more stopping and starting between bouts of faster progress.

One of the most successful applications of paint blinkering in the study of ant navigation is work on foraging in *Cataglyphis* (Wehner and Müller 2006). However, *Cataglyphis* foragers are large bodied and solitary. Hence, foragers can be chosen for study individually and their eyes meticulously painted. Such painted foragers can then be returned to their point of capture to compare their attempts to get home with the behavior of unimpaired foragers who normally go straight back to the nest (Wehner and Müller 2006). Using paint blinkering to study tandem running in *Temnothorax* poses extra challenges, because it is impossible to know, *a priori*, exactly which ants would participate in tandem running and they are often a small minority of the colony's workforce. For these reasons, we had to paint over the eyes of many of the ants in the colony, return them to a new nest and allow the colony to tandem run during an emigration on the next day. In turn, the necessary delay between painting the ants and allowing them to emigrate meant that some of the paint blinkers could be removed, completely, or in part, by the ants either through self-grooming or through allogrooming by their nest mates. However, all but a few of the blinkered eyes at the time of the tandem runs were completely covered in paint and the few exceptions had roughly 90% of their ommatidia completely covered by thick paint. Nevertheless, we have, and will, refer to the ants as being blinkered, *i.e.* visually impaired, rather than totally blind. One intriguing aspect of our study system, however, is that we can ask a supplementary question: do the ants focus grooming on their most visually disabled nestmates or is it haphazard?

Materials and methods

Colonies of *T. albipennis* were collected from the Dorset Coast (UK) in July 2008 and used for laboratory experiments in the following 2 months. The colonies were cultured according to standard protocols (Franks et al. 2003).

We choose six colonies with just over 100 workers each. This is close to the median size of colonies in the field (Franks et al. 2006). Each colony was used once only. We used approximately the same procedure, to paint over the compound eyes of workers that we have used to apply paint marks to workers to uniquely identify them. This involves lightly anesthetizing the ants one at a time with CO_2 (Sendova-Franks and Franks 1993). For one third of the workers in each colony, we painted over just one eye choosing the left or right eye alternately (so that 1/6 of the worker population would be right blinkered and 1/6 left blinkered). One third of the workers had paint applied to both eyes and one third had paint applied to neither eye, but as a control each received a similar amount of paint, as used above, but placed on the occipital region of its head, where it would not interfere with any of the sense organs. We used Testors Pactra paint (Outlaw Black, Racing Finish, Fig. 1). Note, *T. albipennis* workers do not have ocelli, as used by *Cataglyphis* for navigation (Fent and Wehner 1985), so we could focus on their compound eyes alone.

We randomly allocated the ants to the three treatment groups. We did this to avoid bias; for example, if all external workers ended up in the same treatment this could distort the results. Therefore, as we marked the ants, we worked cyclically through the three treatments, to generate an even distribution of the three treatments across the colony. To minimize paint removal through mutual groom-

Fig. 1 A dead *Temnothorax albipennis* worker that had participated in a tandem run, with black paint over the whole of its right eye and beyond. The *scale bar* is approximately 0.1 mm long. (The right antenna has been removed for clarity; Photograph by Saki Okuda)

ing, workers were returned to their colony, when the paint had dried.

The day after marking was completed, each colony was placed in a large arena (82×53 cm) and its old nest was destroyed by removing the top microscope slide to encourage it to choose either of two new nest sites, to which the ants could recruit by tandem running (Fig. 2). The "old nest" had a cavity of 49×34×1.5 mm and a 2-mm wide entrance. The new target nests had the same dimensions as the old one but were made dark with a black cardboard cover. In emigrating *Temnothorax* colonies, the main function of tandem running is to allow the society to focus its recruitment effort towards one of the multiple potential nest sites, each of which may vary in its attributes (Franks et al. 2003; Richardson et al. 2007). So to maximize the number of tandem runs, we made the colonies decide between two identical new nests in opposite directions (Fig. 2). The arena was lit by a combination of natural light from a window and artificial overhead lights. We did not eliminate directional light or other visual cues in the experimental room, because we intended unblinkered ants to be able to navigate normally. This enabled us to identify the effects of blinkering on navigational ability.

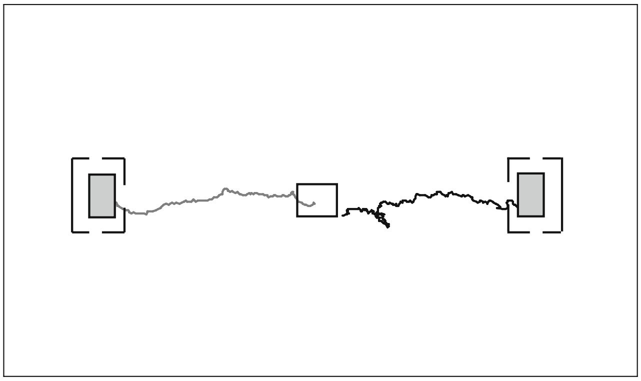


Fig. 2 Experimental set-up: the destroyed old nest in the *center* and the two alternative new intact nest sites at *each end* of the experimental arena. The *light gray* path is the course of a leader in a tandem run in which neither the leader nor the follower is blinkered (*i.e.* LN/FN). The *black* path is the course of a leader in a tandem run in which both the leader and follower are blinkered (*i.e.* LB/FB)

We filmed the entire arena using HD video (Sony HDR-FX1E) and simultaneously directly observed each tandem run to note when and where they started and finished (*i.e.* we recorded start locations and start times and end locations and end times).

