Correspondences

U-turns on ant pheromone trails

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Many ant species use branching networks of pheromone trails for orientation between nest and resources [1–3]. Ants on trails make adaptive U-turns for correcting their course using visual cues [4,5] or trail geometry information [2]. However, the role of seemingly non-corrective U-turns on trails is poorly understood. We found that a minority of ants consistently make frequent and seemingly inappropriate U-turns during foraging bouts. These frequent U-turners were also highly likely to lay pheromone trail, whilst non-turners rarely did so. Our data suggest that U-turning ants make a greater contribution to trail persistence than do non-turners.

We determined the frequency of U-turning in Pharaoh's ants (*Monomorium pharaonis*) by following individuals making a single trip from ramp end to feeder, or the reverse (Figure 1). If an ant made a 180º turn and walked >10 mm, a U-turn was recorded. Otherwise, a non-turning ant walked to the nest (if fed) or found food (if unfed). 'Fed' ants left the feeder with a visibly enlarged gaster. 'Unfed' ants were observed joining the ramp before walking towards the food. In some ants, e.g. *Lasius niger* [6], fed ants are more likely to lay pheromone.

We found no significant differences in U-turning frequencies (mean = 43.2%, range = 39.5–48%) of three study colonies (Chi square = 1.98, df = 2, N = 300, P = 0.372). We therefore pooled data to compare fed and unfed ants, and found that 150 fed ants (N = 50 x 3 colonies) and 150 unfed ants (N = 50 x 3 colonies) performed U-turns with similar probability, 45.1% and 38% respectively (Chi square = 1.73, df = 1, N = 300, P = 0.188). The mean U-turning frequency (43%) on active foraging trails was much higher than that reported by Jackson *et al* [2] for individual ants on an empty trail (~ 7%). The high frequency may be attributable to U-turning ants making frequent U-turns, spending more time on the trail, and therefore being more likely to be observed. We noted that ants making U-turns were highly likely to make subsequent U-turns. U-turners also made significantly fewer contacts with oncoming ants than did non-turners, indicating that U-turns were not due to trail traffic (U-turners N = 128, mean contacts = 1.54, SD = 1.86; non-turners N = 172, mean contacts = 2.92, SD = 2.58; t test, t = 4.97, df = 297, P < 0.0001).

We determined individual fidelity to U-turning behaviour during a foraging bout, using two colonies. From each colony 20 fed and 20 unfed non-turning ants were returned to their start position and followed for a further five such trials. Unfed ants were replaced at the ramp end, and fed ants at the food end (Figure 1). If a non-turner made a U-turn on any of its five trials, the distance was recorded, and the ant was returned to its start position. Otherwise, an ant was only returned to its start position after completing a trial – that is, reaching the end opposite to its

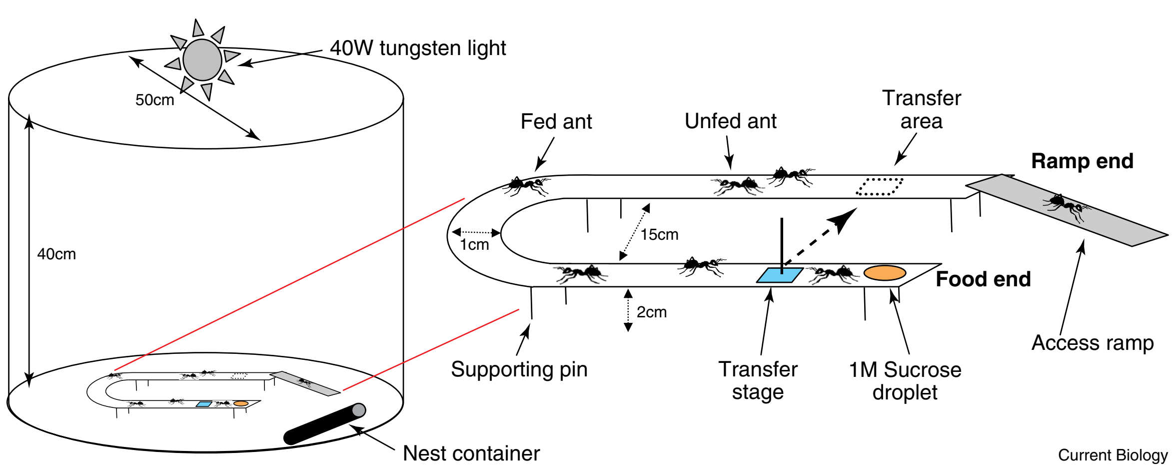

Figure 1. Experimental set-up for studying U-turning behaviour in Pharaoh's ants.

