nature

BRIEF COMMUNICATIONS

Teaching in tandem-running ants

Tapping into the dialogue between leader and follower reveals an unexpected social skill.

The ant *Temnothorax albipennis* uses a technique known as tandem running to lead another ant from the nest to food — with signals between the two ants controlling both the speed and course of the run. Here we analyse the results of this communication and show that tandem running is an example of teaching, to our knowledge the first in a non-human animal[1–3], that involves bidirectional feedback between teacher and pupil. This behaviour indicates that it could be the value of information, rather than the constraint of brain size, that has influenced the evolution of teaching.

An individual is a teacher if it modifies its behaviour in the presence of a naive observer, at some initial cost to itself, in order to set an example so that the other individual can learn more quickly[1]. We suggest that teaching also involves bidirectional feedback between teacher and pupil. To test whether tandem running fulfils these criteria, we measured the acceleration of leaders and followers in response to the stimuli they present to one another.

In our experiments, tandem leaders knew the location of food but tandem followers were naive (for details, see supplementary information). We found that the leader only continued the tandem run when frequently tapped on her legs and abdomen (gaster) by the following ant's antennae[4,5] (Fig. 1a, inset; for movie, see supplementary information). The tandem leader therefore modifies its behaviour in the presence of the follower.

We also found that tandem leading imposes a cost on the leader in that she can proceed four times faster from the nest to the food when not encumbered by a follower (median speed was 1.8 mm s^{-1}, compared with 8.4 mm s^{-1}; Mann–Whitney test, $P<0.0001$). Tandems are slowed by frequent pauses in which the follower loops around, probably in a search for landmarks[6,7]; followers make larger looping movements than do individual explorers (Mann–Whitney test, $P<0.001$; see supplementary information). Indeed, the speed of leader and follower between pauses was significantly higher in the presence of conspicuous landmarks than the speed of controls in the absence of landmarks (mean speed was 7.6 mm s^{-1}, compared with 5.8 mm s^{-1}; analysis of variance (ANOVA), d.f. = 1, $F=22.2$, $P<0.0001$).

We next tested whether the leader provides a demonstration of how to find food. Followers found food more quickly when tandem running than when searching alone (mean time was 201 s, compared with 310 s; ANOVA, d.f. = 1, $F=6.40$, $P=0.016$), indicating that the follower learns more quickly as a result of the leader's help. Moreover, the follower's return path to the nest does not replicate the route of the tandem run: its journey is generally faster and more linear (in 6 out of 8 cases) than that of its leader before the tandem run (see supplementary information). The follower therefore learns the food's location sooner and gains general knowledge about the surroundings of the nest as a result of the leader's example.

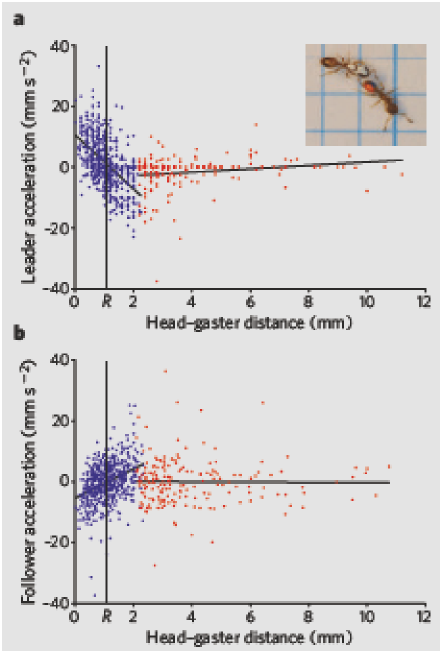

Figure 1 | Tandem running in the ant *Temnothorax albipennis*. **a, b,** Acceleration by ten ants (results pooled) that were **a**, leaders, or **b**, followers, in response to mutual stimuli, as a function of the separation between the leader's gaster and the follower's head. When within twice the distance of the antennal reach (*R*; average *R*, 1 mm) of the follower (blue circles), the ants are too close so the follower decelerates and the leader accelerates; when further apart, the follower accelerates and the leader decelerates. At the average reach of the follower's antennae, both move at constant velocity; when separated by more than twice the antennal reach of followers (red circles), leaders stop and wait as followers loop around. Inset, tandem run over 2-mm squares (for video, see supplementary information).

Bidirectional feedback between the leader and follower is evident from their patterns of acceleration and deceleration as a function of the strength of the stimuli they present to one another (Fig. 1): when the gap between the leader and follower grows too large, the former decelerates and the latter accelerates; both move at the same speed when at the maximal antennal reach of the follower.

Together, our results show that the leader's performance fulfils all the criteria for teaching, with the follower acting as pupil. The lessons learned by tandem followers are transferred when they become tandem leaders[8], so — although tandem runs are slow — they propagate time-saving knowledge among foragers.

Temnothorax albipennis workers may also carry nestmates[9]. Such pairs move three times faster than tandems, but carried ants do not teach others — perhaps because they cannot learn while their head is inverted and pointing backwards during carrying. Other species of ant workers that do not use tandem running[4] are carried with their heads upright: these can learn a route and later recruit others[10].

Bidirectional feedback between teacher and pupil distinguishes teaching from broadcasting. Most recruitment in large ant societies is broadcasting (for example, through pheromone trails)[4], which is effective in big groups. But in small societies, where information is valuable and easily lost, teaching works better. Our identification of teaching behaviour in an ant shows that a big brain is not a prerequisite.

Nigel R. Franks, Tom Richardson
School of Biological Sciences, University of Bristol, Bristol BS8 1UG, UK
e-mail: nigel.franks@bristol.ac.uk

1. Caro, T. M. & Hauser, M. D. *Q. Rev. Biol.* **67**, 151–174 (1992).
2. Shettleworth, S. J. *Cognition, Evolution and Behaviour* 475–522 (Oxford Univ. Press, 1998).
3. Galef, B. G. Jr, Whiskin, E. E. & Dewar, G. *Anim. Behav.* **70**, 91–96 (2005).
4. Hölldobler, B. & Wilson, E. O. *The Ants* (Harvard Univ. Press, Cambridge, Massachusetts, 1990).
5. Möglich, M. & Maschwitz, U. & Hölldobler, B. *Science* **186**, 1046–1047 (1974).
6. Pratt, S. C., Brooks, S. E. & Franks, N. R. *Ethology* **107**, 1125–1136 (2001).
7. Mcleman, M. A., Pratt, S. C. & Franks, N. R. *Insectes Soc.* **49**, 203–208 (2002).
8. Möglich, M. *Insectes Soc.* **25**, 205–225 (1978).
9. Pratt, S. C., Mallon, E. B., Sumpter, D. J. T. & Franks, N. R. *Behav. Ecol. Sociobiol.* **52**, 117–127 (2002).
10. Möglich, M. & Hölldobler, B. *Psyche* **81**, 219–236 (1974).

Supplementary information accompanies this communication on *Nature*'s website.
Competing financial interests: declared none.
doi:10.1038/439153a