We collected each follower and leader when the tandem run naturally broke up near or just before it entered the new nest. Such collection prevented pseudo-replication and by delaying the achievement of a quorum in the new nest should also have maximized the number of tandem runs (Pratt et al. 2002). We collected each tandem leader and follower into a separate and uniquely labeled vial and killed the ants by placing them in a freezer. Later we carefully examined each such ant under a dissection microscope to determine if it was right blinkered, left blinkered, doubly blinkered, or not blinkered. We attempted to video tape at least ten tandem runs from each colony such that we could link each collected pair of tandem runners to its video recording. Immediately after each experiment had been completed, we killed all of the ants in each colony and examined each and every worker to determine how many had been in each blinkered or control treatment at the time of the emigration.

Detailed video analyses were made for tandem runs which were chosen based on the quality of the blinkers (or alternatively lack of paint) of the ants at the time of the tandem run (determined by examination of leader and follower corpses). For tandem participants that were fully sighted, *i.e.* not blinkered, we chose individuals with absolutely no paint on their eyes. Conversely, for tandem participants that were blinkered we chose individuals with at least 90% coverage of the ommatidia in one or both eyes (Fig. 1). We then used a blind trial procedure. The person that chose which tandems should be analyzed did not inform the person analyzing the videos about the blinkered condition of the leaders or followers until after all of the data acquisition had been completed.

We analyzed the video recordings by digitizing them using Adobe Premier Pro 2.0 for playback on Media Player Classic. The paths of tandem leading ants were tracked by plotting their position on a grid in second by second increments. We used the Cell Counter plugin from ImageJ to obtain the coordinates of every increment. From our data, we could determine instantaneous speed, *v(t)*, (distance traveled per second), instantaneous acceleration, $a(t)=v(t)-v(t-1)$, (the change in instantaneous speed per second) and absolute change in instantaneous acceleration per second, $|a(t)-a(t-1)|$, of tandem runs. All three, the instantaneous speed, the instantaneous acceleration, and the absolute *change* in instantaneous acceleration were calculated for each individual and then averaged over each time bin to give the respective mean values. The latter variable allowed us to monitor acceleration in more detail. This is because mean instantaneous acceleration is likely to be approximately constant if the relationship between mean instantaneous speed and log10 of log-binned time is approximately linear (as assumed by our modeling). We also measured tortuosity as $1-D/L$, where D is the direct distance between the first and last points of the path (or net displacement) and L is the path length (Benhamou 2004).

Overall, our study sample consisted of 669 workers from the six different colonies. Out of these 114 were participants in tandem runs. We carried out a detailed video analysis of 40 tandems (*i.e.* 80 workers). There were nine pairs in which the leader was blinkered and the follower blinkered (LB/FB); ten pairs in which the leader was blinkered and the follower not blinkered (LB/FN); nine pairs in which the leader was not blinkered and the follower was blinkered (LN/FB); and, 12 pairs in which neither was blinkered (LN/FN). Since most of the colonies were represented by a subset of the above four types of treatment condition, we did not include colony as a variable in our analyses. The effect of individual tandem as a factor was also omitted to avoid incurring errors from lack of full synchronization in the time data. In other words, we had to analyze the paths of tandem leaders and followers separately because given the temporal resolution of our video recordings we could not guarantee that we began each analysis at exactly the same frame (24 frames per second) for the paired leader and follower.

For each of the four blinkered treatments, we calculated the mean for the instantaneous speed and the mean for the absolute change in instantaneous acceleration. Since tandem duration varied (minimum=32 s, median=166.5 s, maximum=977 s), there were fewer and fewer workers out of the 80 still involved in a tandem with increasing time from the start. To counterbalance this reduction in the sample size, we used logarithmic binning (Sims et al. 2007). To generate the logarithmic bins we logged each second (with logarithm to the base of 10), rounded it up to the first decimal place and then anti-logged it. We did this in Minitab using the formula antilog(ceiling(logt(‘Time (Sec)’),1)). Given that the maximum tandem duration was 977 s, this resulted in 27 bins (or unique values) ranging from 1 to 1,000 s, with only a single original time value falling in the first bin and 183 of the original time values falling in the last bin. With four different tandem classes and with a leader and follower in each, that gave a maximum of $27\times4\times2=218$ data values. However, since only one tandem type represented the maximum duration, the data values for mean instantaneous speed totaled 198 and those for mean absolute change in instantaneous acceleration totaled 182.

The full general linear model (GLM) for the analysis of mean instantaneous speed and mean absolute change in instantaneous acceleration included the following predictor variables: the factor leader/follower with two levels: leader or follower in the tandem; the factor blinkered condition treatment with four levels: LB/FB, LB/FN, LN/FB, LN/FN; the covariate log time (s) and all three binary and single triple interactions. For the analysis of tortuosity, the full model contained the above two factors and their interaction. The mean for each of the two response variables was calculated for each time bin.