To minimise visual cues, *M. pharaonis* colonies (1,000–1,400 workers and 10–50 queens) where housed in a nest container (test-tube sheathed in black paper) placed in an opaque open-topped cylindrical container. The 40W diffused tungsten light was suspended 60cm above the centre to provide non-directional lighting. An access ramp connected the container base to one end of a horseshoe-shaped plastic walkway (45 cm from ramp to food). The walkway was supported on Fluon-dipped pins, making the ramp the only access route. The horseshoe shape allowed us to easily manipulate the ant's direction by transferring them from one walkway arm to the other. As an ant stepped upon the transfer stage, the ant's walking direction was reversed by simple lateral transfer of the stage, as shown. This minimised any disruption to the ant's progress. Neither lateral transfer nor 180º reversal significantly affected U-turning frequency of individuals when compared to U-turning frequency of non-manipulated individuals from a control colony (log-linear likelihood analysis: $G^2 = 0.56$, df = 4, $N_{manipulated} = 100$, $N_{control} = 100$, P = 0.967). In trials, colonies were deprived of syrup for at least 2 days, and then given 20 min to form a foraging trail to the feeder, a drop of 1M sucrose. Ants were only tested during the next 60 min, when trail traffic was high (~70–100 ants per min).

start end. Trials were then conducted on U-turners (again, N = 20 fed and 20 unfed x 2 colonies) in experiments in which an ant observed to U-turn on its first trial was allowed to continue (often U-turning several times) until it reached the food (unfed ants), or the ramp (fed ants). The cumulative distance walked by the ant was recorded. If U-turners returned to their start point, they were rotated 180º using the transfer stage.

For comparative purposes, the number of U-turns per 45 cm (the trial length) was calculated for each ant tested. We found that U-turners scored a mean of 3.20 U-turns per 45cm (SD = 1.92, N = 80 ants). In contrast, non-turners (N = 80 ants) performed on average 0.21 U-turns per 45 cm (SD = 0.33). The difference in mean score (per trial) was highly significant (t test: t = –13.7, df = 83, P < 0.0001). Individuals showed high fidelity to U-turning and non-turning during a foraging bout (see Supplemental Data for more on specialisation). In these experiments, 77/80 ants (96%) identified as non-turners on their initial trial were non-turners in their next trial, whilst 72/80 U-turners (90%) made subsequent U-turns. We found no significant differences between the U-turn frequencies of fed vs. unfed non-turners from either colony (colony 1: t = –0.45, df = 37, N = 40, P = 0.657; colony 2: t = –0.94, df = 36, P = 0.356), or of non-turners in different colonies (fed and unfed non-turners pooled for each colony: t = 1.34, df = 74, P = 0.185). There were also no differences between the frequencies of U-turns by fed vs. unfed U-turners (t = –0.44, df = 77, P = 0.663), or by U-turners in different colonies (fed and unfed U-turners pooled: t = –1.17, df = 75, P = 0.248).

In *Lasius niger* ants, some individuals adopt pheromone-trail-laying postures with very high frequency [7]. In our final experiment, we tested the hypothesis that U-turning ants lay pheromone trail frequently. We identified U-turners (N = 50 fed, N = 50 unfed) and non-turners (N = 50 fed, N = 50 unfed) from each of three colonies (total N = 3 x (2 x 100) = 600) and observed trail laying behaviour by isolated individuals. We categorized U-turners and non-turners based on performance in a single trial. Individual ants were transferred from the walkway onto smoked glass at the end of the trial (pheromone trail deposition by the stinger is visible on smoked glass in the form of continuous lines, streaks, or spots between footprints [2,8,9]). Of U-turners, 263/300 (87.7%) made trail markings, whereas among non-turners, only 67/300 (22.3%) did so. This difference is highly significant (Chi-square = 259, df = 1, N = 600, P < 0.0001), and not affected by colony or nutritional status (log-linear likelihood analysis: by colony, $G^2 = 3.7$, df = 4, N = 200 ants x 3 colonies, P = 0.448; by fed vs. unfed, $G^2 = 2.08$, df = 3, $N_{fed} = 300$, $N_{unfed} = 300$, P = 0.556). The fact that 87.7% of U-turners laid pheromone trail when walking on smoked glass indicated that they could be contributing to the pheromone trail more frequently than non-turners. Given their frequent U-turns, the U-turner minority (7% in [2]) should spend greater time on the trail and should have the opportunity to contribute more trail pheromone than non-turners.

Our data show that many U-turns are neither mistakes nor course corrections, but could be a vital component of the pheromone-trail maintenance process. U-turning ants are well positioned to make decisions on trail persistence because by walking the trails repeatedly, they continually update their knowledge of food availability. This well-informed status contrasts with that of ants not making U-turns because non-turners could easily be misinformed if they fail to access a crowded resource. U-turners may have greater control over abandonment of exhausted food sources, or over the switch to superior food sources. Making quick foraging decisions is vital to colony success, and leaving decision-making to a specialised, well-informed minority [10] would certainly speed the process.

Supplemental data

Supplemental data including Experimental Procedures are available at http://www.current-biology.com/cgi/content/full/16/2/R42/DC1/

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