The final model for mean instantaneous speed contained both factors, the covariate log time (s) and the interaction between blinkered condition treatment and the covariate. The final model for mean absolute change in instantaneous acceleration contained both factors and the covariate.

The final models were obtained by reducing the full models on the principle of parsimony, *i.e.* removing non-significant interactions of the highest order first (in our case starting with three-way interactions). All GLM fitting and other statistical analyses were carried out in Minitab and SPSS.

An alternative approach to modeling mean instantaneous speed and mean absolute change in instantaneous acceleration would have been to treat the factor “leader/follower” as random and fit general linear mixed models (GLMMs), which combine fixed and random factors, instead of GLMs. By focusing on the variation between the profiles of different individuals over time, such models may also largely account for the sequential correlation in repeated measures over time (Maindonald and Braun 2007, p. 334).

Our response variables are means calculated by averaging data over all individuals for each time bin. They are measured at regular intervals over a relatively long period of time on only two “individuals”, an average leader and an average follower, for each of the four levels of the factor “blinkered condition”. This should, at least, in part, obviate issues of repeated measures and a possible correlation between time bins. We fitted several GLMMs to both response variables in R 2.11.1 (www.r-project.org) and used Faraway's parametric bootstrapping method for the likelihood ratio test

Table 1 Participation in tandem runs

	Left blinkered	Right blinkered	Doubly blinkered	Control	Paint-free	Totals
All participants in tandem runs (*i.e.* leaders and followers)						
OBS	22	22	12	32	26	114
EXP	17.21	19.60	16.19	28.46	32.55	
CHI^2	1.333	0.295	1.084	0.441	1.317	
Non-participants (all non-participants in tandem runs)						
OBS	79	93	83	135	165	555
EXP	83.79	95.40	78.81	138.54	158.45	
CHI^2	0.274	0.061	0.223	0.091	0.271	
Totals	101	115	95	167	191	669

Expected counts are printed below observed counts

Chi-square contributions are printed below expected counts

Chi-square=5.387, DF=4, *P* value=0.250

(Faraway 2006, p. 158–161) to compare each of these GLMMs to the respective final GLM, described earlier. Our aim was to check whether treating “leader/follower” as a random factor accounts for enough variation to make a difference to the test statistics for the fixed effects. We found that for both response variables, the GLMMs with “leader/follower” as a random factor do not make a significant difference (please see the Electronic Supplementary Material for more details).

Results

Overall, participants in tandem runs were a random sample of ants from the different blinkering treatments and non-blinkering controls (Table 1). Blinkering does, however, seem to influence whether tandem participants are more likely to be leaders or followers (Table 2). Leaders seem to need at least one good eye (only two leaders had some paint on both of their eyes compared to a random expectation of six and they did not have paint over all of both eyes). Followers can be doubly blinkered (10 observed *vs*. six expected). Leaders are more likely to be those ants without any disabling paint (more are controls or clean 34 *vs*. 30 expected) and finally followers often have some paint (less are controls or clean 24 *vs*. 28 expected).

Table 2 Roles in tandem runs

	Left or right blinkered	Doubly blinkered	Control or paint-free	Totals
Leaders				
OBS	23	2	34	59
EXP	22.77	6.21	30.02	
CHI^2	0.002	2.855	0.528	
Followers				
OBS	21	10	24	55
EXP	21.23	5.79	27.98	
CHI^2	0.002	3.062	0.567	
Totals	44	12	58	114

Expected counts are printed below observed counts

Chi-Square contributions are printed below expected counts

The above is based on pooling singly blinkered ants on the one hand and on the other hand those with no paint on their eyes

Note that in Table 2 there are more leaders than followers because we have excluded gynes or males that followed tandems

Only workers led tandems

Chi-Sq=7.017, DF=2, *P* value=0.030

NB a 2×3 Fisher's exact test gives *P*=0.027

Grooming of blinkered nestmates

Since the painted workers had to be left for 24 h to emigrate into a new nest, they had the opportunity to groom one another and remove the paint we had applied. Hence, we can determine if the ants remove paint indiscriminately or, for example, focus their grooming on the most visually impaired of their nest mates. Such grooming appears to be indiscriminate. For example, if deblinkering is random, the efflux of ants from the 33% that were originally double blinkered into the singly blinkered categories should be the same as the efflux of ants from the originally singly blinkered categories into the cleaned category. Hence the percentages of singly blinkered ants should remain the same and they do (planned 17% left blinkered and 17% right blinkered: realized 15% left blinkered and 17% right blinkered).

So in sum, these data suggest strongly that the ants are not more likely to groom a doubly blinkered ant than a singly blinkered ant. Moreover they are not more likely to continue grooming a doubly blinkered ant until both eyes are cleaned. However, there was somewhat less paint loss from the controls (planned 33%; realized 25%) compared to blinkered ants (total 67%; realized 46%). Hence, ants that are impaired by paint over one of their key organs, their eyes, are slightly more likely to be groomed clean than those with paint in a trivial place.

Table 3 Model parameters and fits for the analyses of mean instantaneous speed and mean absolute change in instantaneous acceleration

Response	Predictor	F	DF	*P*	R^2(adj)%	Normality test
Mean instantaneous speed	L/F	9.96	1,189	0.002	47.56	A-D=0.815,*N*=198, *P*=0.035
	Blinkered condition	8.04	3,189	<0.001		
	Log time (s)	126.96	1,189	<0.001		
	BC*log time (s)	5.55	3,189	0.001		
Mean absolute change in instantaneous acceleration	L/F	7.09	1,176	0.008	24.46	A-D=0.681,*N*=182, *P*=0.074
	Blinkered condition	12.15	3,176	<0.001		
	Log time (s)	27.25	1,176	< 0.001		

* interaction between predictors

L/F, leader or follower; *BC*, blinkered condition treatment; *A-D*, Anderson-Darling statistic

Performance of the ants within tandem runs

Overall, the mean instantaneous speed for followers was 0.15 mm/s greater than that for leaders (*P*=0.002, Table 3, Fig. 3). The form of the blinkered condition treatment also had a significant effect on mean instantaneous speed (*P*<0.001, Table 3). This was entirely accounted for by LN/FN tandems (*i.e.* neither participant is blinkered) having a significantly slower mean instantaneous speed than any of the other three tandem types (Tukey *post hoc* tests for differences between means: LN/FN−LB/FB=−0.27 mm/s, *T*=−4.377, *P*=0.0001; LN/FN−LB/FN=−0.42 mm/s, *T*=−6.339, *P*<0.0001; and LN/FN−LN/FB=−0.42 mm/s, *T*=−6.468, *P*<0.0001; Fig. 3). Overall mean instantaneous speed increased by 0.35 mm/s in log time (*P* < 0.001, Table 3, Fig. 3). However, LB/FN tandems increased their mean instantaneous speed at a higher rate than any of the other three tandem types (*P*<0.001, *P*=0.001, *P*=0.032 for comparison with LB/FB, LN/FB and LN/FN, respectively, Fig. 3). In general, the increase in mean instantaneous speed for tandems with a fully sighted follower was higher than the overall mean of 0.35 mm/s per second in log time and lower for tandems

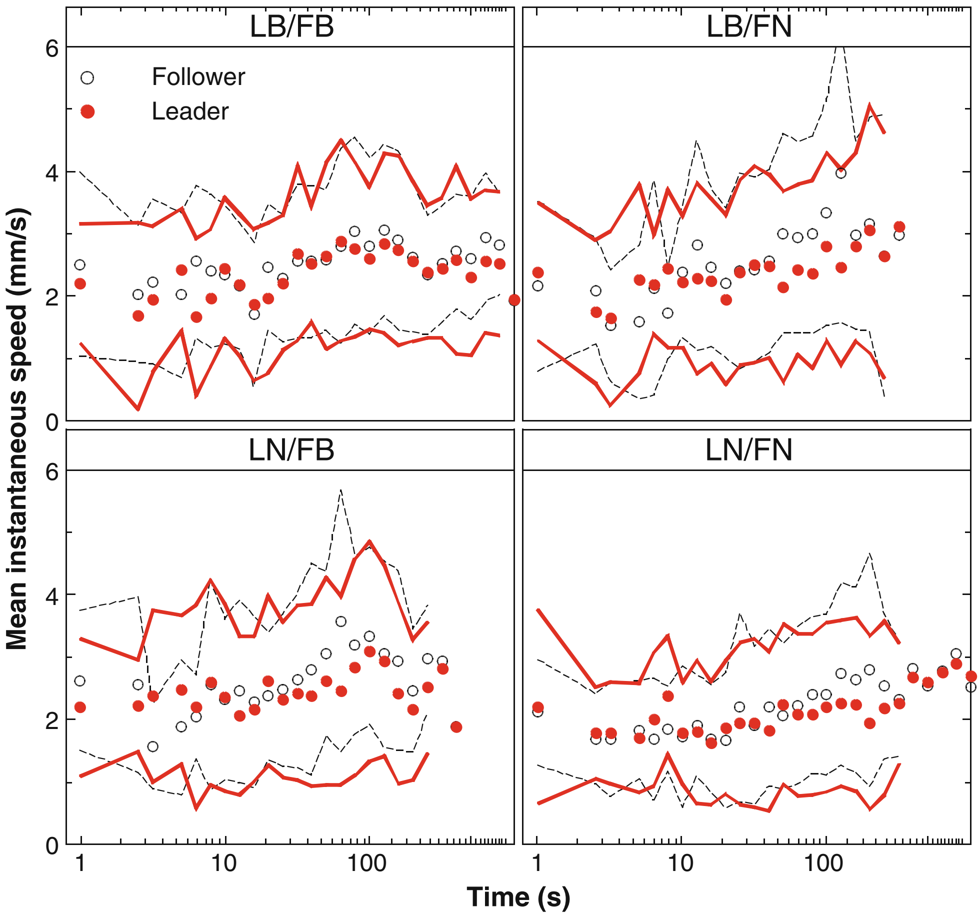


Fig. 3 Change in mean instantaneous speed with time for the four different blinkered condition treatments: *continuous line*, 95% confidence interval envelope for leader; *interrupted line*, 95% confidence interval envelope for follower; *LB/FB*, both leader and follower are blinkered, overall slope=0.2233, *P*<0.001; *LB/FN*, leader blinkered, follower not blinkered, overall slope=0.5614, *P*<0.001; *LN/FB*, leader not blinkered, follower blinkered, overall slope=0.2433, *P*=0.005; *LN/FN*, neither leader or follower is blinkered, overall slope=0.3689, *P*<0.001. The slope for *LB/FN* was significantly greater than any of the other slopes (*P*<0,001, *P*=0.001, *P*=0.032 for comparison with *LB/FB*, *LN/FB*, and *LN/FN*, respectively); time was logarithmically binned before log transformation

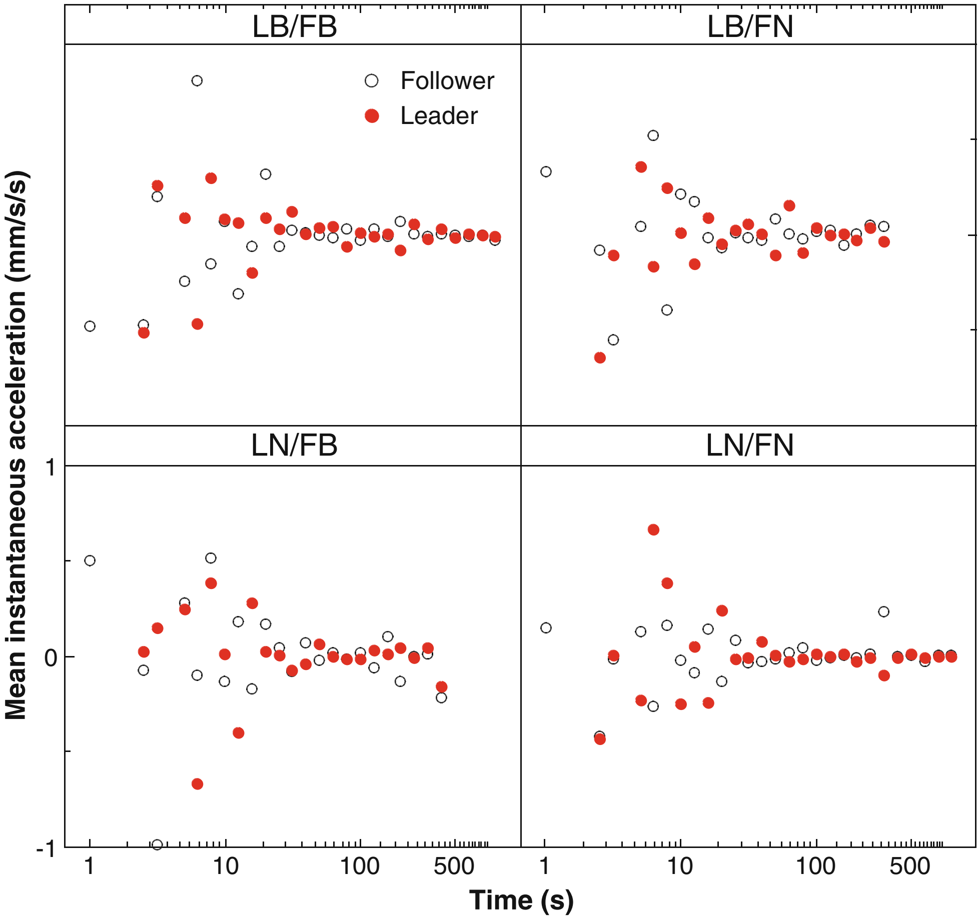


Fig. 4 Mean instantaneous acceleration through time for the four different blinkered condition treatments; key to labels as in Fig. 3; variation early on is emphasized by the log binning

with a blinkered follower (Fig. 3). This suggests that a fully sighted follower is very important for a greater increase in average tandem speed with time.

As expected, the mean instantaneous acceleration was approximately constant over time since mean instantaneous speed was increasing at an approximately constant rate over log10 of log-binned time (Fig. 4). Overall, the mean absolute change in instantaneous acceleration for followers was 0.14 mm/s^2 less than that for leaders (P=0.008, Table 3, Fig. 5). The blinkered condition treatment also had a significant effect on mean absolute change in instantaneous acceleration (P<0.001, Table 3). This was entirely accounted for by LN/FN tandems having a significantly smaller mean absolute change in instantaneous acceleration than any of the other three tandem types (Tukey *post hoc* tests for differences between means: LN/FN−LB/FB=−0.24 mm/s^2, T=−3.480, P=0.0035; LN/FN−LB/FN=−0.37 mm/s^2, T=−5.015, P<0.0001; and LN/FN−LN/FB=−0.38 mm/s^2, T=−5.281, P<0.0001; Fig. 5). Overall mean absolute change in instantaneous acceleration increased by 0.03x10^{-2} mm/s^2 with each second in log time (P<0.001, Table 3, Fig. 5).

There was no strong evidence of any effect of either the factor leader/follower or blinkered condition treatment on tortuosity. However, within each of the four cases, the median tortuosity of followers was greater than that of their leaders (1/2^4 gives P=0.0625, Fig. 6). Furthermore, there is a suggestion that this difference between the tortuosity of followers and leaders is greatest when the followers are fully sighted (LN/FN and LB/FN) and that the path is a little less tortuous when both tandem members are fully sighted (LN/FN).

Across all four classes of tandem run, the progress of both partners was most smooth (*i.e.* changes in acceleration were at a minimum) at 3 mm/s (Fig. 7). This suggests that communication between the partners in tandem runs is non-visual.

Discussion

There are two ways in which *T. albipennis* might use vision during tandem running. One is that the follower might track the movements of the leader by keeping it in sight. The other is that the leader and the follower might be using vision to navigate, in the case of the leader, or to learn the route, in the case of the follower. For example, individual *T.*

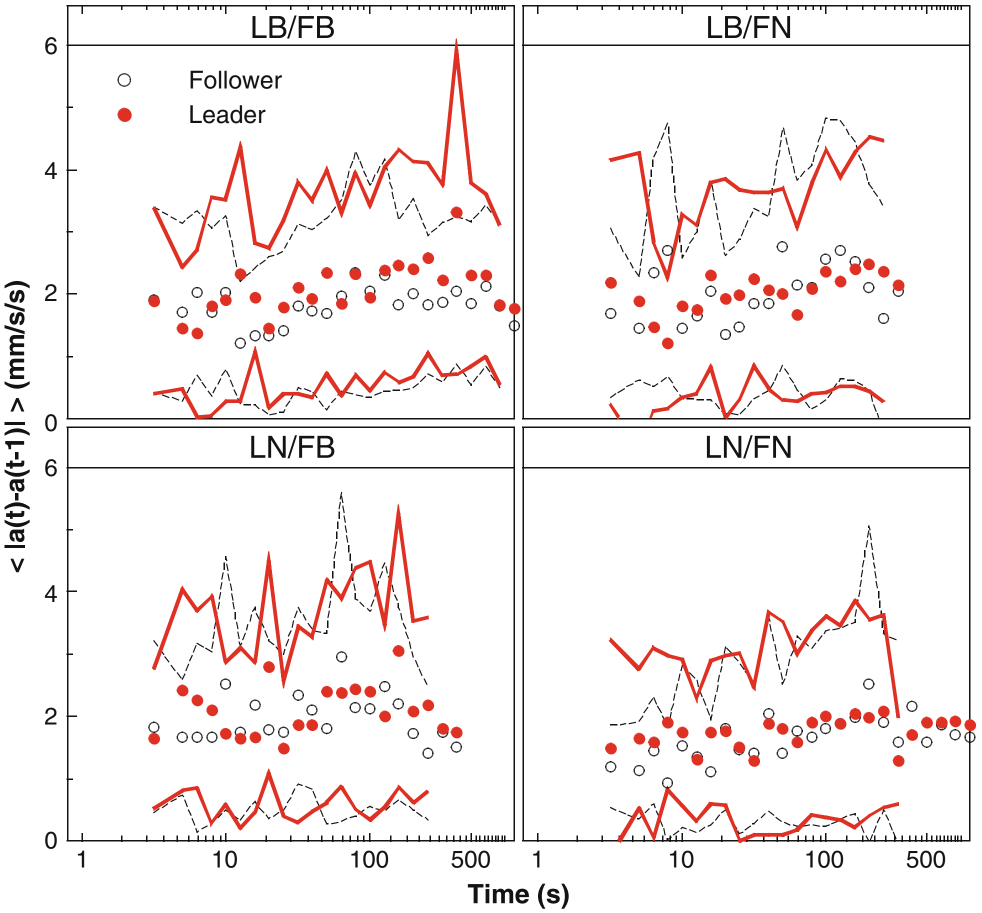


Fig. 5 Relationship between mean absolute change in instantaneous acceleration (calculated as the difference between successive time points at the individual level and averaged over the respective log time bin after taking the absolute value) and time for the four different blinkered condition treatments; key to labels as in Fig. 3. The four slopes are not significantly different from one another. Overall mean absolute change in instantaneous acceleration increased by 0.00026 mm/s^2 with each second in log time; time was logarithmically binned before log transformation

albipennis workers have been shown to navigate by piloting towards landmarks (Mcleman et al. 2002) and by learning to run beside long horizontal structures that parallel the route (Pratt et al. 2001).

Our results strongly suggest that vision has very little role, if any, in enabling the follower to track its leader. Our observation that tandem runs speed up through time, when neither, or one, or both participants have some visual impairment, strongly suggests that the communication between them is both robust and very effective and not very dependent at all on vision. Assuming a spatial resolution of about 7° for the compound eyes of *T. albipennis* (Mcleman et al. 2002) and a maximum value of about 1 mm for the height of workers above the substrate one worker should be able to see another at a distance of about 8 mm. In general, tandem followers are often much closer than this to their leader: indeed, they are often just 1 mm apart (Franks and Richardson 2006). It is thus not clear why tandem followers appear not to use vision to track their leaders. However, the benefit of using pheromonal and tactile signals (Möglich et al. 1974) rather than vision for maintaining the bond between leaders and followers is probably extreme robustness. These signals should work well in low-light conditions and along obstacle-strewn paths and should prevent followers from mistakenly running after other ants.

By contrast, our results suggest that good eyesight does play a role in ants deciding to lead tandem runs with a less important role in ants deciding to follow tandem runs (Table 2). Nevertheless, the effects of blinkering the ants are rather subtle and weak. For example, we needed substantial sample sizes to show these participation patterns at all (*cf.* Tables 1 and 2). Overall, our results suggest that *T. albipennis* do use eyesight in navigating tandem runs but probably use other senses too. One classic response of insects to unilateral blinkering is so called circus movements in which the visually impaired individual may progress overall in a certain direction but often loop either clockwise or anticlockwise before continuing (Fraenkel and Gunn 1961). However, such circus movements only generally occur when the partially blinded subject is orientating towards a beam of light in an otherwise dark room (Fraenkel and Gunn 1961). We saw no such circus movements in our unilaterally blinkered ants probably because they were in a lab well illuminated with both artificial and day light and were probably also using other non-visual systems in their navigation.

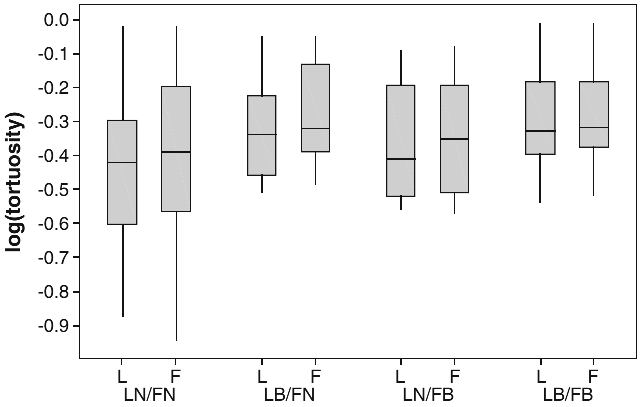


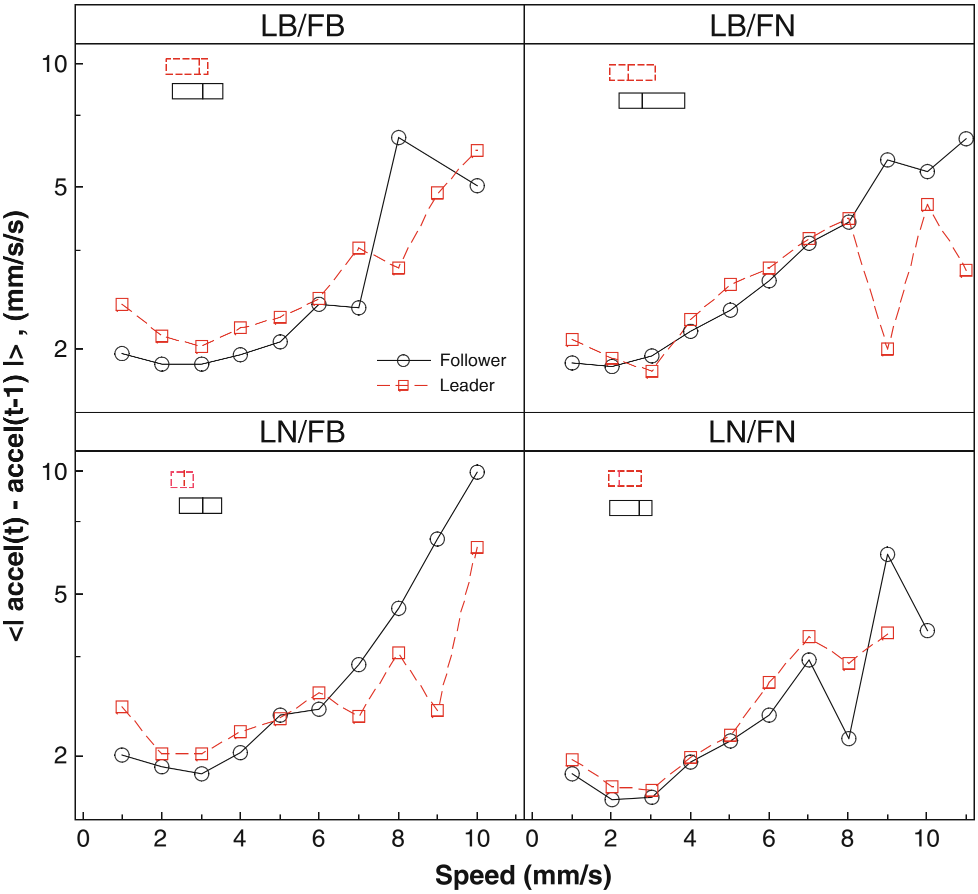
Fig. 6 Log-transformed path tortuosity (see Materials and methods for calculation) according to blinkered condition treatment and whether the worker was the leader or the follower; key to labels as in Fig. 3. The *line within* the *boxes* represents the median, the *box* is delineated by the *lower* and *upper* quartiles, the whiskers extend to the largest/smallest data value within 1.5 times the interquartile range

We were extremely surprised that blinkered ants participate in tandem runs at all and may even do so as leaders. This is even more counterintuitive given that fully sighted ants were abundant in our experiments. Fifty-four percent of the workers in our experiments were not visually impaired during emigrations.

Across all four classes of tandem pairings, mean instantaneous speed increased as the run proceeded. Moreover, in all cases, on average, followers were quicker than leaders. Followers typically have slightly more convoluted paths than leaders as they presumably search for navigational information (Franks and Richardson 2006). Hence, as they have more ground to cover they have to move faster to keep up with their leader. In general, the mean instantaneous speed of tandems with fully sighted followers increased more over time than those with visually impaired followers. This may occur because fully sighted followers can process navigation cues, such as landmarks, more quickly.

Further evidence that members of tandems learn to interact better with one another comes from our analysis of mean absolute change in instantaneous acceleration. It increased significantly over time as participants in all four types of tandem run increased their speeds (Fig. 5). Followers have smaller mean absolute changes in acceleration than leaders because they are continually on the move, whereas leaders must frequently stop and start again as they wait for contact from the antennae of their follower

Fig. 7 Change in mean acceleration as a function of mean speed (rounded to the nearest integer) in all four blinkered condition treatments for leaders (*dotted lines*) and for followers (*solid lines*). The *horizontal box plots* show the interquartile range and the *vertical line within* each *box* shows the median for the average speeds (calculated as the average speed of each ant over its entire tandem run). In all four panels, the tandem runs proceed most smoothly (with minimal changes in acceleration) at about 3 mm/s. The ants are mostly moving (as shown by the *box* plots) at speeds that correspond to these minima. The graphs only depict the data for which we have good sample sizes and comparable speed ranges for leaders and followers



which stimulates their further progress (Franks and Richardson 2006; Richardson et al. 2007). Such contacts are intermittent because the follower, who is presumably gathering new navigational information, has a rather more meandering path than its leader.

The overall increase in speed of tandem runs can probably be attributed to the increasing aptitude of the leader in rapidly stopping and swiftly starting as its follower loses and reestablishes contact with it and to the follower moving increasingly in the right direction. Both trends should facilitate more rapid communication between the participants. Wild-type tandem runs, in which both participants are fully sighted (LN/FN) are slower and have smaller mean changes in acceleration than the other three treatments but speed up more over time than tandems with blinkered followers (LN/FB and LB/FB). Wild-type tandem runs are probably slower because both of their participants are taking time to observe and learn landmarks. In addition, they may be somewhat less tortuous and smoother (less extreme acceleration and deceleration) and speed up well because over time the follower can derive a better sense of the overall direction of the run (see Franks et al. 2010). Tandem runs with a blinkered leader and a fully sighted follower also proceed well; again suggesting that the ability and behavior of the follower is very important.

In general, our results show only a small effect of both leadership or followership and blinkered condition on the overall tortuosity of tandem runs. Indeed, our data suggest that such paths are only very slightly straighter where both participants are fully sighted. This suggests that visual impairment does not have a substantial influence on the ability of the ant to maintain a fairly straight path. Hence, it seems possible and even likely that the ants are using other additional navigation systems than just purely vision-based procedures.

Our observations that blinkered ants seem to be largely unimpaired in terms of tandem running might also help to explain why the ants groom off the blinkers at random rather than focusing on their most visually disabled nest mates.

How might these ants cope with being blinkered? *Temnothorax* ants are generally thought to use individual-specific trail pheromones rather than mass recruitment trails (Maschwitz et al. 1986; Aron et al. 1988; Mallon and Franks 2000). However, just because one worker can distinguish its own trail from those of its nest mates does not mean that other trails cannot be detected (see Aron et al. 1988). Hence, it seems quite possible that as traffic builds to a new nest site, other ants might be able to use these chemically marked paths as orientation cues (see Pratt 2008). In addition, the ants may also be able to use path integration to compute straighter return paths (Franks and Richardson 2006) than those they have executed on the outward leg of their journey.

We know that these ants can learn landmarks; our finding here that blinkered ants are willing and able to participate very effectively in tandem runs suggest that they may use multiple mechanisms to navigate. Other organisms do use multi-modal navigation. For example, homing pigeons may use landmarks, olfaction, and magnetic fields (Walcott 2005) and *Cataglyphis* ants use both visual information (Wehner et al. 1996) and leg-movement odometers (Wittlinger et al. 2006). Moreover, *Cataglyphis* ants use their ocelli to detect polarized light patterns (Fent and Wehner 1985) and their compound eyes to gather both sun compass and landmark information (Wehner and Rossel 1985; Wehner et al. 1996). So perhaps it should come as no great surprise that *Temnothorax* ants can navigate remarkably well when their visual acuity is reduced (see also Maschwitz et al. 1986; Aron et al. 1988).

Franks and Richardson (2006) emphasized the importance of the feedback between leaders and followers during tandem runs and it seems that this is so effective that all possible pairings of blinkered and unblinkered ants are able to speed up over the course of their tandem runs. This finding also shows what sensitive teachers these ants are. As most experienced human teachers have learnt, whether they are teaching children or other small animals, progress in lessons is often determined by the pupil not by the teacher (see also Richardson et al. 2007). Moreover, progress that is slow and steady and even pedantic and pedestrian, as in wild-type tandem runs, may be associated with pupils becoming much better informed.

Acknowledgements We thank the following undergraduates for their help with this project; Clare E. Gray, Katy H. Moran, Sam Ellis and Saki Okuda. We also thank the School of Biological Sciences at the University of Bristol for summer studentships that supported these students. We also thank two anonymous reviewers. NRF and EJHR gratefully acknowledge EPSRC grant EP/D076226/1. NRF also wishes to thank the BBSRC (grant no. BB/G02166X/1) for their support. TOR and ABS-F gratefully acknowledge EPSRC grant EP/E061796/1.

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